Phylogeography of recent Plesiastrea (Scleractinia: Plesiastreidae) based on an integrated taxonomic approach

David J. Juszkiewicz, Nicole E. White, Jarosław Stolarski, Francesca Benzoni, Roberto Arrigoni, Bert W. Hoeksema, Nerida G. Wilson, Michael Bunce, Zoe T. Richards

DOI:
https://doi.org/10.1016/j.ympev.2022.107469

Molecular Phylogenetics and Evolution 172 (2022) 107469

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogeography of recent *Plesiastrea* (Scleractinia: Plesiastreidae) based on an integrated taxonomic approach

David J. Juszkiewicz [a,*], Nicole E. White [a], Jarosław Stolarski [b], Francesca Benzoni [c], Roberto Arrigoni [d], Bert W. Hoeksema [e,f], Nerida G. Wilson [g,h], Michael Bunce [a,i], Zoe T. Richards [a,g]

[a] *Coral Conservation and Research Group (CORE), Trace and Environmental DNA Laboratory (TrEnD), School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia 6102, Australia*
[b] *Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, PL-00-818 Warsaw, Poland*
[c] *Red Sea Research Center, Division of Biological and Environmental Science and Engineering, King Abdullah University of Science and Technology, Thuwal 23955-6900, Saudi Arabia*
[d] *Department of Biology and Evolution of Marine Organisms (BEOM), Stazione Zoologica Anton Dohrn, Villa Comunale, 80121 Napoli, Italy*
[e] *Taxonomy, Systematics, and Geodiversity Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, the Netherlands*
[f] *Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, the Netherlands*
[g] *Collections & Research, Western Australian Museum, 49 Kew Street, Welshpool, Western Australia 6106, Australia*
[h] *School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley, Western Australia 6009, Australia*
[i] *Institute of Environmental Science and Research (ESR), 34 Kenepuru Drive, Porirua 5022, New Zealand*

ARTICLE INFO

Keywords:
Biogeography
Cryptic species
Microstructure
Phylogenetics
Plesiastrea versipora
Systematics

ABSTRACT

Scleractinian corals are a diverse group of ecologically important yet highly threatened marine invertebrates, which can be challenging to identify to the species level. An influx of molecular studies has transformed scleractinian systematics, highlighting that cryptic species may be more common than previously understood. In this study, we test the hypothesis that *Plesiastrea versipora* (Lamarck, 1816), a species currently considered to occur throughout the Indo-Pacific in tropical, sub-tropical and temperate waters, is a single species. Molecular and morphological analyses were conducted on 80 samples collected from 31 sites spanning the majority of the species putative range and twelve mitogenomes were assembled to identify informative regions for phylogenetic reconstruction. Congruent genetic data across three gene regions supports the existence of two monophyletic clades aligning with distinct tropical and temperate provenances. Multivariate macromorphological analyses based on 13 corallite characters provided additional support for the phylogeographic split, with the number of septa and corallite density varying across this biogeographic divide. Furthermore, micromorphological and microstructural analyses identified that the temperate representatives typically develop sub-cerioid corallites with sparse or absent coenosteal features and smooth septal faces. In contrast, tropical representatives typically develop plocoid corallites separated by a porous dissepimental coenosteum and have granulated septal faces. These data suggest that at least two species exist within the genus *Plesiastrea* Milne Edwards & Haime, 1848. Based on examination of type material, we retain the name *Plesiastrea versipora* (Lamarck, 1816) for the temperate representatives of the genus and resurrect the name *Plesiastrea peroni* Milne Edwards & Haime, 1857 for the tropical members. This study highlights how broadly distributed hard coral taxa still need careful re-examination through an integrated systematics approach to better understand their phylogeographic patterns. Furthermore, it demonstrates the utility of integrating micro-, macro-morphological and genetic datasets, and the importance of type specimens when dealing with taxonomic revisions of scleractinian taxa.

* Corresponding author.
E-mail address: david.juszkiewicz@postgrad.curtin.edu.au (D.J. Juszkiewicz).

https://doi.org/10.1016/j.ympev.2022.107469
Received 23 November 2021; Received in revised form 25 February 2022; Accepted 21 March 2022
Available online 26 March 2022

1. Introduction

Species identification is fundamental to biological science and threatened-species conservation (Cracraft, 2002; Mace, 2004; Tahseen, 2014). Cataloguing biodiversity is also integral to understanding the ecological functioning of natural systems (Agapow et al., 2004; Isaac et al., 2004) and interpreting the impacts of climate change (Fišer et al., 2018). In the marine environment, speciation has been prolific (González et al., 2018). As of 2022, over 240,000 marine species have been formally described to date (WoRMS Editorial Board, 2021), approximately one-third of which occur in coral reef ecosystems (Reaka-Kudla, 2005). However, the total number could be at least three times higher once undescribed and undetected marine species are accounted for (Appeltans et al., 2012).

Cryptic species are defined as two or more morphologically similar but genetically distinct species that are erroneously classified under one species name (Bickford et al., 2007; Fišer et al., 2018; Knowlton, 1993; Sáez and Lozano, 2005). Cryptic species often remain undetected until in-depth phylogeographic (Arrigoni et al., 2019, 2020; Fouquet et al., 2007; Mitsuki et al., 2021; Williams et al., 2006) or population genetic studies reveal unexpected divergences (González-Castellano et al., 2020; Griffiths et al., 2010; McKeown et al., 2020). A large proportion of major metazoan taxa contain cryptic species (Pérez-Ponce de León and Poulin, 2016; Pfenninger and Schwenk, 2007); hence cryptic speciation presents ubiquitous and complex challenges to anyone attempting to use morphological similarities to identify species. It also provides significant challenges to managers tasked with protecting biodiversity and implementing effective species conservation strategies (Bickford et al., 2007; Chenuil et al., 2019; Witt et al., 2006).

Scleractinian corals are an ideal model group to study cryptic diversity due to their established propensity for interspecific hybridisation (Richards et al., 2013; van Oppen et al., 2001), morphological convergence (Arrigoni et al., 2014; Benzoni et al., 2012; Budd et al., 2012; Fukami et al., 2004; Gittenberger et al., 2011; Richards et al., 2010) and environmental plasticity (Ow and Todd, 2010; Pfennig et al., 2010; Todd, 2008). Hybridisation promotes diversification in numerous genera (Hobbs et al., 2021) due to gametic admixture during mass spawning events aided by the experimentally-proven ability for many coral species to have semi-permeable reproductive boundaries (Willis et al., 2006). Hybridisation can occur between species with a recent common ancestry or within syngameons (Mao et al., 2018; Richards et al., 2013). It can be a driver of evolutionary novelty (Richards and Hobbs, 2015), but it can also obscure species boundaries (Vollmer and Palumbi, 2002). Where hybrid offspring show morphological similarity to one of the parental lineages, it can lead to morphological gradients and difficulties detecting cryptic species.

Convergent evolution (whereby distinct lineages independently evolve similar traits, i.e. homoplasy) is another process that confounds the ability to reconstruct evolutionary relationships and detect cryptic species (Losos, 2011; Stern, 2013). A study by Richards et al. (2010) discovered an *Acropora* species of uncertain identity ('Pacific Elkhorn') in the Pacific Ocean that shared the same colony architecture and macro-morphological features as the critically endangered Atlantic Ocean species *A. palmata* (Lamarck, 1816). Molecular systematics resolved these biogeographically separated elkhorn corals as highly divergent lineages and distinct species (Richards et al., 2010). Molecular data has also helped identify evolutionary convergence in at least five other scleractinian coral families (Dendrophyllidae: Arrigoni et al., 2014; Fungiidae: Benzoni et al., 2012; Gittenberger et al., 2011; and Mussidae: Merulinidae, and Lobophylliidae, Budd et al., 2012; Fukami et al., 2004).

Intraspecific variation and phenotypic plasticity have also presented challenges to coral taxonomists (Kitahara et al., 2016) and hampered the ability to detect cryptic species. The 'ecomorph' or 'ecotype' concept (Veron, 2013; Wijsman-Best, 1974, 1972) suggests that intraspecific skeletal variations occur as a result of phenotypic and/or genotypic responses to environmental conditions (Gattuso et al., 1991; Veron, 2013). This concept led to the 'lumping' of ecomorphs together (e.g. Wallace, 1999), especially by field biologists, rather than 'splitting' species into more finely resolved units. The *Pocillopora damicornis* complex has been a critical example in helping to understand the relationship between ecomorphs and species (Schmidt-Roach et al., 2014; Veron and Pichon, 1976).

