Zoological Journal of the Linnean Society, 2023, XX, 1–24
https://doi.org/10.1093/zoolinnean/zlad062
Advance access publication 27 July 2023
Original Article

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A *tenuis* relationship: traditional taxonomy obscures systematics and biogeography of the '*Acropora tenuis*' (Scleractinia: Acroporidae) species complex

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ABSTRACT

Molecular phylogenetics has fundamentally altered our understanding of the taxonomy, systematics and biogeography of corals. Recently developed phylogenomic techniques have started to resolve species-level relationships in the diverse and ecologically important genus *Acropora*, providing a path to resolve the taxonomy of this notoriously problematic group. We used a targeted capture dataset (2032 loci) to investigate systematic relationships within an *Acropora* clade containing the putatively widespread species *Acropora tenuis* and its relatives. Using maximum likelihood phylogenies and genetic clustering of single nucleotide polymorphisms from specimens, including topotypes, collected across the Indo-Pacific, we show ≥ 11 distinct lineages in the clade, only four of which correspond to currently accepted species. Based on molecular, morphological and geographical evidence, we describe two new species; ***Acropora rongoi* n. sp.** and ***Acropora tenuissima* n. sp.** and remove five additional nominal species from synonymy. Systematic relationships revealed by our molecular phylogeny are incongruent with traditional morphological taxonomy and demonstrate that characters traditionally used to delineate species boundaries and infer evolutionary history are homoplasies. Furthermore, we show that species within this clade have much smaller geographical ranges and, consequently, population sizes than currently thought, a finding with profound implications for conservation and management of reef corals.

Keywords: Scleractinia; taxonomy; species boundaries; phylogenetic systematics; Indo-Pacific

INTRODUCTION

Reef-building corals are declining globally due to the impacts of climate change and other anthropogenic stressors (Hughes *et al.* 2017, 2018), raising concerns that many coral species might become extinct in coming decades (Carpenter *et al.* 2008). However, understanding population sizes and trajectories of coral species is challenging owing to the inability to identify corals accurately at the species level (Kitahara *et al.* 2016, Bridge *et al.* 2020). The incompatibility of traditional coral taxonomy with systematic relationships revealed through molecular phylogenetics has resulted in substantial revisions to the scleractinian tree of life at all taxonomic levels (e.g. Fukami *et al.* 2004, 2008, Huang *et al.* 2009, 2014, Budd *et al.* 2010, Arrigoni *et al.* 2014, Kitahara *et al.* 2016). Consequently, robust information on the ecology, biogeography, physiological tolerances

Received 13 December 2022; revised 20 April 2023; accepted 8 May 2023

and conservation status of reef corals urgently requires a robust taxonomy that accurately reflects species boundaries and evolutionary relationships.

Historically, coral taxonomy was based almost exclusively on skeletal morphology; however, delineating species boundaries is challenging because many species exhibit morphological plasticity among individuals from different environments and geographical regions (Veron and Pichon 1976, Todd 2008, Paz-García *et al.* 2015). The advent of molecular phylogenetics in the 1990s revolutionized our understanding of coral systematics and demonstrated that many morphological features traditionally used to define species, genera and families are convergent and not taxonomically informative (Romano and Palumbi 1996, Fukami *et al.* 2004, Kerr 2005, Huang *et al.* 2009, 2011, Budd *et al.* 2010, 2012). However, the effectiveness of mitochondrial barcoding markers in anthozoans is limited at lower taxonomic levels (e.g. species, populations) by slow substitution rates (Shearer *et al.* 2002, Hellberg 2006, Huang *et al.* 2008). Consequently, although single-locus markers or a few combinations of nuclear and mitochondrial markers have, in some cases, helped to elucidate the deeper nodes of the coral tree of life (e.g. Fukami *et al.* 2008, Kitahara *et al.* 2010, Budd *et al.* 2012, Arrigoni *et al.* 2014, Huang *et al.* 2014) and provided some insight into species-level relationships in some genera (e.g. Benzoni *et al.* 2010, Luck *et al.* 2013, Schmidt-Roach *et al.* 2014), they have failed to resolve species-level relationships in species-rich genera, such as *Acropora* Oken, 1815, *Montipora* de Blainville, 1830 and *Porites* Link, 1807. Fortunately, next-generation sequencing methods, such as RADseq (Arrigoni *et al.* 2020, Wepfer *et al.* 2020) and targeted capture of conserved loci (Quattrini *et al.* 2018, Cowman *et al.* 2020, Quek *et al.* 2020, Ramirez-Portilla *et al.*, 2022a), which examine a much larger number of independent markers, are proving more effective at resolving species-level relationships in previously problematic coral taxa. These powerful molecular tools, combined with increasing access to type material and original descriptions through digitization of museum collections (Beaman and Cellinese 2012), provide the opportunity to develop a robust taxonomy for reef corals (Bonito *et al.* 2021, Voolstra *et al.* 2021).

Acropora is the most species-rich and numerically abundant coral genus on most Indo-Pacific reefs. The morphological diversity of *Acropora* is illustrated by the fact that > 400 nominal species have been described (Hoeksema and Cairns 2022). However, around two-thirds of the nominal species in the genus were considered junior synonyms or unresolved by taxonomic revisions of the genus in the late 20th century (Veron and Wallace 1984, Wallace 1999), and only 120 extant species were considered valid in the most recent revision and catalogue of the genus globally (Wallace *et al.* 2012). The extensive synonymization of nominal species in *Acropora* and other reef coral taxa was driven primarily by two key assumptions: (1) that most species are 'pandemics' widely distributed across the Indo-Pacific (Potts 1983, 1984, Wallace 1999, Veron 2000); and (2) that most species exhibit significant morphological plasticity as a result of environmental factors rather than variability among species (e.g. Veron and Pichon 1976, Veron and Wallace 1984, Veron 1995, 2000, Wallace 1999). The extensive morphological variation within species and among geographical regions across the Indo-Pacific has also been attributed to extensive hybridization and 'reticulate evolution', to the extent that *Acropora* species were proposed to represent a syngameon rather than evolutionarily distinguishable lineages (van Oppen *et al.* 2001). However, the advent of new molecular techniques, combined with the increasing recognition that gene flow is not necessarily a barrier to speciation (Papadopulos *et al.* 2011, Martin *et al.* 2013, Larson *et al.* 2014), has cast doubt on these long-held assumptions (Ramirez-Portilla *et al.* 2022a).

Molecular phylogenies for the genus *Acropora* (e.g. van Oppen *et al.* 2001, Richards *et al.* 2013, Cowman *et al.* 2020) are largely incongruent with systematic relationships inferred from morphological analysis (Wallace 1999). Molecular data are providing increasingly compelling evidence that at least some putatively widespread *Acropora* species represent multiple distinct evolutionary lineages, which include both sympatric species within geographical regions and allopatric species across the Indo-Pacific (e.g. Ladner and Palumbi 2012, Richards *et al.* 2016, Suzuki *et al.* 2016, Sheets *et al.* 2018, Rose *et al.* 2021). Consequently, it is increasingly clear that the taxonomic revisions of late 20th century (Veron and Wallace 1984, Wallace 1999, Veron 2000) based solely on morphology are unlikely to capture the diversity or reflect systematic relationships within *Acropora* accurately. Despite mounting evidence of overlooked diversity in *Acropora*, there has been little effort to resolve the taxonomic identity of distinct lineages or test the validity of morphological species defined *a priori*; instead, distinct molecular lineages are generally reported as 'cryptic' species (e.g. Ladner and Palumbi 2012, Rosser 2016, Richards *et al.* 2016, Rosser *et al.* 2017, Rose *et al.* 2021). However, recent research examining three co-occurring tabular *Acropora* species in the north-west Pacific identified congruent morphological, molecular and ecological evidence to support species delimitation (Ramírez-Portilla *et al.*, 2022a, b). Furthermore, the three species did not hybridize, suggesting that previous conclusions regarding the porosity of species boundaries in *Acropora* might be attributable to factors such as incorrect taxonomic identifications. The increasing evidence that these recent morphological taxonomic revisions do not adequately capture the genetic diversity within *Acropora* demonstrates the need for formal taxonomic revision using an integrated, quantitative approach.

A recently developed bait set designed for targeted capture of ultraconserved elements (UCEs) and exonic loci (Quattrini *et al.* 2018, Cowman *et al.* 2020) has shown the potential to resolve species-level relationships within *Acropora* (Ramirez-Portilla *et al.*, 2022a) and other scleractinian genera (Grinblat *et al.*, 2021). Importantly, the maximum likelihood (ML) phylogeny presented by Cowman *et al.* (2020) indicates that the genus *Acropora* comprises six distinct clades (referred to as Clades I–VI) that do not correspond to traditional morphological 'species groups' (Wallace 1999). The phylogeny presented by Cowman *et al.* (2020) included only 65 *Acropora* specimens from across the Indo-Pacific, and specimens were selected to maximize coverage of the range of morphologies across the genus, rather than to replicate specimens of a single species or within a location. Consequently, this phylogeny was not sufficient to examine quantitatively the species boundaries within the six clades. Nonetheless, all five morphological 'clades' of Wallace (1999) were not monophyletic in the molecular phylogeny, suggesting that the morphological characters used to delineate species and

evolutionary relationships were not phylogenetically informative.

Here, we use the targeted capture methods for *Acropora* (Cowman *et al.* 2020) to reconstruct a species-level phylogeny of Clade I, the earliest diverging *Acropora* clade (see Cowman *et al.* 2020), and to conduct a taxonomic revision of one of the three subclades within Clade I (termed Clade I-C), which includes *Acropora tenuis* (Dana, 1846) and close relatives. The taxonomy of *A. tenuis* is of particular interest because: (1) it is considered common and geographically widespread, putatively occurring from French Polynesia in the South Pacific to the western Indian Ocean as far south as South Africa and into the northernmost Red Sea (Veron 2000, Richards *et al.* 2014) (virtually the entire geographical range of the genus *Acropora* outside of the western Atlantic); and (2) several nominal species from different locations across the Indo-Pacific were synonymized with *A. tenuis* based on morphological characters (Veron and Wallace 1984). Therefore, this species provides an ideal case study to test whether taxonomic decisions based on morphology alone are congruent with phylogenomic evidence, particularly in light of recent evidence for 'cryptic' lineages of '*A. tenuis*' in Japan (Zayasu *et al.* 2021) and on the Great Barrier Reef (GBR) (Cooke *et al.* 2020, Matias *et al.* 2022). Additionally, *A. tenuis* is frequently used in experiments in coral biology (Ball *et al.* 2021), and there are currently two genomes published under the name *A. tenuis*: one from the GBR (Cooke *et al.* 2020) and another from the Ryukyu Islands, Japan (Shinzato *et al.* 2021). *Acropora tenuis* was considered a member of the *Acropora selago* morphological group by Wallace (1999), along with *A. selago*, *Acropora eurystoma*, *Acropora striata*, *Acropora donei*, *Acropora yongei*, *Acropora loisettae* and *Acropora dendrum*; however, Cowman *et al.* (2020) suggest that their five specimens in Clade I belong to four different morphological species groups (the *echinata*, *selago*, *verweyi* and *rudis* groups). Here, we revisit these hypotheses by indentifying molecular lineages in our phylogeny that are sufficiently divergent to be considered different species. We then test the validity of our species hypotheses using additional lines of evidence, and compare the specimens in each lineage with the type material and original descriptions for all the nominal species in the genus *Acropora*.

MATERIALS AND METHODS

Sampling

We obtained tissue samples from 90 *Acropora* specimens collected from a variety of habitats across a substantial proportion of the latitudinal and longitudinal range of the genus, from the central Indo-Pacific to the western Indian Ocean (Fig. 1; Supporting Information, Table S1). We also harvested UCE and exonic loci from three published whole genomes (see details in 'Ultraconserved element/exon 'harvesting' from whole genomes' below). Sampling was conducted as part of a broader project examining the diversity of Indo-Pacific *Acropora*, and we therefore aimed to collect a representative sample of the *Acropora* fauna in each location. In this study, we focus on nominal species in Clade I-C (see below), which includes the *A. tenuis* complex (Supporting Information, Table S1). The 90 specimens examined from Clade I were added to 61 *Acropora* specimens already published by Cowman *et al.* (2020), allowing us to examine all newly sequenced samples in the context of the six *Acropora* clades outlined by Cowman *et al.* (2020). Of the 61 specimens from the study by Cowman *et al.* (2020), five were reconstructed as members of Clade I and three as members of Clade I-C.

In each sampling location, we specifically prioritized the collection of topotypes of nominal *Acropora* species. The term topotype is broadly used in taxonomy to refer to a specimen originating from the type locality of the species but which is not part of the type series. In this study, we refine the term 'topotype' to refer to the single specimen from the type locality that most closely resembles, morphologically, the original name-bearing type specimen (see Bonito *et al.* 2021). Given that most type specimens consist only of bleached calcium carbonate skeletons and lack preserved tissue, topotypes provide an anchor point within the phylogeny for each nominal species, enabling us to examine both genetic and morphological diversity within and among species.

All specimens (except for specimens from Chagos, which were collected initially for a separate study) were photographed in the field, before a fragment of the colony, sufficiently large for subsequent analysis of skeletal features, was collected as a voucher specimen using hammer and chisel. Voucher specimens were generally 15–30 cm in diameter, although specimens from Chagos were smaller branch fragments owing to permit requirements. A tissue sample from each voucher specimen was immediately preserved in high-grade ethanol for genetic analysis, and the remainder of the sample was bleached for curation in museum collections. Field images and skeletal vouchers of all specimens examined in this study can be viewed at: https://researchassets.qm.qld.gov.au/fotoweb/archives/5071-CoralBank-Research/. The collection location and associated metadata for each specimen are provided in the Supporting Information (Tables S1 and S2).

DNA extraction, targeted capture and post-processing

Coral DNA was extracted using a modification of the previously optimized SDS-based method (Wilson *et al.*, 2002). Briefly, coral fragments (~1 cm^2) were removed from fixing solution (i.e. ethanol) and incubated in 375 µL of digesting buffer (0.1 M Tris-HCL pH 9, 0.1 M EDTA pH 8, 0.1 M NaCl, 1% SDS, and 0.4 mg/mL proteinase K) at 65°C until the tissue was fully lysed. We added 100 µL of 5 M potassium acetate to the tissue lysate before it was transferred to ice for 30 min incubation for protein precipitation. After incubation, the mixtures were centrifuged at 28 000*g* for 15 min. To precipitate DNA, 0.8 vol. of isopropanol was added to the supernatant and incubated at room temperature for 15 min, and centrifuged at 28 000*g* for 15 min. The DNA pellet was washed with 70% ethanol, centrifuged at 28 000*g* for 5 min, and air-dried before eluting in Milli-Q water. DNA quality was assessed using a Nanodrop spectrophotometer, with 260/280 ratios ranging from 1.8 to 2.1 and 260/230 ratios ranging from 1.4 to 3.2. A Qubit 2.0 fluorometer was used to measure the DNA concentration of each sample. We aimed to extract ~1000 ng of total DNA for each specimen for enrichment and sequencing.