The growing body of genetic data obtained across large spatial scales are starting to reveal that corals display complex patterns of genetic structure (Arrigoni et al., 2019, 2020; Flot et al., 2011; Richards et al., 2016; Stefani et al., 2008). Such complexity can only be untangled using multiple lines of evidence (Forsman et al., 2009), including reproductive data, behavioural information, biogeographic data, ecological insight and detailed taxonomic and molecular systematic data (Fišer et al., 2018). It is now becoming apparent in corals (Benzoni et al., 2010; Gittenberger et al., 2011; Kitano et al., 2014; Luck et al., 2013; Luzon et al., 2017) and beyond, that a total evidence approach (also referred to as collaborative [Fisher and Smith, 2008], combined [Malhotra and Thorpe, 2004], integrative [Padial and De la Riva, 2009; Tan et al., 2010], multidimensional [Sbordoni et al., 1991], or multidisciplinary [Lucas et al., 2002; Luckett, 2012]) is needed to formulate robust hypotheses about species relationships (Dayrat, 2005; Pante et al., 2015; Schlick-Steiner et al., 2010).

Plesiastrea versipora (Lamarck, 1816) *sensu lato* is an encrusting to massive zooxanthellate coral present across tropical and temperate waters (Burgess et al., 2009; Cairns and Parker, 1992; Gilmour et al., 2015; Madsen et al., 2014; Precoda et al., 2018; Veron, 2002), which is evolutionarily distinct within the Robust clade of Scleractinia (Benzoni et al., 2011; Kitahara et al., 2016). The genus *Plesiastrea* Milne Edwards & Haime, 1848 is monotypic, but *P. versipora* is the senior synonym of six other nominal species. *Plesiastrea versipora* is unusual among hermatypic corals, in that its wide latitudinal distribution spans Indo-Pacific equatorial waters to as far south as the Bass Straight, Australia (39° S; Ling et al., 2018), where the species must tolerate 12° C water temperatures and low-light levels (Rodriguez-Lanetty et al., 2001). This species is also found across the Indo-Pacific oceans, from the Red Sea (Benzoni et al., 2011) to the eastern Pacific islands of the Tuamotu Archipelago (Adjeroud et al., 2000; Glynn et al., 2007), and as far north as the Ryukyu Archipelago, Japan (24–28° N; Rodriguez-Lanetty and Hoegh-Guldberg, 2002). Preliminary studies of the phylogeography of *P. versipora* as a host for Symbiodiniaceae in the western Pacific Ocean show evidence of unexpected patterns of genetic structuring whereby high-latitude temperate populations are differentiated from tropical populations (Rodriguez-Lanetty et al., 2001; Rodriguez-Lanetty and Hoegh-Guldberg, 2003, 2002). Given the wide distribution of *P. versipora* and evidence of structuring among Symbiodiniaceae, further investigation of genetic structuring within this monotypic genus is warranted.

This study examines the phylogeographic diversity of *P. versipora* in the Indo-Pacific using an integrated taxonomic approach. We hypothesise that the entity currently known as *P. versipora* comprises of more than one distinct species. To test this hypothesis, we examine the level of phenotypic variation exhibited within *P. versipora* across a broad spatial scale and generate mitogenomes and gene trees to explore possible evolutionary relationships amongst morphological variants.

2. Material and methods

2.1. Specimen collection and identification

A total of 86 *Plesiastrea* specimens were collected via SCUBA or snorkelling from 31 Indo-Pacific localities spanning the majority of its known distribution (Fig. 1, Table S1). Specimens that fall between the Tropic of Cancer (latitude 23°26′11.2″N) and Tropic of Capricorn (latitude 23°26′11.2″S) were assigned as "tropical" and everything outside this region "temperate". In this regard, the temperate region

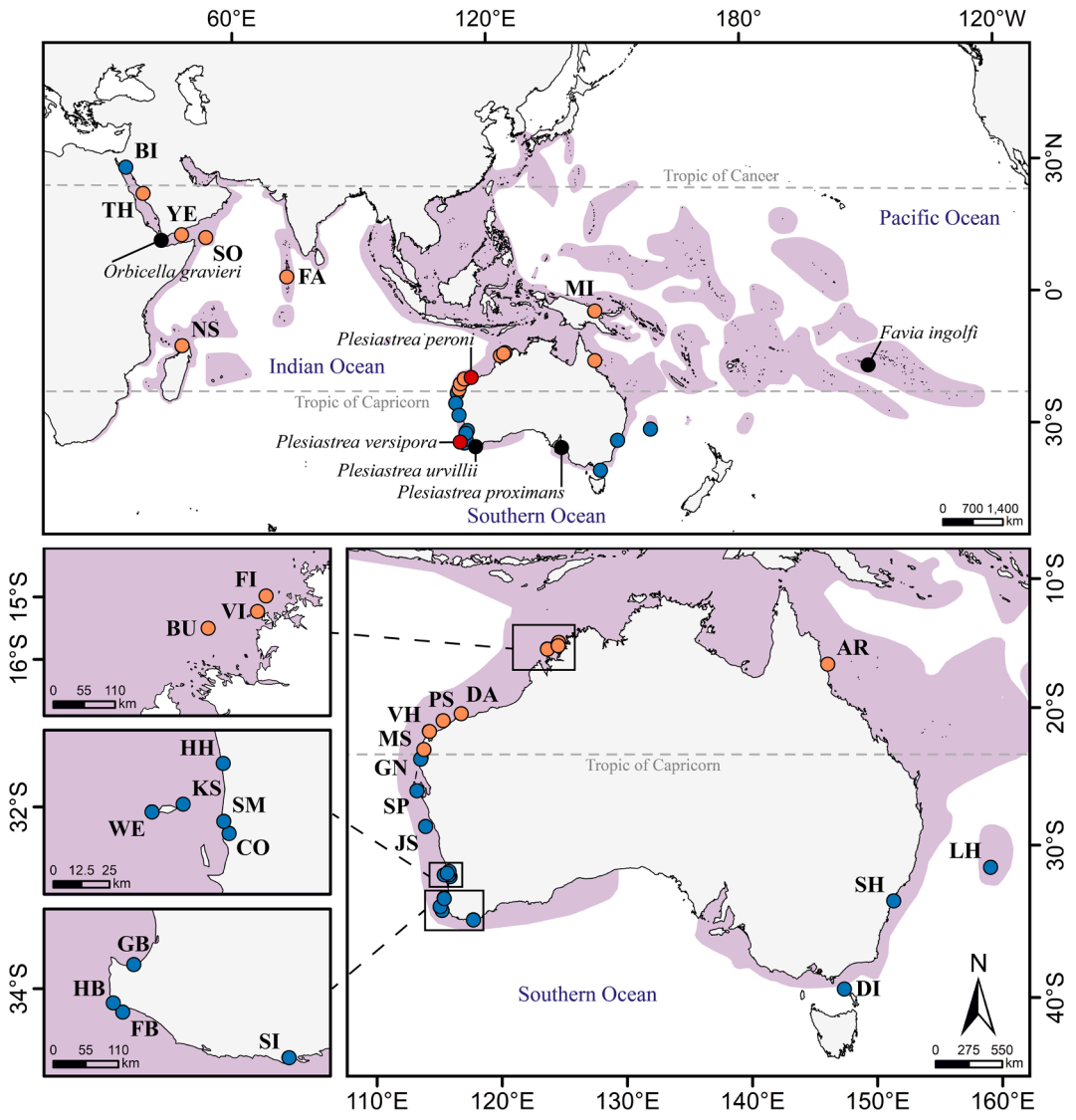

Fig. 1. Map of sampling localities and type localities indicated by dots (blue dots = temperate and orange dots = tropical sampling localities; red dots = holotype localities determined in this study; black dots = type localities of *Plesiastrea* junior synonyms determined in this study). Areas shaded lilac indicate the currently known distribution of material identified as *Plesiastrea versipora* (Best et al., 1989; Huang et al., 2015; Jonker and Johan, 1999; van der Meij et al., 2010; Veron et al., 2016). Location abbreviations are as flows; Arlington Reef, Queensland, Australia (AR); Barkan Island, Saudi Arabia – Red Sea (BI); Buccaneer Archipelago, Western Australia (BU); Coogee, Western Australia (CO); Dampier Archipelago, Western Australia (DA); Deal Island, Tasmania, Australia (DI); Faafu Atoll, Maldives (FA); Flinders Bay, Western Australia (FB); De Freycinet Islet, Western Australia (FI); Geographe Bay, Western Australia (GB); Gnaraloo Bay, Western Australia (GN); Hamelin Bay, Western Australia (HB); Hillarys Boat Harbour, Western Australia (HH); Joe Smith Island, Houtman-Abrolhos, Western Australia (JS); Kingston Spit, Western Australia (KS); Lord Howe Island, Australia (LH); Malamal Island, Papua New Guinea (MI); Maud Sanctuary, Western Australia (MS); Nosy Sakatia, Madagascar (NS); Pilbara Shelf, Western Australia (PS); Fairlight Beach, Sydney Harbour, New South Wales (SH); Shelter Island, Albany, Western Australia (SI); South Mole, Western Australia (SM); Socotra Island, Yemen (SO); Steep Point, Western Australia (SP); Thuwal, Saudi Arabia – Red Sea (TH); Vlaming Head, Western Australia (VH); Vulcan Island, Western Australia (VI); West End, Western Australia (WE); and Yemen – Gulf of Aden (YE).

includes sub-tropical localities (~29-31°N and S). Two additional specimens from the family Merulinidae; *Cyphastrea decadia* Moll & Borel-Best, 1984, and *Favites micropentagonus* Veron, 2000, were collected from the Kimberley, Western Australia, and used as outgroups. Where possible, *Plesiastrea* colonies were photographed in-situ using an Olympus TG-5 camera and depth was recorded using a Shearwater Perdix Dive computer. A 5 × 5-cm^2 fragment of each colony was sampled using hammer and chisel, assigned a unique identification code, and a 1 × 1-cm^2 subsample placed in 100% ethanol. The remainder of the sample was bleached in 30% sodium hypochlorite solution for 48 h to remove any tissue, then rinsed in fresh water and dried. Specimens sampled for this study were deposited at King Abdullah University of Science and Technology, University of Milano-Bicocca, The Australian Museum, and Western Australian Museum (Table S1). Samples were collected or obtained under the appropriate licensing, and export permits see Table S2.

Specimens were identified as *Plesiastrea versipora* (Lamarck, 1816) based on skeleton morphology following Lamarck (1816: p. 264), Milne Edwards and Haime (1848: p. 494; 1849: pp. 118–119), Matthai (1914: pp. 103–104), Veron et al. (1977: pp. 149–153), Wijsman-Best (1977: pp. 93–97), Dai and Horng (2009: p. 150), and Benzoni et al. (2011). Additionally, reference was made to holotype illustrations and descriptions of *Plesiastrea versipora* Lamarck (1816: p. 568; Fig. 2C) and its junior synonyms (see Fig. 2): *Favia ingolfi* Crossland (1931: pp. 386–387), *Orbicella annuligera* (Vaughan, 1907: pp. 252–253), *Orbicella gravieri* Vaughan (1918: pp. 85–86), *Plesiastrea peroni* Milne Edwards & Haime (1857: p. 492; Fig. 2E), *Plesiastrea proximans* Dennant (1904: p. 9), *Plesiastrea quatrefagiana* Milne Edwards & Haime (1849: p. 119), and

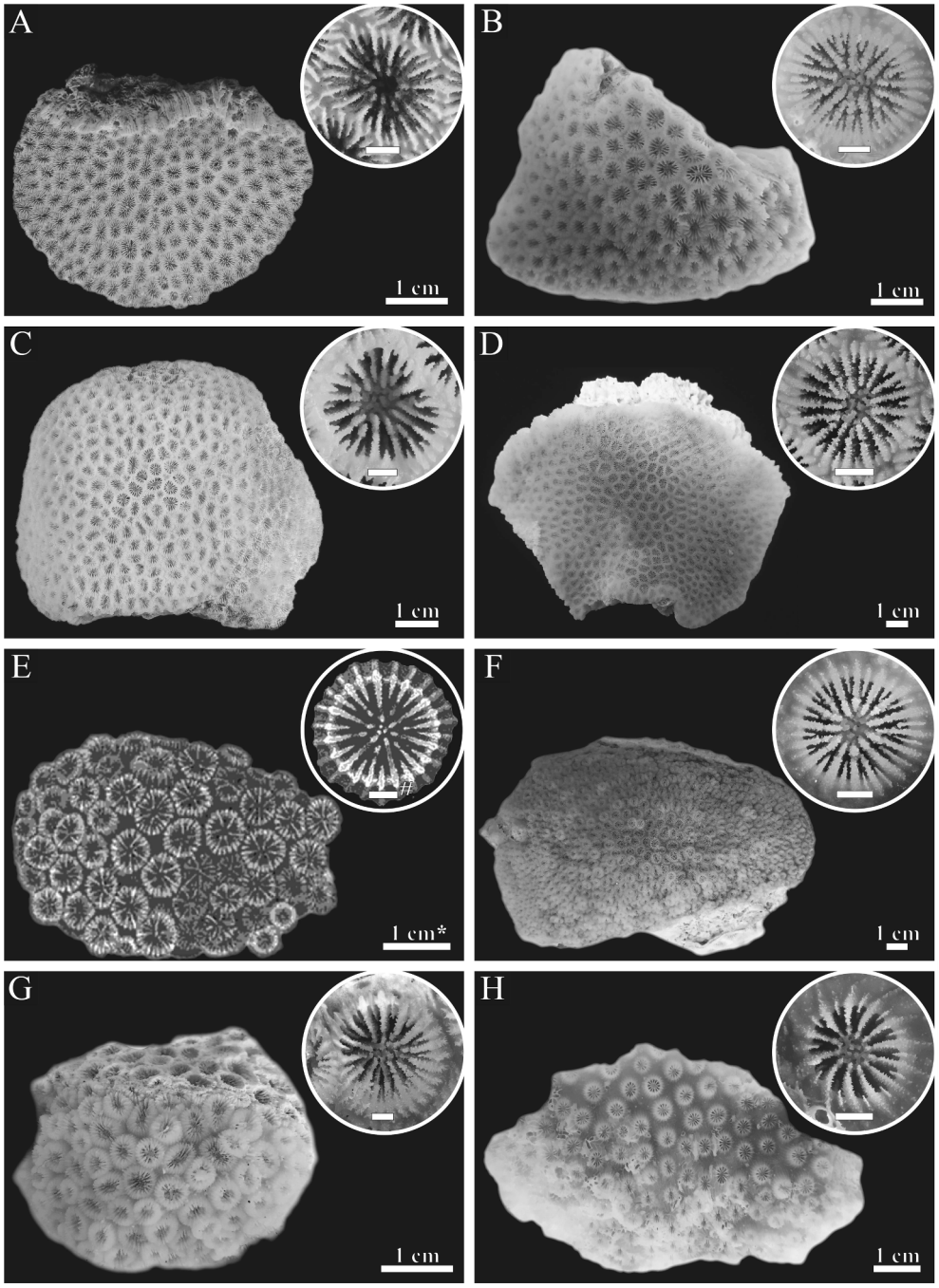

Fig. 2. Colony and corallite morphology of *Plesiastrea* type material and additional specimens (including synonymised taxa and specimens examined in this study). (A) Holotype of *Plesiastrea urvillii* MNHN733. (B) *Plesiastrea* SI 2199 at Shelter Island, Albany, Western Australia (this study). (C) Holotype of *Astrea versipora* Lamarck, 1816; MNHN IK-2012–10624. (D) *Plesiastrea* HB 2144 at Hamelin Bay, Western Australia (this study; topotype of *Plesiastrea versipora* MNHN IK-2012–10624). (E) Holotype illustration of *Plesiastrea peroni* Milne Edwards & Haime, 1857; * ± 0.4 cm. # ± 2 mm. (F) *Plesiastrea* AR 2098 at Arlington Reef, Queensland, Australia (this study). (G) *Plesiastrea* LH 2181 at Lord Howe Island, Australia (this study). (H) *Plesiastrea* FA 2210 at Faafu Atoll, Maldives (this study). White bars in circle inserts are a scale of 1 mm.

Plesiastrea urvillii Milne Edwards & Haime, 1848b (Milne Edwards and Haime, 1849: pp. 117–118; Fig. 2A). For further nomenclatural details see Table S3 and Supplementary file 2.

2.2. DNA extraction and mitochondrial genome library construction and sequencing

Total genomic DNA (gDNA) was extracted from a 2–4-mm^2 subsample from the 86 samples (Table S1) using DNeasy Blood and Tissue kit (Qiagen Inc., Venlo, the Netherlands), with minor modifications to the tissue lysing step. For detailed methods of the DNA extractions, quality, quantification, and PCR amplification, see Table S4.