DNA samples of sufficient quality and quantity were pelleted with 0.3 M sodium acetate and ethanol and sent to Arbor

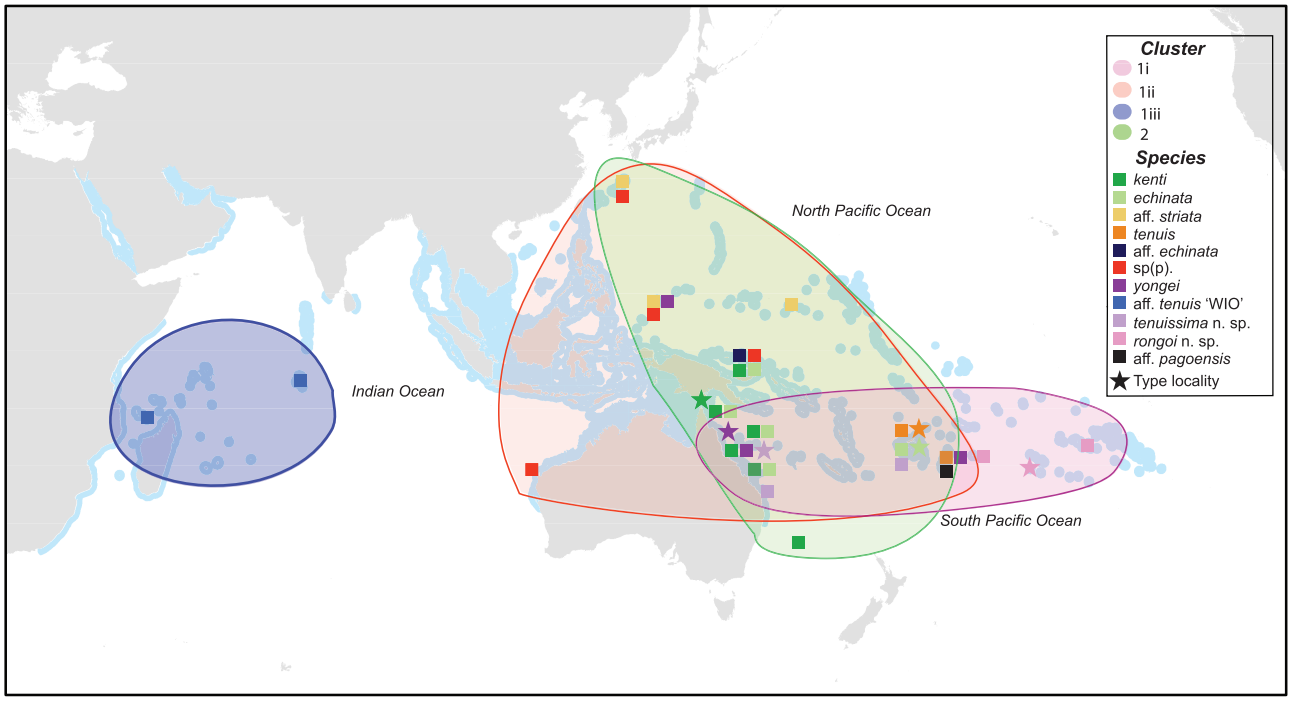

Figure 1. Map of sampling locations and species distributions. Coloured squares indicate the occurrence of each species in each location, and stars indicate the type localities for each nominal species described in this study. Light shading indicates the range of each subclade of *Acropora* clade I-C (purple, cluster 1i; blue, cluster 1ii; orange, cluster 1iii; green, cluster 2), and light blue shading shows the putative range of *Acropora tenuis* according to the IUCN Red List (Richards *et al.* 2014).

Biosciences (Ann Arbor, MI, USA) for downstream library preparation, target enrichment and sequencing, following details given by Cowman *et al.* (2020). Samples were processed using a modified KAPA Hyper Prep Kit (Kapa Biosystems) protocol, where the extracted DNA was sonicated to a target size range of approximately 300 or 500 base pairs. Genomic libraries were prepared using universal Y-yoke oligonucleotide adapters and custom 8-bp indexes. For target enrichment, the Daicel Arbor Biosciences MyBaits v5 protocol was employed to capture pools of up to 12 samples simultaneously. The target-enriched libraries were sequenced using either Illumina HiSeq 4000 PE150 or NovaSeq 6000 S4 PE150 (V1 or V1.5 chemistry), depending on the round of sequencing. The sequencing was performed on either one full and one partial lane of HiSeq 4000 or partial flowcells of NovaSeq 6000 S4, ensuring adequate read coverage for the samples.

Paired end reads of each sample were processed alongside previously published data for 61 specimens from the study by Cowman *et al.* (2020) (for sample details, see Supporting Information, Table S1). Demultiplexed Illumina reads were processed using Phyluce v.1.6 (Faircloth 2016; https://phyluce.readthedocs.io/en/latest/tutorials/tutorial-1.html), with the same pipeline modifications as Cowman *et al.* (2020). Reads were trimmed using the Illumiprocessor wrapper program (Faircloth *et al.* 2012) for Trimmomatic (Bolger *et al.* 2014) with default values. Trimmed reads were then assembled using the stand-alone version of Spades v.3.10 (Bankevich *et al.* 2012, Nurk *et al.* 2013) with the *–careful* and *–cov-cutoff 2* parameters. Ultraconserved element and exon bait sequences were then matched separately to the assembled contigs at 70% identity and 70% coverage using phyluce_assembly_match_contigs_to_probes. Phyluce_assembly_get_match_counts and phyluce_assembly_get_fastas_from_match_counts were used to extract loci into FASTA files. Phyluce_align_seqcap_align was used to align (with MAFFT; Katoh *et al.* 2002) each locus using both edge trimming and internal trimming (via GBLOCKS v.0.91b; Castresana 2000), with default settings. For each alignment type (edge and internal trimmed) alignment matrices were created in which each locus was represented by either 50% or 75% sample occupancy. At the end of this process, UCE and exon locus alignments were combined. The total number of variable sites, total number of parsimony informative sites and number of parsimony informative sites per locus were calculated using phyluce_align_get_informative_sites for alignments across different taxonomic levels [all taxa (N = 154), clade I (N = 93) and subclades within clade I: clade I-A (N = 22), clade I-B (N = 12) and clade I-C (N = 60)] and a number of primary species hypotheses designated in this paper.

Ultraconserved element/exon 'harvesting' from whole genomes

In addition to the newly sequenced data from this study and the previously sequenced samples from Cowman *et al.* (2020), we included UCE/exon loci 'harvested' from published whole genome assemblies published as *A. tenuis* (N = 2; Cooke *et al.* 2020, Shinzato *et al.* 2021) and *Acroporis echinata* (Dana, 1846) (Shinzato *et al.* 2021) (Supporting Information, Table S1). The *A. echinata* genome was included given that the delineation of Clade I by Cowman *et al.* (2020) included two specimens (KM27 and KM32) with morphological affinities to *A. echinata*. We examined images of living colonies and skeletal vouchers of

the specimens sequenced by Cooke *et al.* (2020) (QM G335181 and G335182), but no images or vouchers of sequenced specimens were available for Shinzato *et al.* (2021). Harvesting of targeted loci from whole genomes followed the procedure outlined in Phyluce v.1.6 (https://phyluce.readthedocs.io/en/latest/tutorials/tutorial-3.html). Harvested UCE/exons matching assembled contigs were then included in the alignment procedure outlined above (see Supporting Information, Table S3).

Phylogenomic reconstruction and single nucleotide polymorphism calling

Each of the four alignment matrices (50% and 75% complete edge and internally trimmed alignment) underwent ML analyses in IQ-TREE v.2.1 (Minh *et al.* 2020a). Model selection and partitioning scheme estimation were conducted using the ModelFinder algorithm (Kalyaanamoorthy *et al.*, 2017) in IQ-TREE with the parameter settings '-m MFP+MERGE --merge-model GTR --merge-rate G --rclusterf 10'. For each alignment matrix, ultrafast bootstrap (UFBoot) support approximation with 1000 replicates (Minh *et al.* 2013, Hoang *et al.* 2018) was calculated. UFBoot is a fast and accurate approximation of the standard bootstrap method that can be used to assess branch support on large datasets (Minh *et al.* 2020b). In general, UFBoot values > 95% are considered strong clade support, while values between 90% and 95% are considered moderate support.

In addition, gene and site concordance factors were calculated using IQ-TREE to provide additional insight into agreement and disagreement between gene and species trees (Minh *et al.* 2020b). Gene concordance factors (gCF) measures the degree of agreement between the topologies inferred from individual UCE/exon loci in the dataset by comparing the topologies of each gene tree with a consensus tree that summarizes the relationships across all genes (Minh *et al.* 2020b). It is generally presented as a percentage measure of the gene trees that agree on a particular branch, with higher values indicating greater support for a clade in a phylogeny. Site concordance factor (sCF) measures the degree of agreement between the topologies inferred from different sites across the alignment, expressed as the average proportion of sites that are decisive for a particular branch in the phylogeny. The sCF value is calculated from quartets, where a single site can support only one of three topologies at a node, hence sCF values are rarely below ~33% (Minh *et al* 2020b). Therefore, an sCF measure of 34% is 'decisive' for that node, with a higher value (> 50%) being an indication of strong support (Minh *et al* 2020b).

Individual bootstrap consensus trees (1000 ultrafast bootstrap replicates) for each UCE/exon were also reconstructed in IQ-TREE for downstream multiple species coalescent (MSC) analyses following the ASTRAL III (Zhang *et al.* 2018) online tutorial (https://github.com/smirarab/ASTRAL/blob/master/astral-tutorial-template.md). Before MSC analyses in ASTRAL, branches with low support (< 30% bootstrap support) were removed from individual locus trees. The program TreeShrink (Mai and Mirarab 2018) was used to identify and remove outlier long branches from the individual locus trees and their corresponding sequence alignments. IQ-TREE was used a second time on these resulting alignments to reconstruct individual consensus trees for each locus (1000 ultrafast bootstraps). This set of bootstrapped gene trees was then used to estimate the species tree in ASTRAL III. In total, four ML trees and four ASTRAL trees were reconstructed. Alignment information and supplemental trees are provided in the Supporting Information (Table S3; Fig S1-S2).

Single nucleotide polymorphisms (SNPs) were called from the targeted capture data to delimit species within the *tenuis* clade (Zarza *et al.* 2018, Erickson *et al.* 2021). Briefly, the individual sample with the largest number of UCE/exon contigs was identified using the Phyluce function phyluce_assembly_get_match_counts. This sample served as the reference individual for SNP calling. A FASTA file of UCE/exons only for the reference sample was created using the functions *phyluce_assembly_get_match_counts* and *phyluce_assembly_get_fastas_from_match_count*. Reference loci were then indexed using BWA v.0.7.7 (Li and Durbin 2009). Cleaned and trimmed reads for each sample were then mapped to the reference using BWA-MEM (Li 2013), sorted with SAMTOOLS (Li *et al.* 2009), with duplicates removed using PICARD v.1.106 (Broad Institute 2018). GATK v.3.4 (McKenna *et al.* 2010) was then used to realign BAM files around indels, then call and filter variants using VCFtools (Danecek *et al.* 2011). Only biallelic SNPs with ≥ 25 × coverage per SNP were retained, with one SNP selected per locus for loci < 1000 bp, or one per 1000 bp if loci were ≥ 1000 bp. The SNPs were also subset for each of two main clades within the *tenuis* clade to examine species boundaries further within those lineages.

Species delimitation

Species delimitation was conducted using an integrated approach based on multiple lines of evidence. We use the unified species concept (de Queiroz 2007), which defines a species simply as an 'independently evolving metapopulation lineage', and therefore allows the delineation of distinct evolutionary lineages without requiring species to be distinguishable morphologically or to exhibit intrinsic reproductive isolation. Genetically distinct but morphologically similar species (termed 'cryptic' species) are increasingly recognized across the Tree of Life and must be accounted for in order to capture the diversity and systematic relationships within the clade of interest (Fišer *et al.* 2018). However, species delineation in reef corals is still based almost exclusively on morphological characters, despite widespread evidence of convergence and morphological stasis among deeply diverged taxa (Fukami *et al.* 2004, Bongaerts *et al.* 2021). Although the lack of molecular data for type specimens of virtually all nominal species of Scleractinia still necessitates morphological comparison of sequenced specimens to type material, molecular species delineation methods allow identification of distinct evolutionary lineages both when distinct species appear very similar morphologically and when a single species shows extensive morphological variability. This is particularly useful for delineating allopatric *Acropora* species that have been synonymised on the basis of morphological similarity.

Primary species hypotheses (PSHs) were identified as distinct molecular lineages delineated in the ML phylogeny with robust support values where specimens also shared similar morphological characters. Characters examined included colony morphology, branch length and diameter, size and shape of

axial and radial corallites and the shape and ornamentation of the coenoesteum, following Wallace (1999). This allowed us to designate species names to particular lineages when the type material was available. However, it is important to note that this process does not necessarily capture the intraspecific variation required to delineate species boundaries in the field. Although the capacity to identify species in the field based on morphology is important for many research questions, it is beyond the scope of this study and will require numerous detailed studies focusing on a manageable number of species at a local scale (e.g. Ramírez-Portilla *et al.* 2022a).

We assigned names to each PSH based on comparison of the specimens within each lineage to the type material and original descriptions for all nominal of *Acropora* (Supporting Information, Table S1). To account for differing degrees of certainty with the application of species names, we use an open nomenclature (see Cowman *et al.* 2020). Given that some syntype series are likely to include multiple species, our identifications were made with reference to the name-bearing type, i.e. the specimens designated as lectotypes for *A. echinata* and *Acropora kenti* Brook, 1892 by Wallace (1999). The specimen in our phylogeny that most closely matched the type specimen and original description of a particular nominal species in the morphological characters outlined in the original description and collected from the same location was designated as the 'topotype' (Bonito *et al.* 2021). This process enabled us to assign several PSHs to nominal species, irrespective of whether these species were considered valid by, and therefore included in, recent taxonomic revisions.

The current taxonomic status of each PSH that could be matched to a nominal species was based on the World List of Scleractinia (Hoeksema and Cairns 2022). Additional information on species geographical ranges was obtained by comparing the skeletal vouchers of sequenced specimens with additional skeletal specimens in the Worldwide *Acropora* Collection in the Museum of Tropical Queensland (Wallace *et al.* 2012). Given that our focus is on Clade I *sensu* Cowman *et al* (2020), our sampling included other members of that clade (e.g. *A. echinata*, *A. yongei*). We also included topotypes for two additional species, *A. selago* and *A. donei*, which were placed in the '*selago*' morphological group by Wallace (1999) and therefore presumed to be close relatives of *A. tenuis*.