Twelve morphologically distinct *P. versipora* specimens spanning the widest distribution range possible with the specimens available (Indian and Pacific Oceans, the Red Sea, near equatorial locations, and southern most specimens [Shelter Island, Western Australia and Deal Island, Tasmania, Australia]; see *section 2.5*), and two outgroups (*C. decadia and F. micropentagonus*) were selected for mitochondrial genome sequencing with the aim of identifying new informative barcoding loci based on hyper-variable regions. A larger subset ($n = 74$) of *Plesiastrea* specimens was then sequenced using these newly developed primers (see *section 2.3*).

A gDNA library was prepared for each sample using QIAseq FX DNA library kit (24; Qiagen Inc., Venlo, the Netherlands) targeting the 10 ng of input gDNA to enzyme ratio protocol. Pooled libraries were size selected (200–600 bp) using a Pippin Prep (Sage Sciences; Massachusetts, USA). The genomic library was sequenced on an MiSeq platform (Illumina, San Diego, CA, USA) with standard 500-cycle V2 chemistry (250 bp paired-end sequencing runs). For further detail of the mitochondrial genome library sequencing methods see Table S5.

Construction of the 12 *Plesiastrea* and two outgroups mitochondrial genomes was completed using Geneious version 10.1.3 (Biomatters Ltd, Auckland, New Zealand), with comparison to genomes obtained from GenBank (January 2019) of *P. versipora* (KY094480; Daya Bay, Guangdong, China; 15,320 bp; Niu et al., 2020) and *Orbicella faveolata* (Ellis & Solander, 1786) (NC007226; 16,138 bp; Bocas del Toro, Panama; Fukami and Knowlton, 2005). Three iterations of mitogenome builds were undertaken using the 'Map to Reference' function in Geneious. Further improvement iterations of the mitochondrial genome build involved the extraction of the consensus sequence generated from the first initial build using *O. faveolata* (NC007226) and returning to the raw data (Read1 and Read2) for each sample. Thirdly, additional refinement was carried out with 'Map to *P. versipora* (KY094480)', in addition to providing gene annotations. Assembled mitochondrial genomes were then aligned with *O. faveolata* (NC007226) using the 'Alignment' tool. The gene order and associated annotations were confirmed with the Type SII Scleractinian gene arrangement from Lin et al. (2014). Additionally, the gene order and annotations were cross-referenced with MITOS (Bernt et al., 2013) *de novo* output of the *Plesiastrea* SI 2124 mitogenome assembled in this study because of its largest sequencing coverage (890×). For detailed methods of *P. versipora* mitochondrial genome construction see Table S5. Sequences were submitted to the GenBank database (NCBI) and corresponding accession number are listed in Table S1.

2.3. Mitochondrial and nuclear primer design, sequencing and sequence determination

2.3.1. Primer design

Mitochondrial and nuclear primers were designed using Primer3 version 2.3.7 in Geneious (Table 1). Variable regions within the 12 mitochondrial genomes were identified within the COI (Cytochrome *c* oxidase I – upper section), COIII–COII (partial Cytochrome *c* oxidase III to partial Cytochrome *c* oxidase II) loci for mitochondrial primer design (Table S6). The nuclear primer set ITS (Internal transcribed spacers ITS 1 & 2 including 5.8S; Table S6) were designed around the GenBank ITS sequence of *P. versipora* (HQ203307; Pulau Jong, Singapore; Huang et al., 2011). Similarly to the mitochondrial genome construction, the raw data for each sample (Read 1 and Read 2) was queried using the *'Map to P. versipora* (HQ203307, ITS)'. The consensus ITS was aligned and examined for intraspecies variation areas for targeted primer design. For detailed methods of the *P. versipora* nuclear ITS primer development see Table S7. Both mitochondrial and nuclear primer development followed stringent guidelines for performance and optimisation (Bustin and Huggett, 2017). For details of primer optimisation, validation and testing see Table S8.

2.3.2. DNA amplification and sequencing of COI, COIII–COII and ITS

DNA amplification for Sanger Sequencing involved three PCR assays per sample each with 2ul of gDNA (Table S6). The thermal cycling conditions were: initial denaturation at 95 °C for 5 min, followed by 40 cycles of 95 °C for 30 s, annealing at primer-specific annealing temperature (Table S6) for 30 s, extension at 72 °C for 50 s (longer extension time assigned to larger sized fragments), and a final extension at 72 °C for 10 min. PCR product was purified using Qiagen Qiaquick PCR purification kit (Venlo, the Netherlands) and sequenced via Macrogen Inc. (Seoul, South Korea). Forward and reverse chromatogram, were assembled and manually checked using Geneious and primers were removed. The consensus sequence from each gene and sample was used for further analyses. Sequences were submitted to the GenBank database (NCBI; Table S1).

Table 1
Molecular markers and locus utilised for phylogenetic reconstruction. Total characters (informative) does not include outgroups. Protein-coding gene (PCG).

Locus	Primer Pairs (5′-3′)	Total base pairs (informative)	AIC Model
COI	Pv_COI_14413_F1 Pv_COI_15398_R1	728 (17)	HKY + I + G
COIII–COII	Pv_CO2–3_10805_F1 Pv_CO2–3_11384_R1	447 (13)	HKY + I + G
Mt Genome (13PCGs)	High throughput sequencing	11,682 (96)	HKY + I
ITS	Pv_ITS_827bp_F1 Pv_ITS_827bp_R2	715 (49)	TIM3 + G

2.4. Phylogenetic analyses of mitochondrial and nuclear regions

Three gene alignments were compiled for phylogenetic inference from sequences obtained from Sanger sequencing. Sequences were globally aligned pairwise in Geneious using a cost matrix of 93% similarity (5.0/-9.026168); two mitochondrial loci and one nuclear marker alignment. Mitochondrial loci were COI ($n = 89$; including COI extract from *P. versipora* - KY094480 and outgroups), as well as COIII–COII ($n = 89$; including COIII–COII extract from *P. versipora* - KY094480 and outgroups). The nuclear loci was ITS, where a consensus ITS sequence was compiled for each taxa from this multi-copy marker ($n = 62$; including *P. versipora* - HQ203307 and outgroups). Variable single nucleotide polymorphisms (SNP's) across each loci and taxa were compiled and analysed (Table S9).

Complete annotated mitochondrial genome sequences ($n = 13$; including *P. versipora* - KY094480) were viewed in Geneious 'Sequence Viewer', and each protein-coding gene (PCG) was extracted to produce a mitochondrial genome sequence alignment containing 13 protein-coding genes and a total length of 11,682 bp for further analysis.

Separate phylogenetic analyses for each DNA locus and the mitochondrial PCG sequences were conducted. The optimum phylogenetic models were assessed using the program jModelTest version 2.1.10 (Darriba et al., 2012), under the Akaike Information Criterion (AIC) (Table 1). AIC modelling was chosen for the Bayesian inference analyses as AIC shows more precision in modelling when more complicated substitution models are applied (Kadane and Lazar, 2004; Luo et al., 2010; Posada and Crandall, 2001). COI and COII–COIII sequences were concatenated in TextWrangler version 5.5.2 (Bare Bones Software, North Chelmsford, USA). Phylogenetic analyses were conducted under Bayesian inference. Bayesian inference analyses were performed in BEAST version 2.4.6 (Bouckaert et al., 2014). BEAST file sequence model was created in Beauti version 2.4.6 (Bouckaert et al., 2014) using the Package jModelTest version 1.0.4 (Bouckaert and Drummond, 2017) for Bayesian model test for nucleotide substitution models, gamma rate heterogeneity and invariant sites. ITS and concatenated COI, COIII–CIII were run separately on a relaxed clock log-normal prior using a Coalescent Bayesian Skyline inference (Drummond et al., 2005).

To estimate the relative divergence time, a fossil calibration was applied to the phylogenetic reconstruction of the PCGs using a Coalescent Bayesian Skyline inference and relaxed clock log-normal prior (Drummond et al., 2006; Heled and Drummond, 2012; Sauquet, 2013). Following (Nguyen and Ho, 2020; Simpson et al., 2011) and the Palaeobiology Database (https://paleobiodb.org), the stratigraphically oldest confirmed fossil occurrence of *P. versipora* (specimen Fig. S1) was used to create a calibration prior, probability gamma distributed with a skewed peak. Based on the first appearance datum (*P. versipora* fossil, specimen FLV1.2_53; Bromfield and Pandolfi, 2012), with a time range of 16.0–13.8 Mya, Gamma ShapeScale was set at 2.0α and 18.0β with an offset of 13.8.