Primary species hypotheses identified by the ML phylogeny (excluding the harvested genomes) were subsequently tested using three different species delimitation methods using analysis of SNPs generated from the targeted capture data to define species boundaries. First, we used two standard genetic clustering techniques: discriminant analysis of principle components (DAPC; Jombart *et al.* 2010) and STRUCTURE (Pritchard *et al.* 2000). Second, we used an unsupervised machine learning (UML) approach: t-distributed stochastic neighbor embedding (t-SNE; van der Maaten and Hinton 2008, Derkarabetian *et al.* 2019). Finally, we use the Bayes factor delimitation approach (*BFD; Leaché *et al.* 2014) with SNAPP in BEAST 2.0 to test multiple species hypotheses.

The DAPC method clusters species based on their genetic similarity, providing an estimation of how many populations (K) can be assumed from the data. DAPC (Jombart *et al.* 2010) was conducted using the R package 'adegenet' (Jombart 2008) in R v.4.1 (R Core Team, 2022). We first conducted a principal components analysis (PCA; dudi.pca function) on scaled data, then identified the optimal number of clusters to minimize the Bayesian informaiton criterion using the function *find.clusters*. We used *optim.a.score* to estimate the number of principal component (PC) axes and the discriminant functions (DFs) to retain.

STRUCTURE uses a Bayesian clustering method to infer the population structure in a probabilistic framework, given K populations. We ran STRUCTURE using the parallel version of the program STRAUTOPARALLEL (Chhatre & Emerson, 2017) with 1 million generations and a burn-in of 250 000. We used five runs for each value of K and a maximum K of 13, with results combined and visualized using *POPHELPER* (Francis, 2017) in R. Evanno DeltaK plots (Evanno *et al.* 2005) were used to determine the most likely number of clusters.

t-SNE is a non-linear dimensionality reduction algorithm that aims to preserve probability distributions of distances among samples in a cluster while also repelling samples that are in a different cluster (Derkarabetian *et al.* 2019). t-SNE was executed using the R package *tsne* (Donaldson 2016), using the results of the initial PCA as input, following recommendations for large datasets (Pedregosa *et al.* 2011). Parameters specified in the t-SNE analyses were maximum iterations (max_iter = 10000), perplexity = 5, intial dimensions (intial_dims = 5) and the number of dimensions (k) for the resulting embedding (k = 2). Two sets of clustering analyses were conducted on the t-SNE outputs: (1) Partition around medoids (PAM) clustering with optimal K determined via gap statistic using k-mean clustering and the 'factorextra' package (Kassabara and Munt 2017); and (2) optimal K and clustering determined via hierarchical cluster with the 'mclust' R package (Scrucca *et al.* 2017) using the broken stick method of the 'PCDimensions' package (Coombes and Wang 2018). The t-SNE and clustering analyses were run using modified code from Derkarabetian *et al.* (2019) (github.com/shahanderkarabetian/uml_species_deli).

We conducted a SNAPP coalescence-based analysis using a 75% UCE SNP matrix in BEAST (Bouckaert *et al.* 2014) with *BFD to test alternative species models (Leaché *et al.* 2014). Specifically, three different species models were tested using this framework, reflecting the current taxonomy against our proposed taxonomy with 11 PSHs and our taxonomy with 10 PSHs (*yongei*/spp. grouped together; see Results). SNAPP models were performed in BEAST with 48 path sampling steps, 1 000 000 Markov chain Monte Carlo chains and 1000 pre-burn-in (following Quattrini *et al.* 2019). Convergence of all parameters was assessed using Tracer v.1.7 (Rambaut *et al.* 2018). To determine the support for each of the three species hypotheses, Bayes factors (Kass and Raftery 1995) were calculated as (2 × log likelihood difference).

RESULTS

Targeted capture data

Target capture of UCE/exons based on the Hexacoral v.2 scleractinian bait set resulted in 2425 total loci (1132 UCE and 1293 exons) enriched across the 154 samples and harvested from three published genomes. The numbers of trimmed reads,

assembled contigs and captured loci are given in the Supporting Information (Table S3). Overall, the number of loci recovered per sample sequenced in this study varied from 2008 to 1372 (see Supporting Information, Table S3), with an average of 1565 (±109) loci recovered. The number of loci harvested from previously published whole genomes varied from 1677 ('*tenuis*' genome in Cooke *et al.* 2020) to 1652 ('*echinata*' genome in Shinzato *et al.* 2021). Alignments spanned 2032 and 1850 loci in 50% complete alignment matrices across different taxonomic datasets (Supporting Information, Table S4). The percentage of parsimoniously informative sites varied across different evolutionary scales (from 16% across the entire genus to 7% within Clade I, down to 0.06% in the aff. *striata* lineage; Supporting Information, Table S4). From the targeted capture data, 2046 SNPs were called in a 75% complete matrix.

Phylogenomic assessment

The relationships among the six *Acropora* clades (I–VI *sensu* Cowman *et al.* 2020) and the subclades within Clade I are supported across all datasets and phylogenetic reconstruction methods (ML in IQ-TREE and MSC in ASTRAL; Supporting Information, Figs S1, S2) and their associated support measures (UF bootstrap; gCF and sCF; posterior probability). Differences between all phylogenies are presented in the Supporting Information (Figs S1, S2). All results below are described in relation to the 50% complete edge-trimmed alignments, where phylogenetic relationships were most concordant with morphological assessment. In the 50% complete edge-trimmed tree, 81% of internal nodes received UFBoot support of 100%, 89% of internal nodes had as CF scores of > 34%, and 23% of internal nodes had gCF scores of > 50%. Average sCF and gCF scores across the phylogeny were 46% and 15%, respectively.

The phylogenomic reconstruction places *A. tenuis* and related species within Clade I, the first lineage to branch off in *Acropora* and the sister group to the remaining five clades (Fig. 2A). Within Clade I, our genetic sampling spans three well-supported subclades (labelled here as Clade I-A to I-C; Fig. 2). The *tenuis* complex is found in Clade I-C (Fig. 2B), which we refer to as 'clade C' hereafter. Within clade C, the ML analyses recovered 11 well-resolved lineages with sufficiently high branch support, based on both ultrafast bootstrap (≥ 90%) and decisive site concordance factor values (≥ 34%), to be considered distinct PSHs (Fig. 2B) and subjected to various SNP-based species delimitation analyses to provide quantitative support for species delineation. In general, gene concordance factors were low (< 10%; Supporting Information, Figs S1, S2). Trees recovered from MSC analyses (Supporting Information, Fig. S1) in ASTRAL-III (Supporting Information, Fig. S2) recovered the same three-clade structure in Clade I and very similar topologies in clade C, but topologies varied across alignment matrix types. The phylogeny also outlines striking geographical structure within clade C, with most species being restricted to particular biogeographic regions within the Indo-Pacific and none occurring across the Indo-Pacific (Fig. 1). Specimens from the central-western Indian Ocean, in particular, form a distinct clade.

We recovered > 1600 loci for each whole genome sample (Supporting Information, Table S3). Both *A. tenuis* genomes were reconstructed within clade C, but neither specimen was in the same PSH as the topotype of *A. tenuis* (Dana, 1846) from Fiji (Fig. 2; Supporting Information, Figs S1, S2). The whole genome identified as *A. echinata* from the Ryukyu Islands was recovered within Clade VI, very distant from the topotype of *A. echinata* Dana, 1846 from Fiji in Clade I-C (Supporting Information, Figs S1, S2). Across all reconstructions, the whole genome representing '*A. tenuis*' sampled from the GBR was consistently placed with other specimens from eastern Australia, which we identify as *A. kenti* Brook, 1892 (see Taxonomic Account). The '*A. tenuis*' genome from the Ryukyu Islands was consistently placed with samples from Pohnpei and Palau (Fig. 2; Supporting Information, Figs S1, S2), which we identify as *A.* aff. *striata* (See Taxonomic Account).

Species delimitation and systematic relationships

Based on morphological comparison of topotypes examined in our study with type material (Supporting Information, Fig. S3) and original descriptions, only four PSHs could be identified as a nominal species: *A. tenuis* (Dana, 1846), *A. echinata* (Dana, 1846), *A. kenti* (Brook, 1892) and *A. yongei* Veron & Wallace, 1984. The remaining seven lineages could not be matched with the type material of any single nominal species. Two of these represent new species (*Acropora tenuissima* n. sp. and *Acropora rongoi* n. sp.) described (see Taxonomic Account). Of the remaining five PSHs, four [*A.* aff. *striata*, *A.* aff. *tenuis* 'Western Indian Ocean' ('WIO'), *A.* aff. *echinata* and *A.* aff. *pagoensis*] contain specimens that bear some resemblance to a nominal species but require further study to confirm their identity, while *A.* sp(p). contains a topotype for *A. akajimensis* Veron, 1990 along with other specimens with a wide range of morphologies that cannot be resolved here.

The STRUCTURE analyses initially highlighted that the 11 PSHs spread across two discrete genetic clusters ($K = 2$; Supporting Information, Fig. S4): cluster 1 included seven PSHs: *A. tenuissima*, *A. rongoi*, *A.* aff. *pagoensis*, *A.* aff. *tenuis* 'WIO', *A. yongei* Veron & Wallace, 1984, *A.* sp(p) and *A.* aff. *echinata*; and cluster 2 contained the remaining four PSHs: *A. tenuis* Dana 1846, *A.* aff. *striata*, *A. echinata* Dana 1846 and *A. kenti* Brook 1892 (Fig. 3A). One sample was placed with almost equal probabilities in both clusters (74-1950, 0.50/0.49; Supporting Information, Fig. S4), and the phylogenetic placement of this sample also varied among alignment datasets (see Supporting Information, Figs S1, S2). One PSH (*Acropora* aff. *echinata*; see Taxonomic Account) was included in cluster 1 and sister to *yongei*/sp(p) in STRUCTURE (Fig. 3), but at the base of cluster 2 in the ML phylogeny (Fig. 2).

Additional STRUCTURE analyses were run for each of the two clusters independently and, subsequently, for two clusters identified within cluster 1 (clusters 1i and 1iii; Fig. 3A, lower panel; Supporting Information, Fig. S4). Within cluster 1, Evanno DeltaK plots indicated that $K = 3$ and $K = 6$ genetic clusters were the most likely, with $K = 6$ having a slightly higher DeltaK than $K = 3$. At $K = 3$, the analyses placed *A. tenuissima*, *A. rongoi* and *A.* aff. *pagoensis* in one group (cluster 1i), *A.* aff. *tenuis* 'WIO' in a second (cluster 1ii), and *A. yongei*, *A.* aff. *echinata and A.* sp(p) in a third (cluster 1iii). At $K = 6$, the genetic distinction is less clear, but again *A. rongoi*, *A.* aff. *pagoensis A. tenuissima* and *A.* aff. *echinata* are overall assigned to separate genetic clusters from *A.* sp(p) and *A. yongei*.

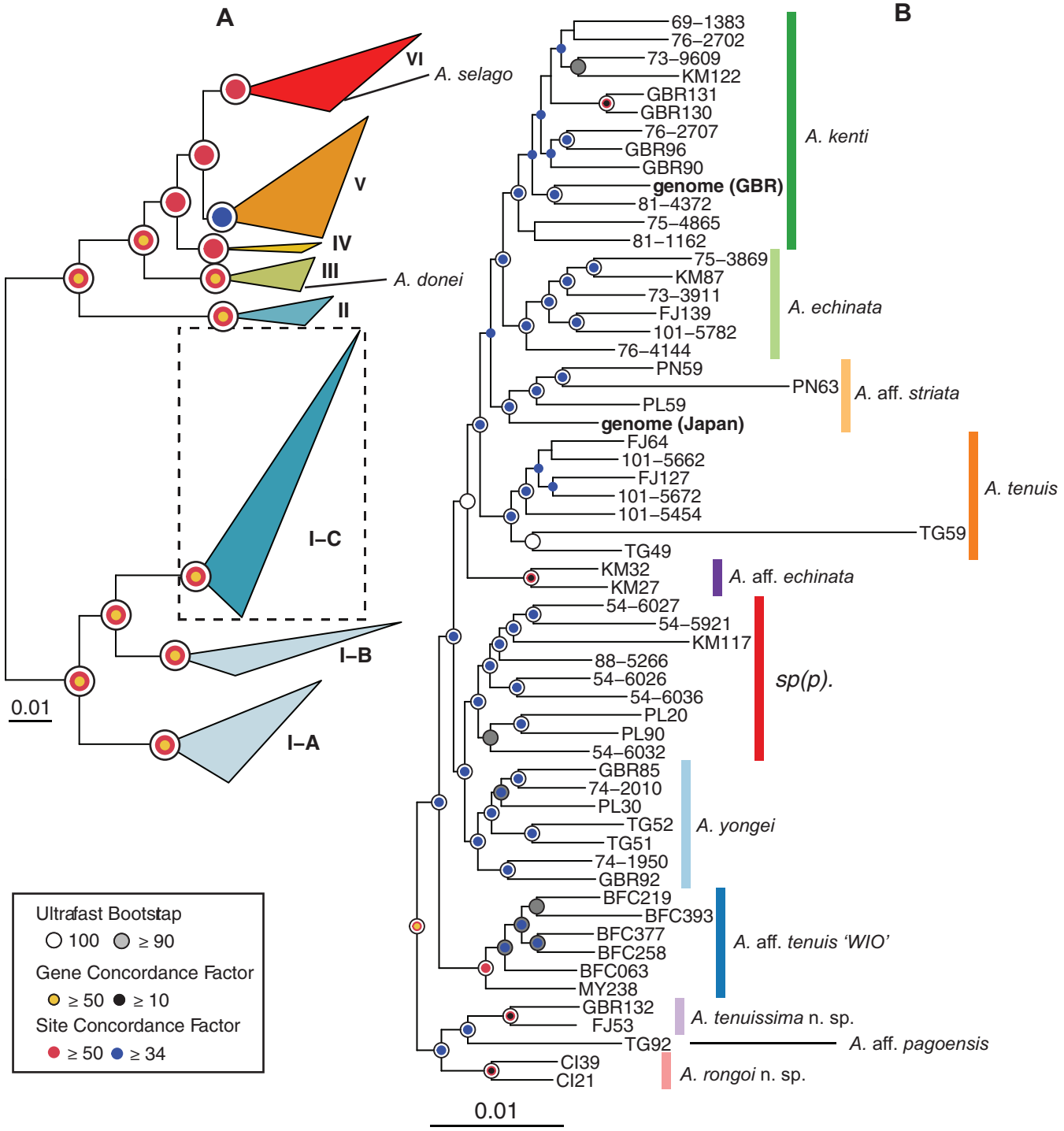

Figure 2. Maximum likelihood (ML) phylogeny based on the 50% complete edge-trimmed alignment matrix (2032 loci). A, inset phylogeny depicts the relationships among all six major *Acropora* clades (*sensu* Cowman *et al.* 2020) and the three subclades within clade I. Clade I-C is indicated by the dashed box. The position of *Acropora selago* (Clade VI) and *Acropora donei* (Clade III) are indicated. B, ML phylogeny of clade I-C. Ultrafast bootstrap support and gene/site concordance factors are indicated at the nodes (see key). Primary species hypotheses (PSHs) are indicated by clade labels. Field codes for each specimen (tip labels) also reflect the collection location: Great Barrier Reef (73-, 74-, 76-, GBR); Coral Sea (75-); Lord Howe Island, south-east Australia (81-), Fiji (101-, FJ), Tonga (TG); Rarotonga, Cook Islands (CI); Kimbe Bay, Bismarck Sea, Papua New Guinea (69-, KM); Palau (PL); Pohnpei (PN); Ningaloo Reef, Western Australia (88-); Ryukyu Islands, Japan (54-); Chagos (BFC); and Mayotte (MY).

To further resolve species boundaries within cluster 1, we ran additional analyses on two subsets of cluster 1 (cluster 1i and 1iii; Fig. 3A, lower panel). The analysis of cluster 1i indicates $K = 2$ genetic clusters that separate *A. tenuissima* and *A. rongoi*, with *A.* aff. *pagoensis* placed with nearly equal probability in between the two clusters. In cluster 1iii, $K = 2$ genetic clusters

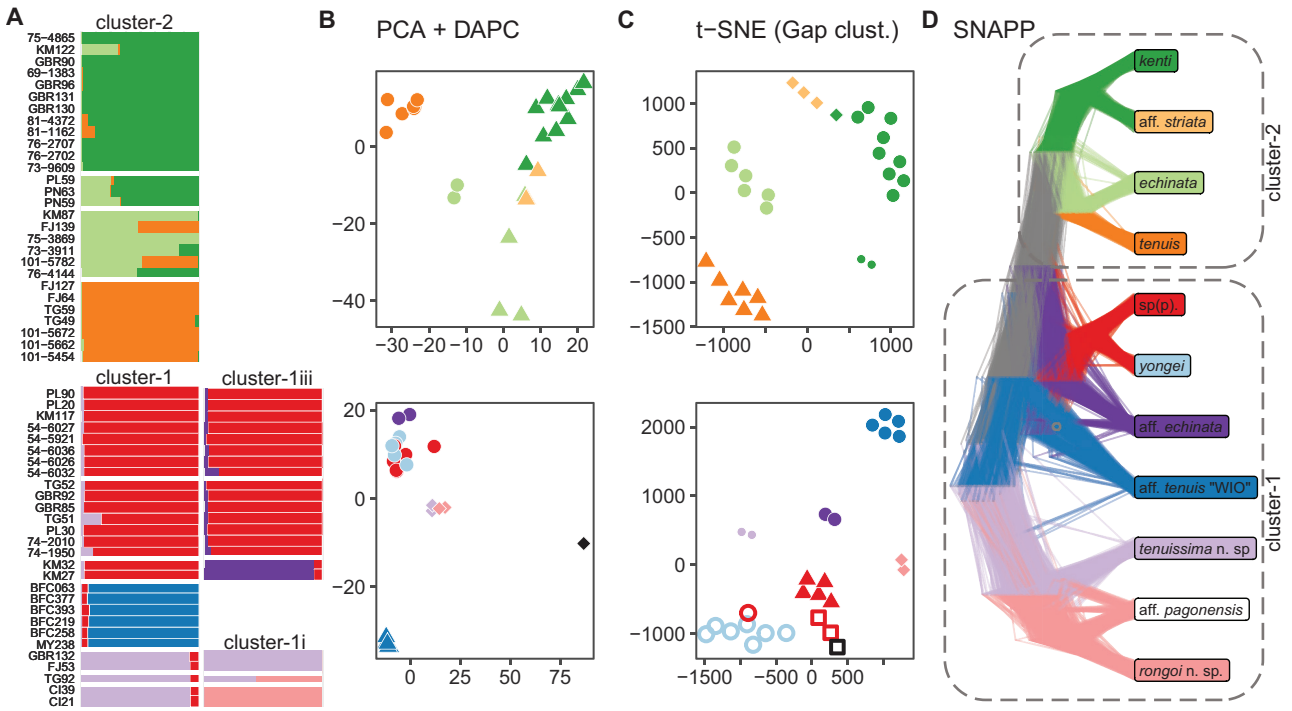

Figure 3. Results from multiple species delimitation methods of Clade I-C. A, STRUCTURE result for cluster 1 ($K = 3$) cluster 1i ($K = 2$) and cluster 1iii ($K = 2$) in lower panel and cluster 2 ($K = 3$) in upper panel. Additional STRUCTURE plots are available in the Supporting Information (Fig. S4). B, principal components analysis (PCA) plots for DAPC analysis for cluster 1 in the lower panel and cluster 2 in the upper panel. DAPC clusters are indicated by shape for cluster 1 ($K = 3$; diamond, triangle and filled circle) and cluster 2 ($K = 2$; triangles and filled circles). Colours of shapes match the PSH designation from Figure 2. C, unsupervised machine learning method t-SNE clustering of samples using Gap algorithm clustering for cluster 1 and cluster 2. Genetic clusters are indicated by shape, while colour matches the PSH designation. Cluster 1 is shown in the lower panel; alternative clustering methods and detailed labelled plots are shown in the Supporting Information (Fig. S5). D, species tree cloudogram of Clade I-C. Cloudogram of the posterior distribution of SNAPP trees from 2046 SNPs mined from targeted capture data. Tip labels indicate species designated from phylogenetic and morphological assessment. (see Supporting Information Fig. S4).

was the most likely, with *A.* aff. *echinata* placed separately from a cluster containing samples identified as *A. yongei* and *A.* sp(p). Within cluster 2, $K = 3$ was the most likely number of clusters, with *A. tenuis* designated as a clearly separate cluster from *A. echinata* and *A. kenti*, while samples *A.* aff. *striata* mostly cluster with the *A. kenti* samples but also show some genetic affinity with *A. echinata* (Fig. 3A, upper panel). Three samples within the *A. echinata* PSH have affinity with the *A. kenti* cluster (76-4144) and the *A. tenuis* cluster (101-5782 and FJ139), while one *A. kenti* sample (KM122) shows affinities with *A. echinata*.

Based on initial STRUCTURE results, all PCA, DAPC and t-SNE an Clyses were conducted on separate SNP datasets for cluster 1 and cluster 2 (Fig. 3). Before the PCA, DAPC, t-SNE and SNAPP analyses, two samples from cluster 1 that had proportions of missing data > 30% were removed from the analyses (BFC393 and TG52). The DAPC clustering on PCA axes (Fig. 3B, lower panel) showed three clusters in cluster 1 that did not correspond to PSHs, but delineated the *A.* aff *tenuis* 'WIO' samples from a cluster containing *A. tenuissima*, *A. rongoi and A.* aff. *pagoensis* and a cluster containing *A.* aff. *echinata*, *A. yongei* and *A.* sp(p) from the central-west Pacific and eastern Indian oceans. In cluster 2, DAPC results showed two clusters that also do not align to PSHs: all samples of *A. tenuis* and two *A. echinata* from Fiji in one cluster, which was distinct from all other samples (Fig. 3B, upper panel).

The t-SNE analyses resolved more discrete genetic clustering of samples within both clusters than DAPC, and although there was minor variation in cluster membership between the two clustering methods (PAM and hierarchical; Supporting Information, Fig. S5), some general patterns were clear. Based on PAM clustering of the 75% SNP dataset, seven clusters were recognized in cluster 1 (Fig. 3C, lower panel), with individual groups corresponding to PSHs for *A.* aff. *tenuis* 'WIO', *A. tenuissima*, *A. rongoi*, *A.* aff. *echinata*, and three groups consisting of a mix of samples from the PSHs *A. yongei*, *A.* sp(p) and *A.* aff. *pagoensis*.

The SNAPP analyses supported the 11 PSHs described above (Fig. 3A). The SNAPP consensus topology indicated that the majority of trees with the 11 PSHs were congruent, although some alternative topologies were apparent, particularly within cluster 1. *BFD indicated that 11-PSH taxonomy was the better model (Maximum Likelihood Estimation [MLE] = −26 225, Bayes Factor [BF] = −26 374) than a 10-species model (MLE = −26 284, BF = −26 256), while both were substantially better than the current morphological taxonomy (MLE = −39 412). A detailed taxonomic account of *Acropora* Clade I-C is provided below.

DISCUSSION

Our study represents the first taxonomic revision of *Acropora* based on phylogenomic data, and our results are clearly

incongruent with recent taxonomic revisions based on morphology (Veron and Wallace 1984, Wallace 1999) that are widely used in coral reef science. Importantly, our results demonstrate that: (1) the diversity of *Acropora* is higher than currently recognized; and (2) the putatively widespread nominal species, *A. tenuis* represents multiple distinct species with restricted geographical distributions. These findings highlight the urgent need to revisit the taxonomy, systematics and biogeography of *Acropora* more broadly.

Both hybridization and introgression are processes that involve the mixing of genetic material from different populations or species. The key difference between the two is that hybridization produces a single hybrid population with a new generic pattern, whereas introgression leads to the gradual assimilation of genes from one group to another through repeated hybridization and backcrossing. Distinguishing the two processes in phylogenomic research is difficult because they can produce similar patterns in molecular data; however, understanding how different processes have shaped the evolutionary history of corals is important for accurate species delimitation. Despite some evidence for introgression in a small number of specimens, our results do not support the persistent belief that widespread hybridization has blurred species boundaries in *Acropora* (e.g. Veron 1995, van Oppen *et al.* 2001, 2002). Only one specimen (74-1950) in our study had a phylogenetic placement that varied substantially between ML phylogenies and might, potentially, represent a recent hybrid (Supporting Information, Figs S1, S2). However, the low number of loci captured (Supporting Information, Table S2) might also explain its uncertain placement in the ML phylogenies (Supporting Information, Figs S1, S2) and conflicting association in STRUCTURE (Supporting Information, Fig. S4). Morphologically, the specimen is similar to *A. yongei*, but the radial corallites differ from other *A. yongei* specimens.

Both unsupervised machine learning and Bayesian coalescent based methods were able to delineate species effectively. Only 6 samples sequenced in clade C showed a genetic signal that 'blurred' the PSHs delineated on the basis of phylogenetic reconstructions (e.g. 74-1950) and genetic clustering techniques (e.g. TG92, 76-4144, 101-5782, FJ139 and KM122; see details below). Consequently, we show that recently developed species delimitation techniques combined with genomic-scale datasets can resolve species boundaries even in previously challenging groups (Quattrini *et al.* 2019, Erickson *et al.* 2021, Quek and Huang 2022, Hobbs *et al.* 2022). Importantly, our results provide further evidence that hybridization in *Acropora* is not particularly common and does not preclude robust species delimitation in the genus (Ramirez-Portilla *et al.* 2022a).

Despite evidence for only a single recent hybrid individual (74-1950), our data do show evidence of incomplete lineage sorting or hybridization/introgression in some UCE/exon loci of specimens in clade C. For example, the STRUCTURE analysis indicated that specimens identified as *A. echinata* from Fiji (FJ139 and 101-5782) show some affinities with *A. tenuis* across the SNP dataset (Fig. 3A), whereas those from the GBR (76-4144 and 73-3911) show affinities with *A. kenti* (Fig. 3B). These genetic results are also reflected in their morphology: FJ139, 101-5782 and 73-3911 all closely resemble the *A. echinata* type, and the first two are also from the type locality; however, 76-4144 clusters phylogenetically with *A. echinata*, but its morphology is intermediate between *A. echinata* and *A. kenti*. Similarly, KM122 is phylogenetically reconstructed within *A. kenti*, but is morphologically more similar to *A. echinata*, a finding also reflected in the STRUCTURE results.

It is increasingly clear that species boundaries can be maintained even in the presence of gene flow (Papadopulos *et al.* 2011, Martin *et al.* 2013, Larson *et al.* 2014, Jackson *et al.* 2017); therefore, the evidence of hybridization within some specimens does not indicate that *Acropora* species represent a syngameon. Instead, it is likely that *Acropora*, like most other taxonomic groups, can maintain species boundaries despite hybridization in their evolutionary history. Although population structure within species can also obscure species boundaries (Sukumaran and Knowles 2017), multiple lines of evidence support our conclusion that the 11 lineages outlined here represent distinct species and are not simply an artefact of isolation by distance: (1) sister species often differ substantially in morphology (e.g. if *A. kenti* were synonymous with *A. tenuis*, then so must be the bottlebrush species *A. echinata*); and (2) each species represents a reciprocally monophyletic group within all phylogenomic analyses (with the exception of *A.* sp(p) and *A. yongei*). In addition, there is increasing evidence that long-distance dispersal in corals is very rare; the peak in larval competency for most coral species tested to date is 7–14 days (Connolly and Baird 2010, Figueiredo *et al.* 2013), and the average dispersal distance is measured in tens of kilometres, not hundreds or thousands (Figueiredo *et al.* 2013, 2022, Underwood *et al.* 2020). Consequently, it is not surprising that many coral species ranges are far smaller than currently assumed.

The most recent taxonomic accounts of the genus *Acropora* based on morphological characters (Veron and Wallace 1984, Wallace 1999, Veron 2000) suggested that the majority of *Acropora* species have large geographical ranges spanning the central Pacific through to the western Indian Ocean. However, our results suggest limited overlap in species composition between the Pacific and Indian Oceans within clade C, with distinct biogeographical structure within the Pacific. Furthermore, many species appear confined to relatively small regions: *A. tenuis* Dana, 1846 appears restricted to Fiji and Tonga, while *A. rongoi* is known only from the Cook Islands, Niue and French Polynesia in the central South Pacific (Supporting Information, Fig. S6). These findings suggest that previous research showing strong genetic differentiation between '*A. tenuis*' in numerous locations, including Western Australia and Indonesia (Rosser *et al.* 2020) and across the western Indian Ocean (van der Ven *et al.* 2022), probably reveal the presence of two or more distinct species identified incorrectly as *A. tenuis* (Dana, 1846).