Four Markov chains of 100 million generations were implemented in ten separate runs, saving a tree every 1000th generation. Markov Chain Monte Carlo (MCMC) convergence among runs was monitored using Tracer version 1.7.1 (Rambaut et al., 2014) and checked for effective sampling size (ESS) including unimodal posterior distribution. The first 10% of trees sampled were discarded as burn-in following indications by Tracer, and summarised output trees were compiled using

TreeAnnotator version 2.4.6 (Bouckaert et al., 2014). Tree files for the respective analysis were combined using Log Combiner version 2.4.6 (Bouckaert et al., 2014). Combined tree posterior probability was visualised in FigTree version 1.4.4 (Rambaut, 2012) and final tree figure edited in Adobe Illustrator version 21.1.0 (San Jose, USA).

2.5. Macro-morphological analyses

2.5.1. Skeletal morphometrics

To explore the extent of morphological variation in specimens across their distribution range, macro-morphological characterisation was carried out on 80 *Plesiastrea* colonies (Table S1). Seventeen informative characters were chosen pertaining to the corallum and the internal features of the calice (Budd and Stolarski, 2011; Cairns and Kitahara, 2012; Huang, 2012; Rocha et al., 2014; Veron, 1993; Veron et al., 1977; Veron, 2000); Fig. S2, Table S10, definitions in Table S11). Character states were quantified from six randomly-selected corallites per colony observed with a Fluorescent Stereo Microscope Leica M165 FC with an integrated CCD Camera Leica DFC7000 T, using Leica Application Suite X Version 4.9.0 LAS software. Corallite choice randomisation was carried out by inputting a skeletal colony image into CPCe version 4.1 (Kohler and Gill, 2006) and using the point overlay tool to randomly choose six corallites for analysis.

2.5.2. Macro-morphological skeletal analyses

Morphological variability in 17 characters was initially examined using a draftsman plot to investigate the collinearity of characters using PRIMER-E version 7 (Clarke and Warwick, 2001; Fig. S3). Three characters, C14 (number of primary septa; S_1), C15 (number of secondary septa; S_2), C16 (number of tertiary septa; S_3; Table S10) displayed linear combinations with C17 (total number of septa) and were removed from the analyses. Additionally, C12 (columella state) was also removed because only a single character state was conserved across all samples. Similarity matrices of the remaining 13 morphometric characters of all *Plesiastrea* specimens ($n = 80$) and a subset of those collected from Western Australian (W.A.) localities ($n = 60$) were constructed using the Euclidean distance measure (Clarke and Warwick, 2001; Table S12).

To address the hypothesis that undetected phylogeographic structuring exists within *Plesiastrea*, we examined colony morphology using multivariate techniques across the range of samples, testing for differences between plausible groups based on geographic locations (using ecoregions as defined by Spalding et al., 2007), between Indian and Pacific Oceans, and either side of the Tropic of Capricorn. These analyses were necessary to help infer whether significant spatial morphological variation was present, and to identify the morphological character(s) driving variation. These findings were then applied to groups identified by phylogenetic analyses to support these results under the integrated approach (see *section 2.5.3*).

A One-way Analysis of Similarity (ANOSIM; 999 permutations) was performed to test for significant differences between sampling locations. Data were then grouped according to defined marine ecoregions (Table S13) and a two-way nested ANOSIM was used to examine differences between 14 ecoregions nested within their respective oceans (Indian or Pacific). Along the Western Australian coast, sampling covered six ecoregions spanning the Kimberley (Bonaparte) ER141 to South-West Australia (Leeuwin) ER209 (Fig. 1, Table S13), these ecoregions were examined for significant differences in morphometrics using a one-way ANOSIM (Table S16).

A hierarchical CLUSTER analysis (group average) was constructed to group localities based on Euclidean distance (Fig. S4), and any significant separation overlayed on the PCoA of localities. Spearman rank correlation of > 0.1 was overlayed on the PCoA of ecoregions. Finally, a Similarity Percentages Analysis (SIMPER) was performed to identify unifying morphological characters within ecoregions and key discriminating characters between ecoregions.

2.5.3. Integration of skeletal macro-morphology, molecular work and analysis of type specimens

To investigate whether morphometrics were significantly different across clades established from the concatenated COI, COIII–COIII phylogenetic analysis, samples were grouped according to their respective clades (temperate $n = 48$, tropical $n = 32$). A one-way ANOSIM (999 permutations) was used to test for significant differences based on morphometrics between clades, and SIMPER analysis was used to identify key characters contributing to differences. After distinguishing key discriminating characters (using SIMPER, see *section 2.5.2*), images of type specimens were examined and these characters recorded, where possible. A similarity matrix (Euclidean distance) was constructed and an nMDS ordination produced to visually compare the alignment of type specimens with clades identified in molecular analyses, based on informative morphological characters.

The multivariate analysis described above allows the identification of morphological characters driving differences between clades (via similarity matrices), however, it does not distinguish additional characters related to the corallum that are expressly useful for taxonomic identification. Thus, each character was subject to a one-way ANOVA in R (R Version 3.6.2) to determine whether it differed significantly between clades, which allowed further investigation of the usefulness of that character for traditional taxonomic morphological identification. Assumptions of normality (Shapiro-Wilk Test) and homogeneity of variance (Levene's test, Q/Q-plots and boxplots) were tested using package 'car' (Version 3.0-6). Character C11 (average distance among corallites) was log-transformed prior to analysis to meet normality for analysis of variance. Characters C3 (corallite density per 10 mm^2), C5 (calyx longest diameter), C6 (shortest corallite diameter), C7 (columella maximum diameter), C8 (corallite height), C9 (average primary septa thickness over theca) and C11 (met normality for analysis of variance) were individually fitted to a general linear model and tested using a one-way ANOVA with Clade as factor. Characters C2 (type of budding), C4 (corallite longest diameter), C10 (number of adjacent corallites), C13 (orders of septa), C14, C15, C16 and C17 were not from a normal distribution based on Shapiro-Wilk Test and were tested using the non-parametric Kruskal-Wallis rank sum test (Zar, 2010). Additionally, C1 (corallite structure) was ordinal data and tested using the Kruskal-Wallis rank sum test.

2.6. Skeletal micro-morphological and micro-structural analyses

Skeletal micro-morphology was visualised using Thermo Fisher (Philips) XL20 scanning electron microscope (SEM); all samples were sputter coated with platinum and photographed. SEM was also used to visualize the micro-structural features of polished sections that were lightly etched in Mutvei's solution following Schöne et al., (2005). Skeletal micro-structure was also examined using polished sections and photographed with Nikon Eclipse 80i transmitted light microscope fitted with a DS-5Mc cooled camera head. Thin sections and skeletal fragments attached to microscope stubs are housed at the Institute of Paleobiolgy, Polish Academy of Sciences (ZPAL; Table S1). 3D visualization of the internal structure of the coralla was made with Zeiss XRadia MicroXCT-200 system (referred to as Micro-CT). Scans were performed using the following parameters: voltage: 60 kV, power: 10 W, exposure time: 6 s, pixel size: 19.47 μm, 1201 projections. Three-dimensional images were obtained by processing with the AVIZO7.1 Fire Edition software. All micro-morphological and micro-structural analyses were performed at the Institute of Paleobiology, Polish Academy of Sciences.

3. Results

3.1. Mitochondrial genome architecture

Mitochondrial genome architecture followed Type SII scleractinian gene arrangement (Lin et al., 2014; Fig. 3). The level of single nucleotide

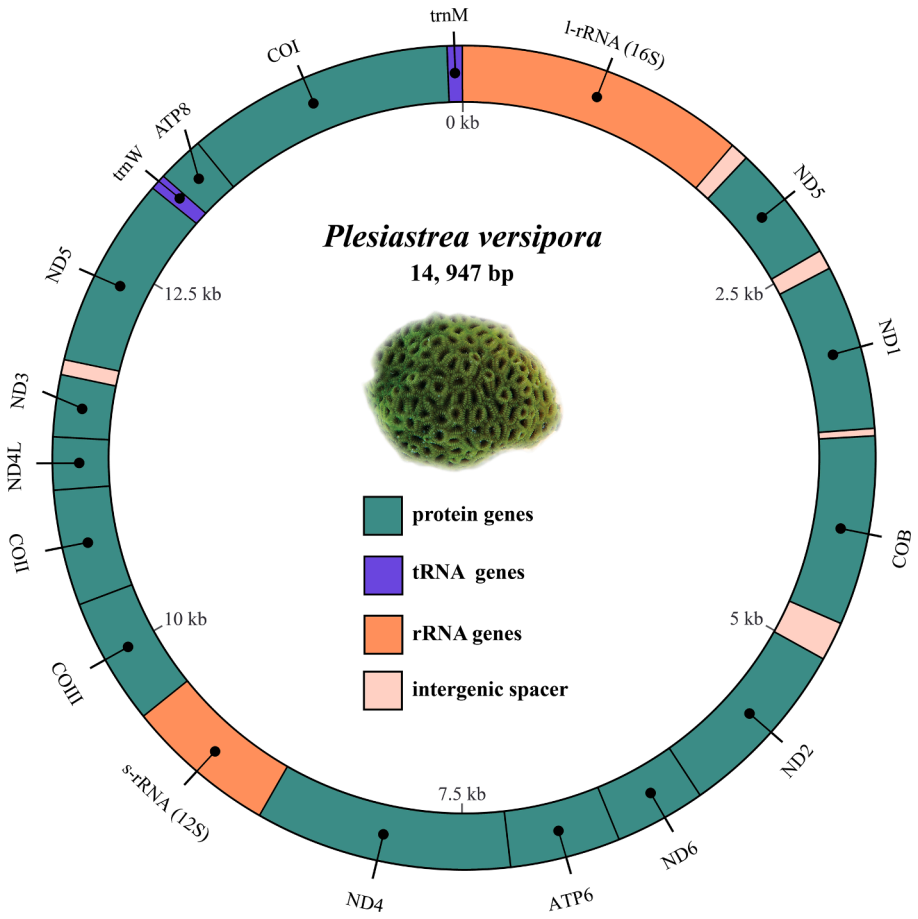

Fig. 3. Mitochondrial genome architecture of *Plesiastrea versipora* based on Type SII Scleractinian (Lin et al., 2014). Gene arrangement and mitochondrial sequence length were determined from 12 mitochondrial genomes. Inside scale markers indicate sequence length positions of 2.5 kb.

polymorphism (SNP) variation observed in the 12 novel *P. versipora* mitochondrial genomes (sequence coverage ranged from 31× to 890×; Table S14) was 100 SNPs (0.7%) with no indels observed. 93 SNPs (0.8%; Table S9) occurred among the 13 protein-coding genes used in the mitochondrial phylogenetic analysis and three more were found when a published mitogenome of *P. versipora* (KY094480) was included in the alignment. Among the 13 protein-coding genes, the COI gene was identified as the longest contiguous gene (1516 bp; Table S15), noting the ND5 gene occurred in two different regions (ND5 Part 1 and Part 2) and totalled 1,820 bp. ATP8 was the shortest PCG (198 bp; Table S15).

3.2. Concatenated COI, COIII to COII phylogeny

Eighty-nine sequences from 32 locations were used in the phylogeographic analysis. A segment (1175 bp) consisting of concatenated COI and COIII–COII mitochondrial loci were aligned, and 30 informative sites (COI and COIII–COII combined; Table 1). The consensus tree was from drawn from ten independent BEAST runs that resulted in effective sampling size (ESS) values > 250. The COI and COIII–COII phylogenetic tree showed two strongly supported clades (posterior support 0.98) that correlated with a divide at the Tropic of Capricorn (herein referred to as temperate and tropical clades; Fig. 4).

The tropical clade contained 39 samples with a southern-most latitude of 23°26′11.2″S (Tropic of Capricorn). There was 0.98 posterior probability support for samples from Lord Howe Island to group in the tropical clade, with samples from Arlington Reef (Great Barrier Reef); the Kimberley (W.A.); Papua New Guinea; the Gulf of Aden; the Maldives; the Red Sea; and Madagascar (Fig. 4). Additionally, the Red Sea sample from Barkan Island, Saudi Arabia (BI) located 27°54′21.2″N latitude fell within the tropical clade.

The temperate clade contained 47 samples with a northern-most latitude 23°26′11.2″S (Tropic of Capricorn). There was 0.94 posterior probability support for Western Australian samples from Gnaraloo Bay, Shark Bay and Abrolhos Islands to cluster with samples from Geographe Bay (Fig. 4). Overall, the samples within *Plesiastrea* created two distinct, highly supported, reciprocally monophyletic lineages in the mitochondrial gene tree. It is important to note Gnaraloo Bay samples (GN), which belong to the temperate clade, were only geographically separated from the Maud Sanctuary (MS) samples (which fell in the tropical clade) by 70 km (Fig. 1).

3.3. Nuclear ITS locus phylogeny

To examine if the tropical/temperate division was also present in the nuclear DNA, a phylogenetic tree was built from an alignment of 61 ITS sequences from 28 geographic locations (715 bp in length with 49 polymorphic sites and five indels observed; Table 1).

The ITS region amplification was a challenge for Sanger sequencing due to its multi-copy nature leading to overlapping peaks and signal loss in the electropherogram. Hence the ITS phylogeny is a subset of terminals from the mitochondrial phylogeny. The consensus tree was drawn from ten independent BEAST runs that resulted in ESS values > 380. The nuclear ITS phylogenetic tree was found to be congruent with the mitochondrial COI and COIII–COII 1186 bp dataset, revealing two strongly supported clades; tropical and temperate (posterior support 1.0; Fig. 5).

In contrast to the mitochondrial reconstruction, based on the ITS phylogeny, Gnaraloo Bay (W.A.) samples clustered within the tropical