Molecular evidence has revealed that the widely-used morphological taxonomy underestimates species diversity within regions across a range of coral taxa. However, in many cases distinct lineages revealed by genetic data exhibit ecological rather than morphological differences (Prada and Hellberg 2013, Boulay *et al.* 2014, Johnston *et al.* 2022). Recent population genomic studies indicate the presence of 'cryptic' species within '*A. tenuis*' in Japan (Zayasu *et al.* 2021) and on the GBR (Cooke *et al.* 2020, Matias *et al.* 2022). Unfortunately, these studies lack the voucher specimens and field images necessary to examine potential morphological differences between these putatively cryptic species

(see Voolstra *et al.* 2021). The number of specimens examined in this study precludes population genomic assessment of *A. kenti*, but our SNP analyses (e.g. t-SNE; Fig. 3) suggest the presence of population structure that is not attributable to geographical distance alone. Consequently, there might be additional species currently lumped as '*A. tenuis*' on the GBR in addition to *A. kenti*, and further taxonomic work will be required to confirm the identities, geographic ranges and habitat preferences of these species. Irrespective of their true taxonomic identities, our results clearly demonstrate that the putatively widespread species '*A. tenuis*' actually comprises multiple distinct species across the Indo-Pacific, and the supposed widespread distribution of *A. tenuis* (Veron 2000, Wallace *et al.* 2012, Richards *et al.* 2014) is an artefact of taxonomic lumping. This problem is likely not to be restricted to *A. tenuis*, because similar 'cryptic lineages' have been observed in several putatively widespread *Acropora* (Richards *et al.* 2016, Suzuki *et al.* 2016, Sheets *et al.* 2018) and numerous other coral species (e.g. Keshavmurthy *et al.* 2013, Bongaerts *et al.* 2021).

Our results show that at least some morphological characters traditionally used to delineate species and species groups are homoplasies and that many species can vary widely in gross morphology (Fig. 2; Supporting Information, Fig. S1). For example, bottlebrush growth form has clearly evolved multiple times in different lineages: species with this morphology occur in at least four of the six molecular clades (I, III, V and VI) and two of the three subclades of Clade I (I-B and I-C) (Supporting Information, Fig. S1; Cowman *et al.* 2020). In each case, clades with bottlebrush species also include species with a range of different morphologies, including staghorn, corymbose and other hispidose specimens, demonstrating that the *echinata* species group (Wallace 1999), which included all bottlebrush species, is not monophyletic. This finding highlights the limitations of morphological characters and, particularly, morphological 'species groups' for a range of research questions, especially for understanding evolutionary history in *Acropora*. Although morphological groups retain some utility for fields such as functional ecology where growth form can be linked to demographic traits (e.g. Alvarez-Noriega *et al* 2016), it is clear that identifying specimens (e.g. fossils) to morphological species groups defined by homoplasies cannot provide reliable insights into the evolution and diversification of *Acropora* (e.g. Wallace and Rosen 2006, Wallace and Bosellini 2015, Wallace *et al.* 2020).

Given the increasing awareness that traditional morphological taxonomy underestimates coral diversity, the next important step to facilitate future coral reef research is to develop a robust taxonomic framework, consistent with the International Code for Zoological Nomenclature, to enable these findings to be incorporated by non-taxonomists and field researchers (Bonito *et al.* 2021). The term 'cryptic species' is widely used but is often a misnomer, because the problem is often not that there are no morphological characters that differentiate species, but that phylogenetically informative characters do exist but have not yet been identified. Although molecular studies can provide insight into species boundaries and systematic relationships, an increased focus on morphological taxonomy and visible field characteristics is required to go beyond simply identifying 'cryptic' lineages and towards a robust, trait-based taxonomy for reef corals at the species level that can be used to identify species in the field. Although sequencing type specimens (e.g. holotypes and paratypes) would be preferred, this approach is not feasible for the majority of scleractinian taxa that lack preserved tissue. Therefore, the 'topotype approach' can link molecular sequences to nominal species by comparing high-quality field images and skeletal voucher specimens that have molecular data with type specimens for which molecular data are lacking. This approach enables molecular studies to move beyond simply identifying distinct evolutionary lineages and towards applying names that identify species without ambiguity (Bonito *et al.* 2021). The application of species names to distinct evolutionary lineages represents a significant step towards resolving the taxonomy of the Scleractinia and will facilitate the uptake of a more robust taxonomy by field scientists, ecologists and other non-taxonomists.

Our findings highlight a fundamental issue for addressing questions that rely on accurate assessments of species geographical ranges or population sizes, such as IUCN Red List assessments. *Acopora tenuis* is not currently listed as threatened because it is considered geographically widespread and comparatively resilient to habitat loss owing to a large effective population size (Richards *et al.* 2014). However, this assessment is based on a taxonomy that incorrectly lumps numerous distinct species with much smaller geographical ranges and population sizes. Clearly, there is a need to replace 'list thinking' with 'lineage thinking' (Hazevoet 1996) when assessing extinction risks in corals. Current species lists are of little value for conservation, and future assessments of extinction risk must be underpinned by a robust taxonomy capable of identifying species accurately. In the meantime, population assessments at local to regional scales are required to provide any indication of species population trajectories (Bridge *et al.* 2020).

TAXONOMIC ACCOUNT

Specimens within *Acropora* Clade I-C vary widely in gross morphology and include corymbose (Fig. 4A–C), hispidose (Fig. 4D–F), arborescent (Fig. 4J–L) and caespitose (Fig. 4M, N) specimens. Morphological variability is also present within species, potentially attributable to the specimens originating from different habitats and depths. Nonetheless, species in clade C generally share a number of key features, including labellate to cochleariform radial corallites, sometimes with flaring lower walls, although in some specimens, particularly hispidose colonies, radial corallites can become appressed tubular. Axial corallites are generally tubular and exsert, and the coenosteum is costate, with simple spinules or no spinules at all.

Based on the combination of morphological comparison with type material, phylogenomic reconstruction of targeted capture loci, genetic clustering of SNPs and a number of species delimitation techniques, we propose that the specimens examined in this study comprise at least 11 distinct species. Cluster 1 contains five clearly delineated species [*A. rongoi*, *A. tenuissima*, *A.* aff. *tenuis* 'WIO', *A.* aff. *echinata* and *A. yongei*, in addition to the unresolved clade *A.* sp(p) and *A.* aff. *pagoensis*, for which we sequenced only one specimen], and cluster 2 contains four species (*A. tenuis*, *A. echinata*, *A.* aff. *striata* and *A. kenti*). Although STRUCTURE did not differentiate between *A. yongei* and *A.* sp(p) clusters, both the ML phylogeny and t-SNE indicated that *A. yongei* specimens from the type

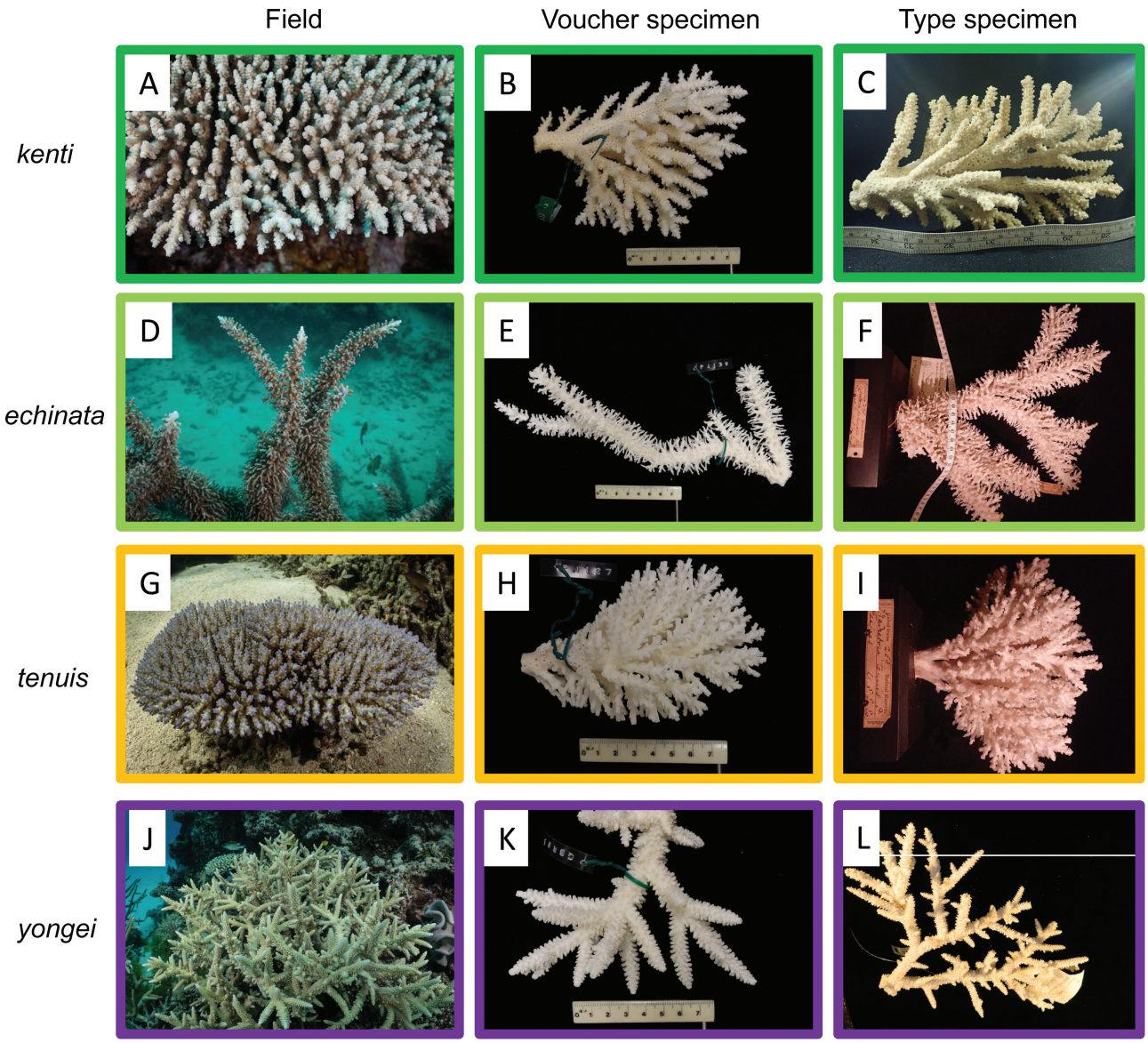

Figure 4. Nominal species of *Acropora* identified in this study. A, B, *Acropora kenti* (Brook 1892) topotype GBR130/G80247, Myrmidon Reef, GBR. C, *A. kenti* lectotype *NHM 1892.6.8.202*, Thursday Island, Australia. D, E, *Acropora echinata* Dana, 1846 topotype FJ139/G78322, Viti Levu, Fiji. F, *A. echinata* lectotype *USNM 275*, Fiji. G, H, *Acropora tenuis* Dana, 1846 topotype FJ127/G78323, Viti Levu, Fiji. I, *A. tenuis* holotype *USNM 259*, Fiji. J, K, *Acropora yongei* Veron & Wallace, 1984 topotype GBR85/G78644, Lodestone Reef, GBR. L, *A. yongei* holotype *G55079*, Britomart Reef, GBR. A field image (left column), skeletal image (middle column) and type specimen (right column) are shown for each species. M–V, specimens examined in this study that could not be assigned to nominal species: PN63 *Acropora* aff. *striata*, Ant Atoll, Micronesia (M, N); KM27/G71345 *Acropora* aff. *echinata*, Kimbe Bay, Papua New Guinea (O, P); 54-5921/RUMF-ZG-04792 *Acropora akajimensis* Veron, 1990 topotype specimen placed within Acropora sp(p). clade, Ryukyu Islands, Japan (Q, R); 54-6036/RUMF-ZG-04796 *Acropora* sp., Ryukyu Islands, Japan (S, T); and BFC219 *Acropora* aff. *tenuis* 'WIO', Chagos, Indian Ocean (U, V).

locality (central GBR) were distinct from specimens from the NW Pacific. In addition, the model with 11 PSHs [*A. yongei* and *A.* sp(p) split] was the top-ranked species model in *BFD analyses, with a higher marginal likelihood estimate compared with the 10-species model that combined *A. yongei* and *A.* sp(p). Conseqently, based on the available evidence and the considerable morphological differences, we conclude that *A. yongei* Veron & Wallace, 1984 from the GBR is a distinct species from *A.* sp(p), although the geographical, genetic and taxonomic boundaries of *A. yongei* cannot be resolved in this study.

Only 4 of the 11 species delineated above can be identified reliably as nominal species: *A. tenuis* (Dana, 1846), *A. echinata* (Dana, 1846), *A. kenti* (Brook, 1892) and *A. yongei* Veron & Wallace, 1984 (Fig. 4). Of the remaining seven lineages, two (*A. tenuissima* n. sp. and *A. rongoi* n. sp.) are described below, while a further three (*A.* aff. *striata*, *A.* aff. *echinata* and *A.* aff. *tenuis* 'WIO') are also likely to be undescribed, but require further investigation before a formal description is warranted. *Acropora* aff. *echinata* is represented by two specimens published in Cowman *et al.* (2020), and molecular comparison of these specimens with topotypes for *A. echinata* Dana, 1846 in this study