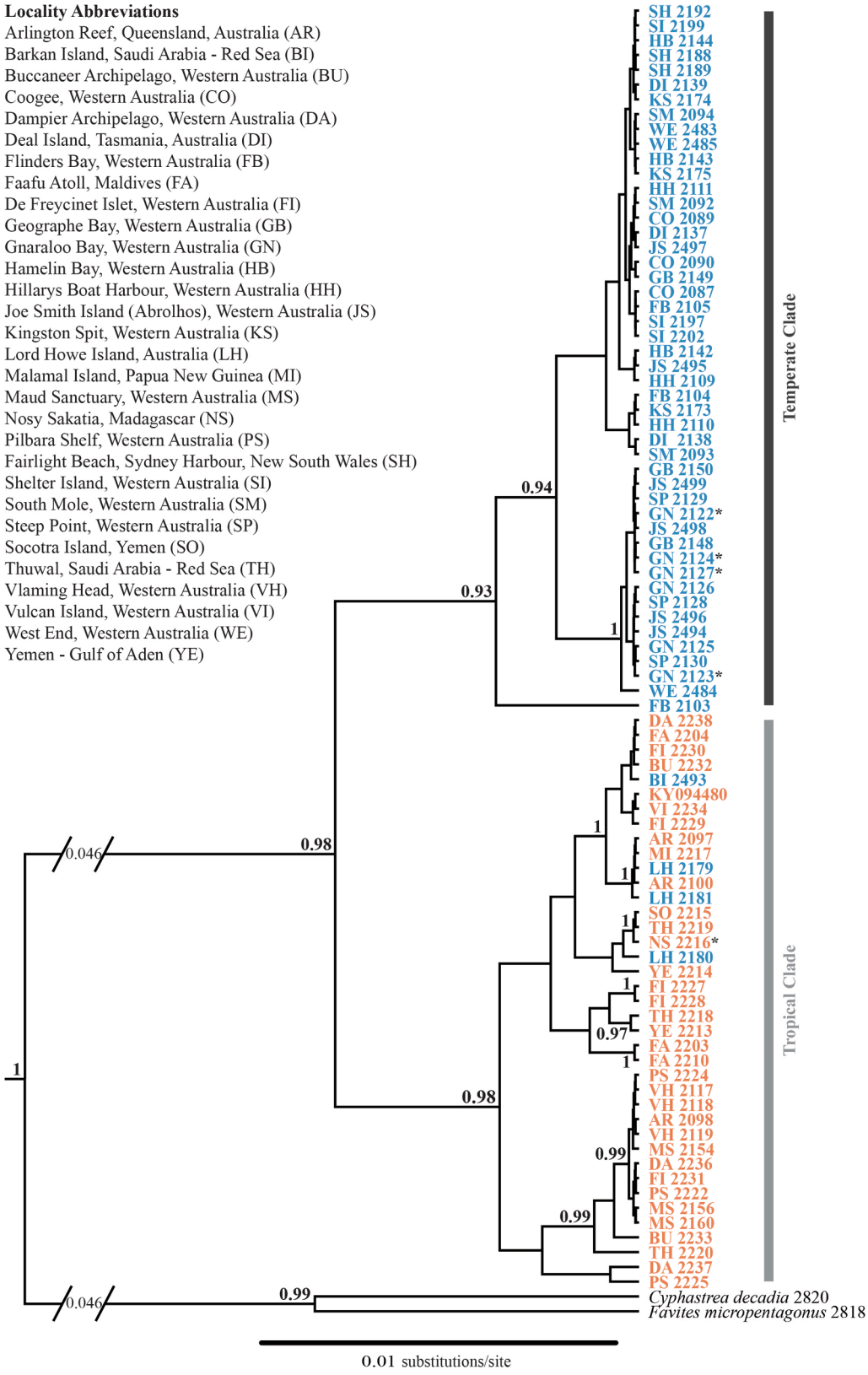

Fig. 4. Bayesian phylogenetic analysis of *Plesiastrea* based on concatenated 1175 bp mitochondrial protein-coding genes; COI, and COIII-COII. Branch support values at nodes represent Bayesian posterior probabilities ≥ 0.9. For ease of interpretation, the two main clades are labelled as tropical and temperate based on a split at the Tropic of Capricorn. Orange labels = tropical collection locality; Blue labels = temperate collection locality. (*) Indicates specimens where there is discordance between the mitochondrial (COI-COIII-II) and nuclear (ITS) phylogenies (compare Fig. 5).

clade (posterior support 0.9; Fig. 5) (with Maud Sanctuary and Cape Vlaming Head) (Figs. 5, 6). This discordance was also noted for a sample from Nosy Sakatia, Madagascar, which in the ITS phylogeny clustered in the temperate clade (Fig. 5), but clustered within the tropical clade of the mitochondrial phylogenies (Figs. 4, 6). Samples from Lord Howe Island were present in the tropical clade (Fig. 6), consistent with the concatenated mitochondrial reconstruction (Fig. 4). Overall, the ITS analysis showed weak internal node support within the temperate and tropical clades.

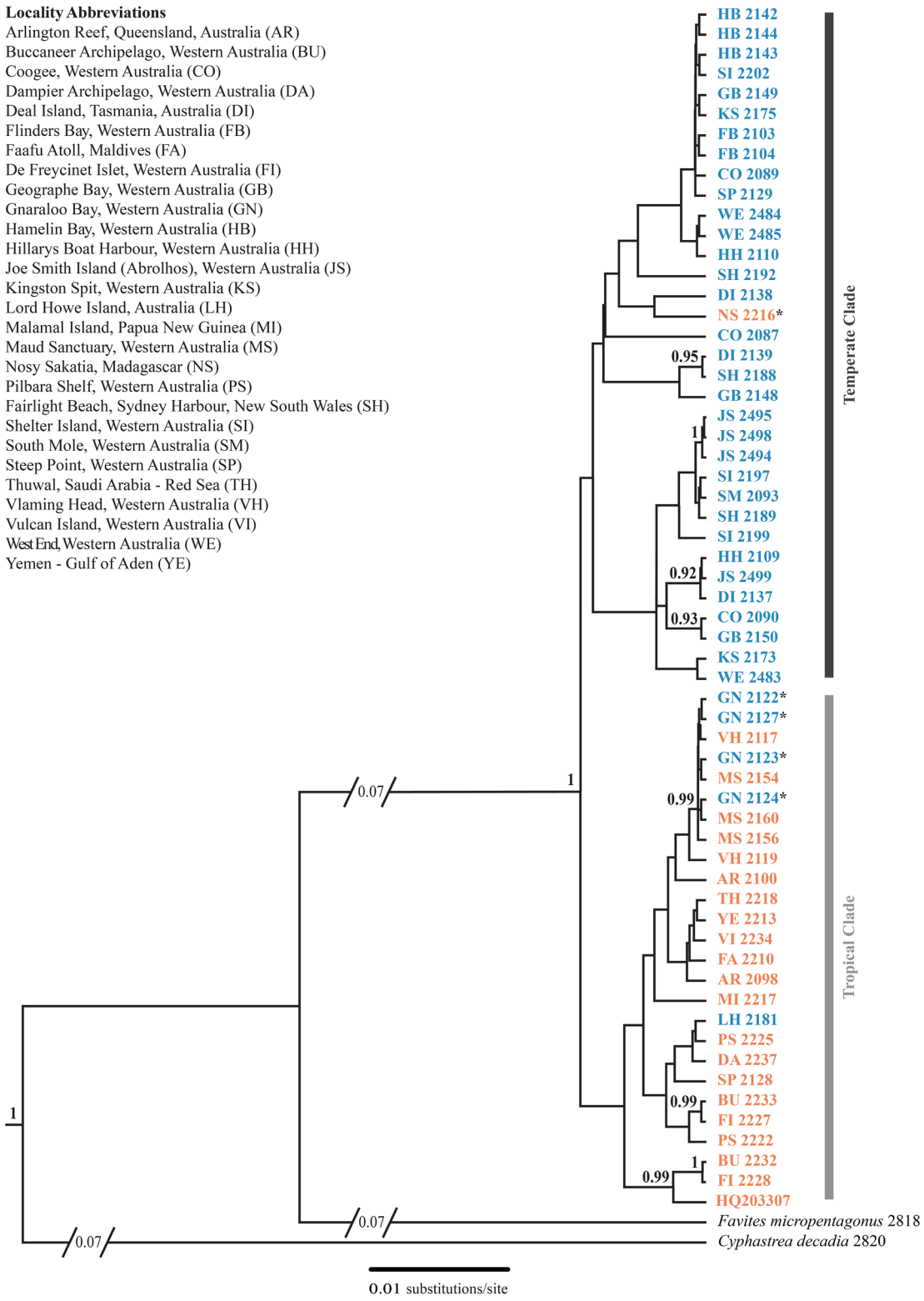

Fig. 5. Bayesian phylogenetic analysis of *Plesiastrea* based on nuclear ITS. Branch support values at nodes represent Bayesian posterior probabilities ≥ 0.9. For ease of interpretation, the two main clades are labelled as tropical and temperate based on a split at the Tropic of Capricorn. Orange labels = tropical collection locality; Blue labels = temperate collection locality. (*) Indicates specimens where there is discordance between the mitochondrial (COI-COIII-II) and nuclear (ITS) phylogenies (compare with Fig. 4).

3.4. Mitochondrial genome phylogeny and tropical vs temperate clade divergence timing

The Bayesian analysis of the full mitochondrial genomes recovered a congruent phylogeny with the ITS and concatenated mitochondrial analysis separating tropical and temperate clades (≥ 0.98; Figs. 4–6). Like the concatenated mitochondrial analysis, the full mitochondrial genome analysis also places the samples collected from Gnaraloo Bay (a