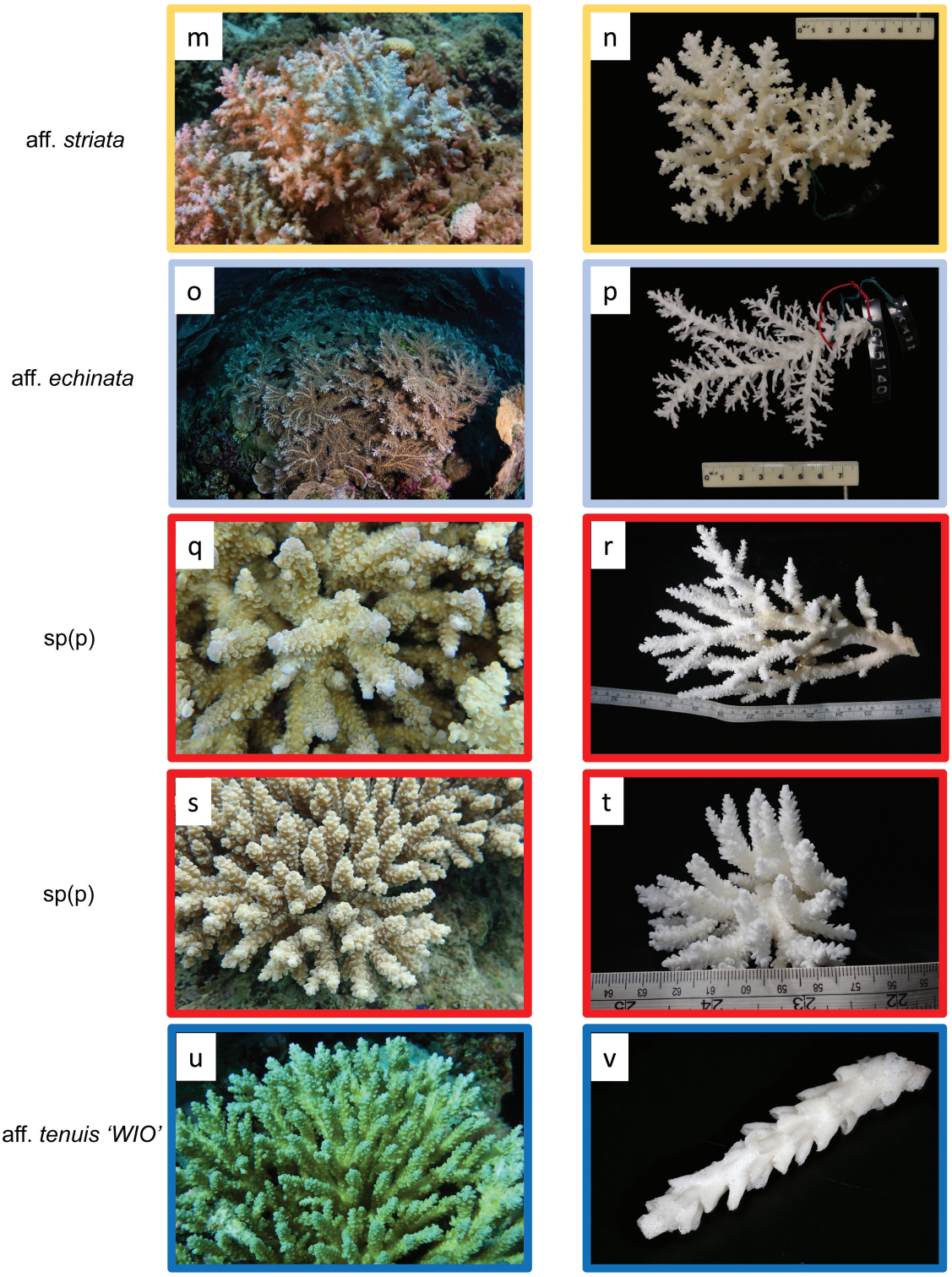

Figure 4. Continued

confirms that the two species are distinct. *Acopora* aff. *pagoensis* is represented by a single specimen from Tonga and shows some morphological similarities to *Acropora pagoensis* (Hoffmeister, 1925), originally described from American Samoa. However, further specimens, including a topotype, are required to confirm the identity of this species.

The final lineage, designated 'sp(p)', we consider an unresolved clade requiring further sampling and analysis. This lineage includes specimens that vary considerably in gross morphology, including specimens with resemblance to the types of *A. kenti* Brook, 1892, *A. donei* Veron & Wallace, 1984, *Acropora akajimensis* Veron, 1990 and *A. yongei* Veron & Wallace, 1984. The specimen that closely resembles the type of *A. akajimensis* (54-5921/RUMF-ZG-04792), collected from the type locality, is phylogenetically distant from our specimens from the GBR that most closely resemble the holotype of *A. donei* Veron & Wallace,

1984, which are in Clade III. Consequently, the species referred to as *A. donei* in Japan is likely a different species to *A. donei* Veron & Wallace, 1984 from the GBR and that the synonymization of *A. akajimensis* Veron, 1990 with *A. donei* Veron & Wallace, 1984 by Wallace (1999) was incorrect. The wide range of morphological variability within the sp(p) clade indicates that it probably includes multiple species from the NW Pacific that cannot be resolved without further sampling and species delimitation analysis. However, based on the distant relationship between *A. donei* from the GBR and the topotype of *A. akajimensis*, we remove the latter species from synonymy (see below).

This study examines specimens within the morphological range of *A. tenuis* sensu Wallace (1999) from a number of geographical regions across the Indo-Pacific. We show that *A. tenuis* Dana, 1846 is not geographically widespread across the Indo-Pacific, but restricted to the South Pacific (Fiji and Tonga). This finding has important implications for the taxonomy of the group because it provides evidence that nominal species from different parts of the Indo-Pacific that were synonymized with *A. tenuis* Dana, 1846 based on morphological characters represent distinct species that require resurrection. Therefore, below we formally revise the taxonomic status of four nominal species previously considered junior synonyms of *A. tenuis* Dana, 1846: *Acropora macrostoma* Brook, 1891 from Mauritius; *A. kenti* Brook, 1892 from north-eastern Australia; *Acropora bifaria* Brook, 1892 from Java; and *A. africana* Brook, 1893 from South Africa. We sampled numerous colonies of *A. kenti* from the south-west Pacific that are clearly distinct from *A. tenuis*. The other three nominal species are not included in our molecular phylogeny, but are resurrected because: (1) they have type localities a long distance from Fiji; and (2) they show morphological differences from the holotype of *A. tenuis* (discussed below). This biogeographical and morphological evidence, combined with the strong geographical variation in numerous other studies of '*A. tenuis*', warrants resurrection of these nominal species. Although it is clear that these species are distinct from *A. tenuis*, additional sampling, particularly in the Indian Ocean, will be required to confirm their taxonomic boundaries.

The four nominal species identified within clade C belong to two different morphological groups delineated by Wallace (1999): the '*selago* group' (*tenuis*, *kenti* and *yongei*) and the '*echinata* group' (*echinata*), with the latter being characterized by a bottlebrush colony morphology. Species with bottlebrush morphology occur across the six molecular clades within *Acropora* (Supporting Information, Fig. S1) and do not form a monophyletic group. Likewise, other species from the *selago* group occur in other molecular clades, including *A. selago* (Studer, 1878) (Clade VI) and *A. donei* Veron & Wallace, 1984 (Clade III) (Fig. 2A).

Below, we provide a summary of taxonomic changes to species within *Acropora* Clade I-C. When listing material examined, specimens sequenced in this study are highlighted in **bold**, and * indicates a topotype specimen.

Museum abbreviations are as follows: MNB, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MTQ, Museum of Tropical Queensland, Townsville, Queensland, Australia; NHM, Natural History Museum, London, UK; RUMF-ZG, Ryukyu University Museum, Fujukan, University of the Ryukyus, Japan; and USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Order Scleractinia Bourne, 1900

Family Acroporidae Verrill, 1901

Genus *Acropora* Oken, 1815

Acropora tenuissima Bonito, Bridge, Fenner & Baird, 2023 n. sp.

Holotype: ***G78705***, collected from 7 m depth on the eastern fore-reef of Myrmidon Reef, GBR, Australia (Fig. 5A, B).

Paratypes: **G78343**, 7 m depth, fore-reef of Namaqumaqua, Viti Levu, Fiji (Fig. 5C); and **G81179**, collected from 1 m depth at Blue Pools, Heron Island, GBR, Australia.

Other material examined: MTQ: GBR G30675, Davies Reef, Queensland, Australia; G30677, Fitzroy Reef, Queensland, Australia.

Holotype: Colony shape corymbose with determinate growth form. Primary branches long (> 10 cm), thin and terete, 3–5 mm in diameter and vertically orientated (Fig. 5D, E). Axial corallites tubular, 1.2–2.0 mm outer diameter and 0.8–1.0 mm inner diameter (Fig. 5F). Radial corallites closely positioned but not touching, predominantly appressed tubular with extended lower lip and large oblique or nariform openings, but become labellate towards branch tips. Septa on both axial and radial corallites are weakly developed; primary septa up to one-quarter of the radius of the calyx, secondary septa absent or some present as points (Fig. 5F, G). The coenosteum is costate, with some spinule development in the paratype specimen (Fig. 5H).

Molecular phylogeny: The two specimens sequenced of this species, from the GBR and Fiji, are recovered as a reciprocally monophyletic group in all phylogenetic trees (Figs 2, 3; Supporting Information, Figs S1, S2). The species is sister to *A.* aff. *pagoensis* in the ML reconstructions, but the SNAPP species tree places *A.* aff. *pagoensis* as sister species to *A. rongoi* (Fig. 3D).

Remarks: Forms small corymbose clumps, generally 15–30 cm in diameter. Colonies are compact cushions with short branches in high-energy environments. In more sheltered habitats, colonies can form taller, more upright corymbose colonies. Generally, an iridescent yellow–orange to pinkish/orange colour, especially pronounced at the branch tips and axials, but can also be greyish/brown in colour. Polyps lower on the branches are generally extended during the day and brownish in colour. The species is clearly differentiated morphologically from all other species in clade I-C by its thin, neat branches. Within cluster 1i, *A.* aff. *pagoensis* has much thicker branches, whereas *A. rongoi* has thick branches and an indeterminate growth form. *Acropora tenuis* and *Acropora azurea* Veron & Wallace, 1984 can co-occur with *A. tenuissima* and can have similar colony shape, but *A. tenuissima* is distinguished from *A. tenuis* by its thinner branches and smaller corallites, whereas *A. azurea* has appressed radial corallites that are nariform rather than tubular. Specimens of *A.*

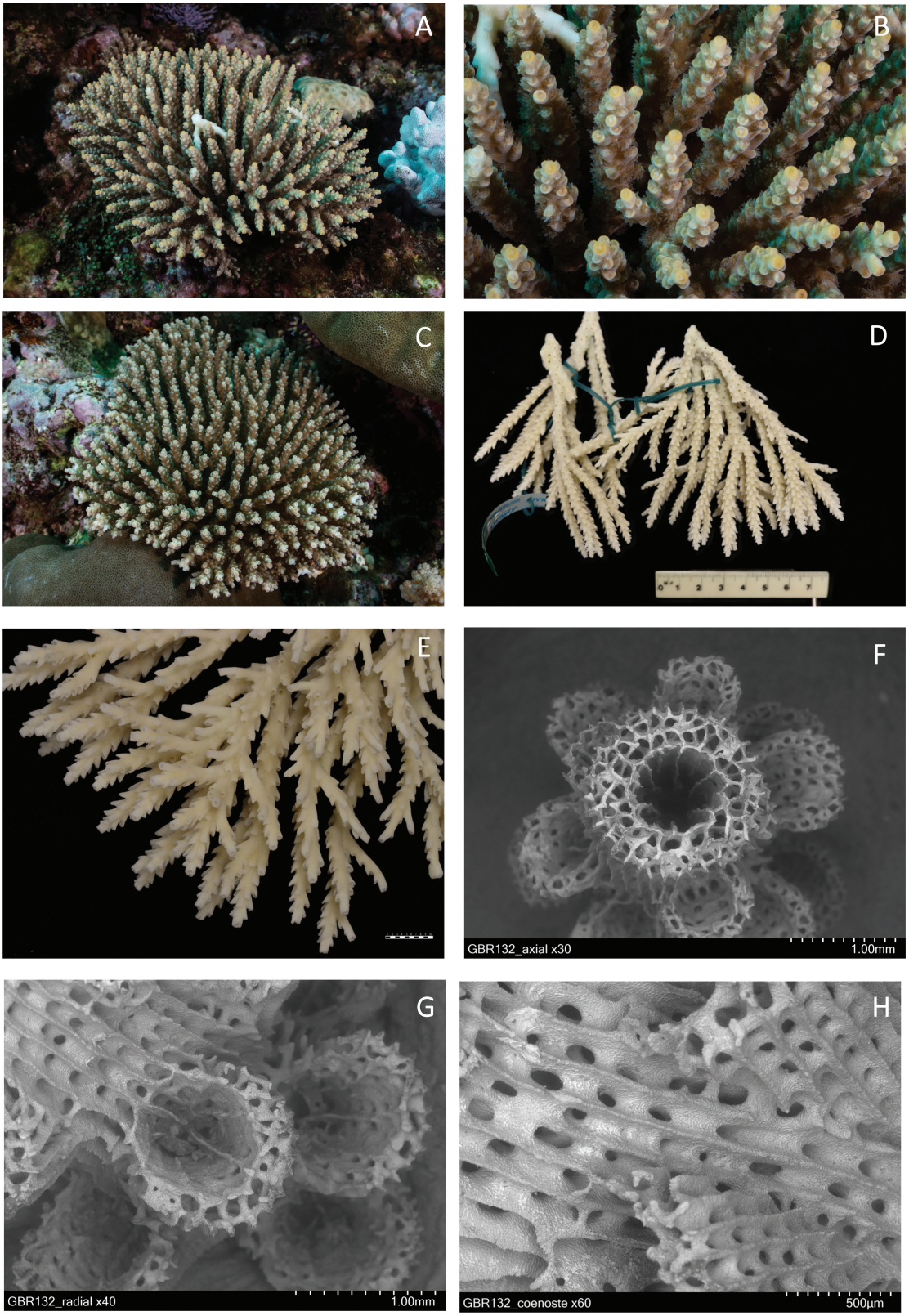

Figure 5. ***Acropora tenuissima***. Holotype MTQ *G78705* in the field at Myrmidon Reef, Great Barrier Reef (A, B); paratype MTQ G78343 from Namaqumaqua, Viti Levu, Fiji (C); holotype skeletal details (D, E); and scanning electron microscope images of axial corallite (F), radial corallites (G) and coenosteum (H) of the holotype.

tenuissima in the MTQ collection are identified as *Acropora nana* (Studer, 1878); however, the holotype of *A. nana* (*MNB 1941*) has tubular to nariform radial corallites, which extend from the branch at an obtuse angle, rather than the acute to appressed angle of *A. tenuissima*. The coenosteum of the *A. nana* holotype also exhibits a heavily ornamented coenosteum, whereas the

coenosteum of *A. tenuissima* is costate and lacks spinules. A specimen of *A. tenuissima* from Fiji is included in the series of images illustrating *A. subulata* by Veron *et al.* (2016) http://www.coralsoftheworld.org/media/images/0073_C04_01.jpg; however, the holotype of *A. subulata* is a fragement of a large tabular or corymbose colony with tightly packed, labellate radial corallites reminiscent of *Acropora squamosa* (Brook, 1892) but very distinct from *A. tenuissima*.

Distribution: Currently recorded only from Fiji and the central-southern GBR, but likely to occur elsewhere in the south-west Pacific (Supporting Information, Fig. S6).

Etymology: Meaning 'very thin' in Latin, *tenuissima* refers to the thin branches characteristic of this species and which distinguish it from *A. tenuis* and *A. kenti*, both of which co-occur with *A. tenuissima* across its range.

Acropora rongoi **Bridge & Cowman, 2023 n. sp.**

Holotype: ***MTQ G78411***, collected from 1 m depth in the lagoon at Rutaki, Rarotonga, Cook Islands.

Paratypes: **MTQ G78418**, collected from 17 m depth on the outer reef slope at Papua, Rarotonga, Cook Islands; MTQ G80232 collected from 12 m depth on the fore-reef slope at 'Ōpūnohu Bay, Mo'orea, French Polynesia; MTQ G80233, collected from 10 m depth on the fore-reef at 'Ōpūnohu Bay, Mo'orea, French Polynesia.

Other material examined: MTQ: Cook Islands: G35728 Rarotonga, G35712, G55536 Aitutaki; Niue: G54667, G54670, G54671; Society Islands: G44034, G58650 Mo'orea.

Holotype: Irregular hispidose colony ~75 cm in diameter (Fig. 6A). Primary branches ≤ 300 mm long and 10–20 mm in diameter, secondary branches ≤ 100 mm long and 10–15 mm in diameter, and tertiary branches 5–15 mm long and 2–4 mm in diameter. Axial corallites tubular and exsert, outer diameter 1.8–2.2 mm, inner diameter 0.9–1.2 mm. Radial corallites closely positioned but not touching, outer diameter 1.2–1.8 mm, inner diameter 0.7–0.8 mm, haphazardly arranged and ranging in shape from tubular with oblique to dimidiate openings through to labellate with flaring lower lips (Fig. 6B–D). Both axial and radial corallites often show two prominent directive septa one-half to three-quarters of the radius of the calyx, but otherwise septa are weakly developed (Fig. 6G, H). The coenosteum is costate (Fig. 5H).

Molecular phylogeny: The two specimens sequenced of this species from Rarotonga (Cook Islands) are recovered as a reciprocally monophyletic group in all phylogenetic trees (Figs 2, 3; Supporting Information, Figs S1, S2). The species is sister to a group containing *A.* aff. *pagoensis* and *A. tenuissima* in ML reconstruction, but appears as a direct sister species to *A.* aff. *pagoensis* in the SNAPP species tree.

Remarks: Colony growth form is irregular caespitose to hispidose, with indeterminate growth. The holotype, from the shallow lagoon of Rarotonga, has upright branches (Fig. 6A), whereas paratypes from higher-energy outer reef slopes show thicker, flatter branches with fewer incipient axial corallites. Radial corallites are densely packed (touching in some specimens but not on the holotype), of mixed sizes and shapes and often flaring, giving the colony a spikey, messy appearance. Colour varies from cream to brown. Specimens of *A. rongoi* in the collection at MTQ were previously identified as *A. striata* (Verrill, 1866), *Acropora elseyi* (Brook, 1892) and *Acropora florida* (Dana, 1846), attributable to the variability in gross morphology of *A. rongoi* in different habitats. Verrill's holotype of *A. striata* from the Ryukyu Islands has similar radial corallite shape but is clearly distinguished from *A. rongoi* on the basis of molecular and biogeographical evidence. Furthermore, the interpretation of *A. striata* as hispidose (Shirai 1980, Veron and Wallace 1984, Wallace 1999) is likely to be incorrect because the holotype lacks tertiary branching (see below for further discussion on *A. striata*). *Acropora elseyi* can have similar gross morphology, but radial corallites are tubular to appressed tubular with thick walls and prominent septa, and the coenosteum is composed of elaborate spinules. Colonies from outer reef slopes can also superficially resemble colonies identified as *A. florida* when tertiary branches become stunted and resemble the ramiculi of *A. florida*. However, the colony shape of *A. florida* (Dana, 1846) is arborescent, not hispidose. *Acropora affinis* (Brook, 1893), synonymized with *A. florida* by Veron and Wallace (1984), may be hispidose, but this species is in clade III (Cowman *et al.* 2020; Fig. 2).

Distribution: Currently known from the Cook Islands, Niue and the Society Islands, French Polynesia in the South Pacific (Supporting Information, Fig. S6).

Etymology: Named for Dr Teina Rongo in recognition of his contribution to research and conservation of coral reefs and the marine environment in the Cook Islands.

Acropora tenuis **Dana, 1846**

Madrepora tenuis Dana 1846: 451; Ortmann 1888: 152.

Acropora tenuis (Dana): Verrill 1902: 219.

Madrepora macrostoma Brook 1891. Here removed from synonymy with *Acropora tenuis* (Dana) *contra* Veron and Wallace 1984: 279.

Madrepora kenti Brook 1892. Here removed from synonymy with *Acropora tenuis* (Dana) *contra* Veron and Wallace 1984: 279.

Madrepora bifaria Brook 1892. Here removed from synonymy with *Acropora tenuis* (Dana) *contra* Veron and Wallace 1984: 279.

Madrepora africana Brook, 1893. Here removed from synonymy with *Acropora tenuis* (Dana) *contra* Veron and Wallace 1984: 279.

Specimens examined: NMNH-SI: *USNM 259*, *Madrepora tenuis* holotype, Fiji; MTQ: Fiji: **G80284**, **G80281**, **G80280**, **G78334**, **G78323***; G40941; Tonga: **G80240**, **G80237**.

Remarks: Acropora tenuis is described in recent revisions as having a neat, regular arrangement of branches with few sub-branches and evenly sized cochleariform radial corallites neatly arranged in rows (Veron and Wallace 1984, Wallace 1999). However, these characters are not consistent with the holotype, which is described by Dana as being caespitose with branchlets that are 'very slender, subterete and proliferous', while

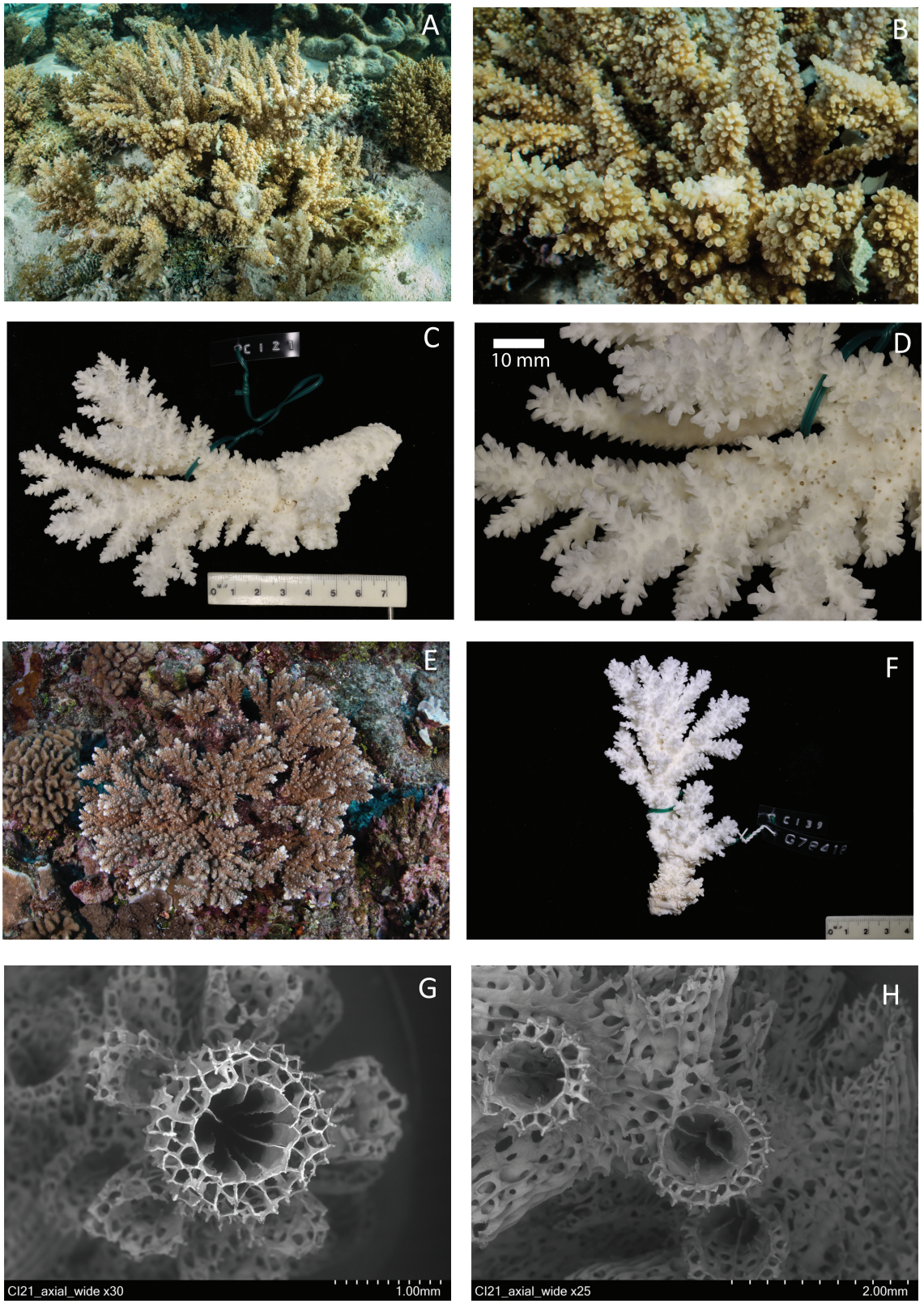

Figure 6. ***Acropora rongoi***. Holotype MTQ *G78411* in the field the lagoon at Rarotonga, Cook Islands (A, B) and in the laboratory (C, D); paratype MTQ *G78418* in the field on the outer reef slope at Papua, Rarotonga, Cook Islands (E, F); and scanning electron microscope images showing axial (G) and radial corallite and coenosteum details (H) of the holotype.

the radial corallites are 'appressed-tubiform, irregular, elongate and slender' (Supporting Information, Fig. S3).

The specimens in the present series vary in gross morphology, but FJ127 (G78323) and 101-5454 (G80284), from the reef flat on the southern coast of Viti Levu, Fiji, closely resemble Dana's holotype (Fig. 4), confirming that these specimens are *A. tenuis*. Other specimens sequenced here illustrate the range of variation within this species. G80281, also from Fiji, and G80240

from Ha'apai, Tonga, have thicker branches than the holotype, while 101-5672 (G80280) is intermediate between these specimens. TG59 (G80237), also from Tonga, differs considerably in gross morphology, growing as a thick bottlebrush rather than a corymbose clump or table. However, close examination of the branch ends shows that the branching structure and corallite shape are consistent with the thicker specimens in the present series. The large range of variation in gross morphology within *A. tenuis* could present a challenge when defining morphological characters for identification of this species in the field; however, it is clear that many of the species with overlapping morphological features previously considered within the range of variation of *A. tenuis* have distinct geographical ranges that do not overlap.

Acropora tenuis is currently known only from Fiji and Tonga in the South Pacific (Supporting Information, Fig. S6); all other *tenuis*-like specimens from other regions are likely to represent distinct species that require additional taxonomic investigation. Consequently, given the support of numerous other population genetic studies demonstrating strong geographic structure within specimens identified as *A. tenuis* based on gross morphology (e.g. Rosser *et al.* 2020, van der Ven *et al.* 2022), combined with morphological differences between the type specimens (Supporting Information, Fig. S3) discussed below, *A. macrostoma* Brook, 1891 stat. rev. from Mauritius, *A. kenti* Brook, 1892 stat. rev. from Torres Strait, *A. bifaria* Brook, 1892 stat. rev. from Java, and *A. africana* Brook, 1892 stat. rev. from South Africa (listed as a synonym of *A. tenuis* by Veron and Wallace 1984 and considered a probably junior synonym of *A. tenuis* by Wallace [1999]) are hereby removed from synonymy with *A. tenuis* Dana, 1846. Additional taxonomic research, particularly the collection of topotypes, is required to establish the geographical and morphological ranges of these species and to identify additional species that might co-occur in these regions.

Of these four nominal species, *A. macrostoma* and *A. bifaria* resemble *A. kenti* in morphology, with neatly arranged cochleariform radial corallites and minimal tertiary branching (Supporting Information, Fig. S3). Three specimens in the Museum of Tropical Queensland (G51822, G51823 and G51824) from Baie Aux Tortues, Mauritius, closely resemble Brook's type of *A. macrostoma* owing to their comparatively thick branches, lack of incipient axial corallites and flaring, cochleariform corallites and are therefore re-identified as this species. The species identified as *A. tenuis* by Pillay *et al.* (2002: 78–79) is also likely to be *A. macrostoma*. The type of *A. africana* is corymbose, but the branches are thicker and axial dominated, and the radial corallites are described by Brook (1893) as 'appressed nariform to tubiform', rather than labellate or cochleariform (Supporting Information, Fig. S3). *Acropora plana* Nemenzo, 1967 was also synonymized with *A. tenuis* by Veron and Wallace (1984) and considered a junior synonym by Wallace (1999) but recognized as a valid species by Veron (2000) and Veron *et al.* (2016). The holotype of *A. plana* appears to be a fragment of a large tabular colony with relatively thin branches, and the radial coralites are appressed with round openings (Supporting Information, Fig. S3). These morphological differences, combined with the type location of *A. plana* in the Philippines, indicate that this species is unlikely to be a synonym of *A. tenuis*. However, we have not examined the holotype, and further research is needed to resolve the status of this species.

Acropora echinata (Dana, 1846)

Madrepora echinata Dana 1846: 464, plate 36, fig. 1.
Acropora echinata (Dana): Verrill 1902: 214.
Madrepora durvillei Milne Edwards and Haime 1860: 148.

Specimens examined: NMNH-SI: *USNM 275*, *Madrepora echinata* holotype, Fiji; *MNHN 282a*, *Madrepora durvillei* holotype, Fiji; MTQ: G28406, G28460, G28461, G28409, G28458, G56982, **G80268** GBR; **G78007** Papua New Guinea; G60537, G60571, **G80259** Coral Sea; **G78322***, **G80278** Fiji.

Remarks: Dana's description of *A. echinata* is clearly based on *USNM 275* (Fig. 4F), designated as the lectotype by Wallace (1999). It is a large specimen (~50 cm in diameter) from Fiji, which matches Dana's description of an arborescent corallum with branches that are 'very neatly bristled with delicate branchlets' that give it an 'even cylindrical outline', 'smooth tubiform calices' and a costate coenosteum. We sequenced two specimens from the type locality (G78322 and G80278) with characters that very closely match the lectotype. These specimens confirm the identity of *A. echinata*, but the morphology of specimens in our study, from the GBR, the Coral Sea and the Bismarck Sea, show considerable morphological variability. In particular, specimen G80259 from Marion Reef in the Coral Sea is more bushy than the lectotype and topotype specimens from Fiji, while G78007 from the Bismarck Sea has thicker, less dense branches. However, all specimens of *A. echinata* have terete incipient axial corallites with square walls, compared with the thicker, more rounded tubular walls of other bottlebrush species. The coenosteum of *A. echinata* is costate, whereas other bottlebrush species often have elaborate spinules [e.g. *Acropora subglabra* Brook, 1891 (G71541)]. Additional specimens in the collection of MTQ also possess all these characters, providing strong morphological support for their identification as *A. echinata*.

Madrepora durvillei Milne Edwards & Haime, 1860 from Fiji and *Madrepora procumbens* Brook, 1891 from the 'South Seas' were considered junior synonyms of *A. echinata* by Veron and Wallace (1984) and Wallace (1999). Milne Edwards and Haime (1860) note that *M. durvillei* is very similar to *M. echinata*. The *M. durvillei* holotype (MNHN *Z282a*) is described as having 'echinated ribs' by Milne Edwards and Haime (1860), which presumably refers to the coenosteum, and is from the same type locality as *A. echinata*, supporting previous decisions that the species is a junior synonym of this species. However, the type of *A. procumbens* (NHM *1841.12.11.3*) has more rounded corallite walls and spinules on the coenosteum, and therefore more closely resembles bottlebrush species from Clade V [e.g. *A. subglabra* G71541 and G71543] than those from Clade I. Consequently, although *A. procumbens* does not appear to be a junior synonym of *A. echinata* (Dana, 1846), further research is required to determine its taxonomic status and phylogenetic affinities.

The *A. echinata* genome assembled from a specimen collected from the Ryukyu Islands (Shinzato *et al.* 2021) is reconstructed in our study in Clade VI (labelled clade IV by Shinzato *et al.* 2021), deeply diverged (> 50 Mya; Shinzato *et al.* 2021) from *A. echinata* (Dana, 1846) sampled from the type locality, which we reconstruct in Clade I (concordant with Clade I in the study by Shinzato *et al.* 2021). Unfortunately, there is no voucher or field image associated with this genome, hence we cannot comment on any morphological differences between these species. However, it

is possible that the Coral Triangle / north-west Pacific region supports another distinct species with morphological similarities to *A. echinata*. Consequently, we do not include any specimens from these regions as *A. echinata*, pending further study. Based on the specimens we examined here, the current geographical range of *A. echinata* extends from the type locality in Fiji west across the Coral Sea to the Great Barrier Reef and north to the Bismarck Sea (Supporting Information, Fig. S6).

Acropora kenti (Brook, 1892) status revised

Madrepora kenti Brook 1892: 458; Brook 1893: 110, plate 11, fig. B.

Acropora kenti (Brook); Wells 1954: 493.

Here removed from synonymy with *Acropora tenuis* (Dana, 1846) *contra* Veron and Wallace 1984; 279. See also Cooke *et al.* 2020; Mattias *et al.* 2022.

Specimens examined: Madrepora kenti lectotype: NHM 1892.6.8.202, Thursday Island, Torres Strait, Australia; syntype: NHM: 1892.6.8.203, Low Woody Island, GBR, Australia; MTQ: G27054, G27078, G27236, G27245, G27280, G27281, G27282, G27284, G27285, G27286, G27287, G27288, G27289, G27292, G27298, G27711, G28444, G29061, G29064, G29899, G29903, G29905, G31175, G32447, G32448, G32455, G32456, G34149, G35014, G35015, G35138, G35139, G35140, G35141, G35142, G35638, G35879, G40909, G41100, G41101, G41102, G41103, G48325, G49331, G58409, **G78648**, **G78750**, **G78778**, **G80247**, **G80266***, **G80256**, **G80256**, **G78750**, **G335181, G335182** GBR; G35638, G35897, G53273, G53275, G53281, G53284, G53288, **G78014**; G78046, G78064, **G80270**, Papua New Guinea; G27291, G28448, G35879, G60564, G63895, **G80258** Coral Sea; G60131, **G80251**, **G80250** Lord Howe Island.

Description: Corallum horizontal or corymbose, main branches 2.0–2.5 cm thick. Corallites large, round, appressed tubular. Radial corallites appressed tubular, crowded and prominent, with the outer part of the wall forming a rounded lip with no inner wall. Septa moderately developed, with two directive septa prominent.

Remarks: The lectotype of *A. kenti* (Supporting Information, Fig. S3) differs from the holotype of *A. tenuis* in having thicker branches that lack tertiary branching and incipient axials, and in possessing cochleariform radial corallites arranged in neat rows. Of the specimens sequenced in this study, G80266 from Great Detached Reef and G80247 from Myrmidon Reef most closely resemble the lectotype, NHM 1892.6.8.202, designated by Wallace (1999) from Thursday Island, Torres Strait. Brook's syntype, NHM 1892.6.8.203, from Low Woody Island near Cooktown in the northern GBR is morphologically similar to the lectotype and is almost certainly the same species. Like *A. tenuis*, the specimens of *A. kenti* in our phylogeny show considerable variation in gross morphology, in terms of both branch thickness and the neatness of the radial corallites. Two colonies collected adjacent to each other at Myrmidon Reef, GBR, and sequenced in the present series, G80247 and G78778, demonstrate the range of variation in the length and neatness of the radial corallites. Specimens also show variation in branch thickness within and between colonies, some of which might be attributable to environmental factors, such as wave exposure. Despite morphological variability within the species, molecular data clearly demonstrate that *A. kenti* (Brook, 1892) is distinct from *A. tenuis* (Dana, 1846); therefore, we formally resurrect the former species. Consequently, the species commonly referred to as *A. tenuis* on the GBR and elsewhere in eastern Australia (*sensu* Veron and Wallace 1984), including the genome published as *A. tenuis* from the GBR (Cooke *et al.* 2020) is *A. kenti*. Unlike many published genomes, images were taken of the live colonies from Orpheus Island, GBR, that provided the material for the *A. kenti* genome. Voucher specimens from these colonies were also deposited in the collection of the Queensland Museum (G335181 and G335182), and the morphology of the specimens closely matches the *A. kenti* lectotype. Based on the specimens examined here, the geographical range of *A. kenti* extends from Lord Howe Island north along the GBR to the Bismarck Sea and east to the Coral Sea (Supporting Information, Fig. S6).

Acropora macrostoma (Brook, 1891) status revised

Madrepora macrostoma Brook 1891: 464; Brook 1893: 105, plate 19, fig. B.

Acropora macrostoma (Brook); Crossland 1952. Here removed from synonymy with *Acropora tenuis* (Dana, 1846) contra Veron and Wallace 1984; 279.

Specimens examined: NHM: *1878.2.4.7, Madrepora macrostoma* holotype, Mauritius; MTQ: G51822, G51823 and G51824, from Baie Aux Tortues, Mauritius.

Remarks: See remarks under *A. tenuis* (above). This species is currently confirmed to occur only in the type locality of Mauritius. There are literature records from other locations (e.g. Mozambique; Sheppard 1987), but further research is needed to establish its distribution.

Acropora bifaria (Brook, 1892) status revised

Madrepora bifaria Brook 1892: 453; Brook 1893: 110, plate 30, fig. A. Here removed from synonymy with *Acropora tenuis* (Dana, 1846) *contra* Veron and Wallace 1984; 279.

Specimens examined: NHM: *1859.12.12.2, Madrepora bifaria* holotype, Java

Remarks: See remarks under *A. tenuis* (above). This species is currently confirmed to occur only in the type locality of Java, Indonesia. Further research is needed to establish its distribution.

Acropora africana (Brook, 1893) status revised

Madrepora africana Brook 1893: 83; plate 35, fig. B.

Acropora africana (Brook); Crossland 1948. Here removed from synonymy with *Acropora tenuis* (Dana, 1846) *contra* Veron and Wallace 1984; 279.

Specimens examined: NHM: *40.9.30.9, Madrepora africana* holotype, South Africa

Remarks: See remarks under *Acropora tenuis* (above). Brook notes that the collection location of the holotype specimen was

recorded as the Cape of Good Hope, but that he believed the specimen came from the south-east coast. Therefore, the specimen is most likely to be from subtropical east Africa. The species is reported from Mozambique and Sri Lanka based on literature records provided by Sheppard (1987), and the type locality for the species was incorrectly recorded as Sri Lanka by Veron and Wallace (1984), but further research is needed to establish its distribution.

Acropora akajimensis Veron, 1990 status revised

Acropora akajimensis Veron 1990: 102–106.
Here removed from synonymy with *Acropora donei* Veron & Wallace 1984 *contra* Wallace, 1999 p. 224. See also Hatta and Matsushima 2008; Morita *et al.* 2019.

Specimens examined: MTQ *G32475 Acropora akajimensis* holotype, Ginanotatejyan, Aka-jima, Japan; G47767 Aka-jima, Japan; RUMF-ZG-04792, Sesoko Island, Japan.

Remarks: Acropora akajimensis Veron, 1990, from Aka-jima, Japan, was considered a junior synonym of *A. donei* Veron & Wallace, 1984 by Wallace (1999), a decision supported by Hoeksema and Cairns (2022). Veron (2000, 2016) continues to recognize *A. akajimensis* as a distinct species, noting that it is 'readily distinguished by its larger, sprawling, indeterminate branching pattern as compared with the determinate growth … of *A. donei*' (Veron 2016). Veron's opinion is supported by the type specimens and original descriptions of both species: *A. donei* is described as forming colonies that are 'caespito-corymbose or large corymbose plates or tables' (Veron and Wallace 1984), whereas *A. akajimensis* is 'irregularly arborescent' (Veron 1990). The species has been the subject of several reproductive studies in Japan (e.g. Hatta and Matsushima 2008, Morita *et al.* 2019) and was generally referred to as *A. donei*. Recently, Baird *et al.* (2022) applied the name *A. akaijimensis* to the species with tabular-branching growth form and labellate to cochleariform radial corallites that spawns at ~19:30 h on the reefs surrounding Sesoko Island, ~20 km from the type locality of Aka-Jima, Japan, on the basis that the morphology more closely resembles the type of *A. akajimensis* than *A. donei*. Our study includes one specimen from Sesoko Island (54-5921/RUMF-ZG-04792; Fig. 4Q, R) that closely resembles the type of *A. akajimensis*. This specimen occurs within the unresolved sp(p) clade. In addition, two specimens that resemble the type of *A. donei* collected from the north-central GBR (G78708 and G80265) are in Clade III *sensu* Cowman *et al.* (2020) and therefore not closely related to the *A. akajimensis* specimen from Sesoko. Consequently, we resurrect *A. akajimensis* as a valid species and suggest that *A. donei* is unlikely to occur in Japan. Further research is required to confirm the taxonomic identity and geographic range of *A. donei* and to establish the relationship between *A. akajimensis* and other species within Clade I-C in the north-west Pacific.

Additional taxonomic remarks on species in the clade I-C

Although it is clear that the morphological entity of *A. tenuis sensu* Veron and Wallace (1984) and Wallace (1999) comprises numerous species, additional taxonomic and molecular phylogenomic research is required to confirm the identities of nominal species considered junior synonyms and to identify and formally describe new species. For example, *A.* 'aff. *tenius* WIO' (*A.* aff. *tenuis* in the study by Colin *et al.* 2021) from Chagos and Mayotte is clearly distinct from *A. tenuis* (Dana, 1846). However, additional sampling across the western Indian Ocean is required to establish whether it is a single species or multiple species. None of the specimens from Chagos in this study or in the MTQ collection closely matches the types of either *A. macrostoma* or *M. africana* (Supporting Information, Fig. S3) or other nominal *Acropora* species, suggesting that it is most likely to be an undescribed species. Resolving the taxonomic identity of this species will require the sequencing of topotypes of these nominal species.

Although the systematics of Clade I-C in the north-west Pacific is unresolved, our study nonetheless provides important information about the biogeography of the group. It is clear that none of the specimens in the unresolved sp(p) clade is *A. tenuis*, *A. kenti* or *A. donei*, suggesting little overlap of species between the north-west and south-west Pacific. Recent molecular studies indicate the presence of at least two distinct but co-occurring lineages within '*A. tenuis*' around Okinawa (Zayasu *et al.* 2021), which might include nominal species such as *A. striata* (Verrill, 1866) (discussed below) or represent undescribed species.

Acropora striata Verrill, 1866 from the Ryukyu Islands, Japan, was considered valid by Wallace (1999) and described as 'distinctive clumps of upright hispidose branches'. The species *A.* aff. *striata* in cluster 2 includes specimens from the north-west Pacific (Palau and Pohnpei) and a genome identified as *A. tenuis* from Japan. Morphologically, specimens PL59 from Palau and PN63 from Pohnpei correspond to the interpretation of *A. striata* by recent authors, including Shirai (1980), Veron and Wallace (1984) and Wallace (1999). However, this interpretation does not match the type specimen (Supporting Information, Fig. S3), and the description by Verrill states that the species is 'shrubby or arborescently branched'. Both Shirai (1980) and Wallace (1999) presume that it is hispidose; however, the holotype is caespitose and lacks tertiary branching. Shirai (1980) interpreted *A. striata* as a bottlebrush, and the skeleton illustrated (p. 487) is definitely hispidose; however, the accompanying field image lacks labellate radial corallites and does not closely resemble the holotype. Likewise, the specimens used to illustrate *A. striata* by Wallace (1999) do not closely resemble the holotype and are not from the type locality. Unfortunately, our present series does not include a topotype with all the skeletal characters required to match Verrill's type confidently; therefore, although *A. striata* is likely to be a valid species, its exact identity must remain unresolved. Our *A.* aff. *striata* is likely to be an undescribed species, but given the morphological variability within the species, further sampling is required to confirm this. In our series, PN59, from ~25 m depth in the lagoon at Ant Atoll, Federated States of Micronesia, has a bottlebrush morphology and sparser radial corallites than PN63 or PL59, which were collected from shallower depths and have a bushy, upright morphology reminiscent of the interpretation of *A. striata* by Shirai (1980) and Wallace (1999). Given that both PN59 and PN63 were collected from the same site but different depths, the bottlebrush version could represent a deep-water morphology of this species.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We thank all those who assisted with fieldwork and providing specimens, including Gus Crosbie, Hanaka Mera, Paul Muir, Francesca Benzoni, Pat Smallhorn-West, Ed Roberts, Steve Lindfield, Sonia Rowley, Dave and Tris Sheen, Nelson Sikatoa, Mahonia Na Dari, Pat Colin and Lori Bell, Coral Reef Research Foundation. We also thank the national management agencies that provided permission to conduct research and make collections. We gratefully acknowledge the curators and collection managers at NHM, USNM-SI, MNHN and Yale Peabody Museum that enabled our examination of type material and Jen Klunk from Daicel Arbor Biosciences for all her efforts with the sequencing analysis. This research was supported by the ARC Centre of Excellence Programme (CE140100020) to A.H.B., ARC DECRA Fellowships to P.F.C. (DE170100516) and T.C.L.B. (DE180100746), and the Queensland Museum's Project DIG.

CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

Images of all specimens examined in this study are available on the Queensland Museum website: https://researchassets.qm.qld.gov.au/fotoweb/archives/5071-CoralBank-Research/. Molecular data for specimens not included in the paper by Cowman *et al.* (2020) are available at: BioProject PRJNA977819, SAMN35547948-48037, SAMN35547948-48037, BioSample #SAMN35547948-48037. Data from Cowman *et al.* (2020) are available at: BioProject PRJNA601826, SRA GenBank SUB6852542, BioSample #SAMN13871686-1781; Hexacoral bait set: Appendices C and D, Data Dryad Entry https://doi.org/10.5061/dryad.9p8cz8wc8.

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