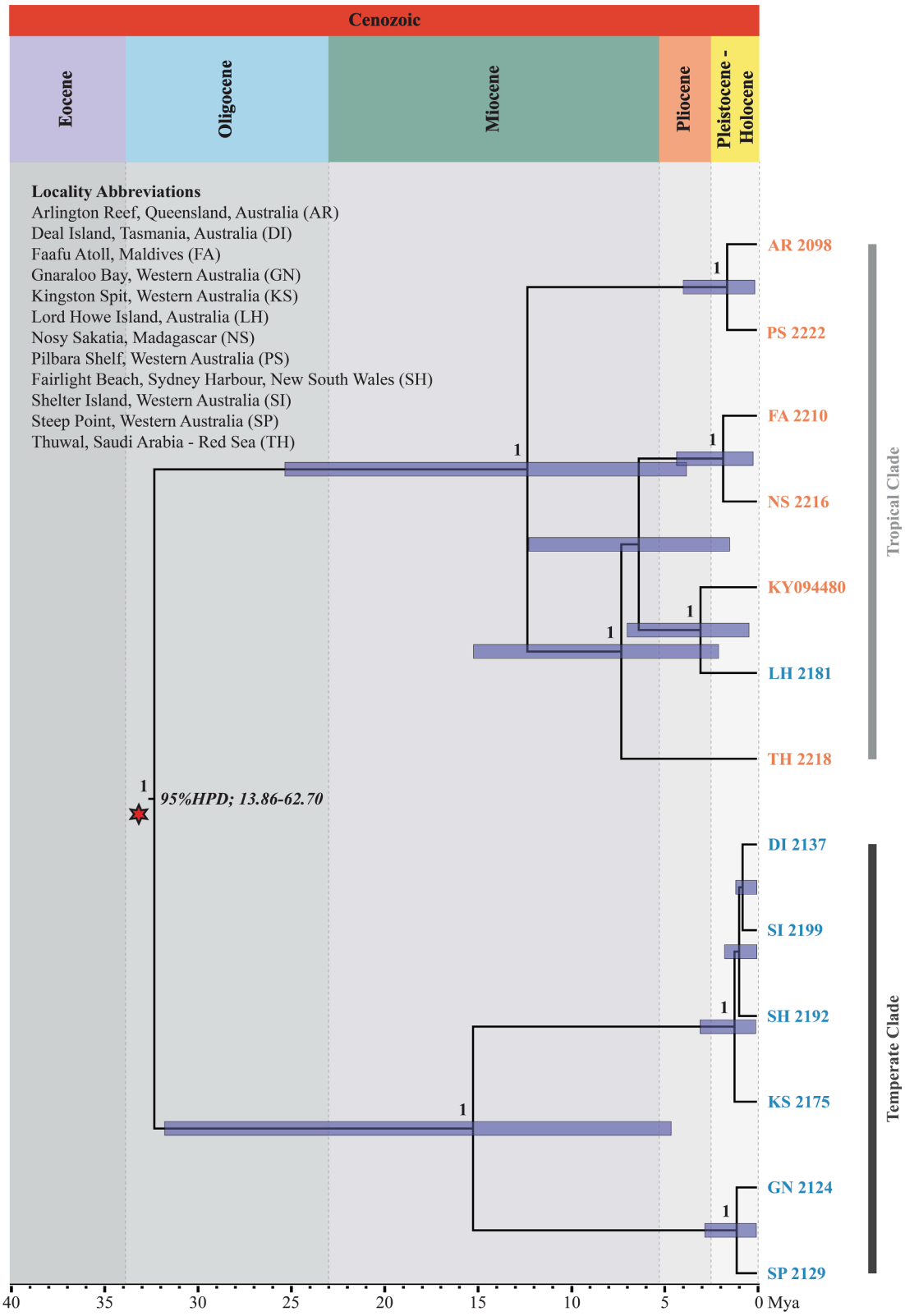

Fig. 6. Bayesian phylogenetic analysis of *Plesiastrea* based on 13 mitochondrial protein-coding genes (11,682 bp). Red star = node of minimum age constraint with the oldest stratigraphically fossil occurrence of *Plesiastrea versipora*, 16.0 – 13.8 Ma (Bromfield and Pandolfi, 2012). Node values are posterior probabilities (≥0.9), violet bars display 95% highest posterior density (HPD) interval of node ages unless stated in italics, orange labels = tropical collection locality, blue labels = temperate collection locality. The two main clades are labelled as tropical and temperate based on a split at the Tropic of Capricorn.

tropical location and part of the Ningaloo Reef system), in the temperate clade (Fig. 6) yet they cluster in the tropical clade within the ITS phylogeny (Fig. 5). Lord Howe Island (LH) samples, which were collected at latitude 31°33′S, in a temperate location, was recovered in the tropical clade in all phylogenetic reconstructions (Figs. 4–6).

There is also evidence of further sub-structuring within the major clades (Fig. 6). For example, within the temperate clade there was posterior probability support of 1 for samples from Gnaraloo, W.A. (GN) and Steep Point, Shark Bay W.A. (SP) to be a sister group to samples from Rottnest Island, W.A. (KS); Albany W.A. (DI); Tasmania (DI); and Sydney N.S.W (SH). Within the tropical clade, there was also posterior probability support of 1 for samples collected from the Pilbara W.A. (PS) and Great Barrier Reef (AR) to belong to a sister group to those collected in the Red Sea (TH); Maldives (FA); Madagascar (NS); Lord Howe Island (LH); and Daya Bay, Guangdong, China (KY094480; Niu et al., 2020).

Our mitochondrial time-calibrated phylogeny suggest that the most common recent ancestor of the *Plesiastrea* tropical and temperate clades lie in a 95% highest posterior density (HPD) interval between 13.85 and 62.70 Mya (Fig. 6). The divergence time estimate for both the *Plesiastrea* tropical (12.314 Mya, 95% HPD; 3.77–25.32; Fig. 6) and temperate (15.228 Mya, 95% HPD; 4.6–31.77; Fig. 6) clades suggest they occurred in the Miocene epoch.

3.5. Comparative skeletal macro-morphometrics

Multivariate analysis revealed that the morphology of *Plesiastrea* did not differ at an oceanic scale (Indian vs. Pacific Ocean, Global R = 0.054, $p = 0.6$; Fig. S5A). However, there were distinct differences in morphology based on whether samples were collected north or south of the Tropic of Capricorn (23°26′11.2″S). Character C17 (total number of septa) was found to be the character driving differences between tropical and temperate locations. Colonies collected in tropical locations consistently had between 23 and 42 ($\bar{x} = 30 \pm 5.4$) septa whereas colonies in temperate locations had 28 – 45 ($\bar{x} = 36 \pm 3.1$ SD). 87.5% tropical and 85.4% temperate samples were correctly identify based on the total amount of septa at $\leq$ 35.6 ($\bar{x}$ + SD) and $\geq$ 32.9 ($\bar{x}$ - SD) respectively. Character C3 (corallite density per 10 mm^2) was also a distinguishing character with tropical colonies being more widely spaced than temperate colonies (compare Fig. 2A–D with Fig. 2E–H). For further details of character variations see Table S16.

Significant differences were observed between 14 ecoregions nested within oceans (Global R = 0.37, $p = 0.001$; Fig. S5B). Furthermore, individual localities differed from one another ($n = 29$; Global R = 0.362, $p = 0.001$), clustering into two groups at the > 10.0 resemblance slice (Fig. S4) using hierarchical cluster analysis (Cophenetic correlation coefficient = 0.77; Fig. S5C). Statistical comparisons of samples collected in the six Western Australian ecoregions revealed significant differences in macro-morphology ($n = 6$, Global R = 0.223, $p = 0.001$). Morphology did not differ between the two temperate ecoregions (ER211, ER209, all pairwise ANOSIM $p > 0.05$) however samples collected from the tropical Kimberley, W.A. (ER141), and Exmouth to Broome (ER144) differed from Ningaloo Reef (ER145) and Shark Bay (ER210), see Table S16. This suggests morphological affinities may occur within *Plesiastrea* specimens either south or north of the Tropic of Capricorn.

3.6. Macro-morphological skeletal features: Congruence with molecular data and Plesiastrea type specimens

A consistent result of this study is that the samples split into two main clades falling north and south of the Tropic of Capricorn. With a small number of exceptions, there was congruence between all gene trees and with morphometric data. Characters C17 (total number of septa) and C3 (corallite density per 10 mm^2) were the key distinguishing characters driving the significant difference between tropical and temperate clades ($n = 2$; Global R = 0.322, p = 0.001; Fig. 7).

Univariate tests found that all morphological characters, except for C2 (type of budding) and C14 (number of primary septa; S_1), were significantly different between tropical and temperate clades (Table S17 and S18), including the characters identified by SIMPER to be distinguishing between clades (C3: $F_{1,78} = 4.108$, $P = 0.046$; C17: χ^2 (1) = 22.466, $P = <0.001$). However, these characters were not useful for distinguishing between the tropical and temperate clades (i.e. as a taxonomic key) because of high variation and overlap.

Measurements for the two key distinguishing characters (C17, C3) were made on images of the type specimens of species that are currently synonymised with *Plesiastrea versipora* and visualised in multivariate space. The MDS visualisation showed type specimens of *F. ingolfi; O. gravieri*; *P. peroni* fell within the ordination space of the tropical clade and type specimens of *P. urvillii*; *P. quatrefagiana*; *P. versipora* fell within the temperate clade (Fig. 8). From these combined results, it is inferred that *Plesiastrea versipora* belongs to the temperate clade and the tropical members may be either *F. ingolfi*, *O. gravieri* or *P. peroni*. For further nomenclatural discussion, see section *4. Systematic Account.*

3.7. Micro-morphological, micro-structural skeletal features: Congruence with molecular data

As a final test of the congruence of morphological and molecular data, and our principal finding that *Plesiastrea* samples belong to two main clades (tropical and temperate), micro-morphological and micro-structural features were examined with SEM and Micro-CT. From this work, one of the most distinct differences between representatives of both tropical and temperate groups is the extent of inter-corallite contact (Fig. 9). Representatives of the tropical clade typically develop plocoid

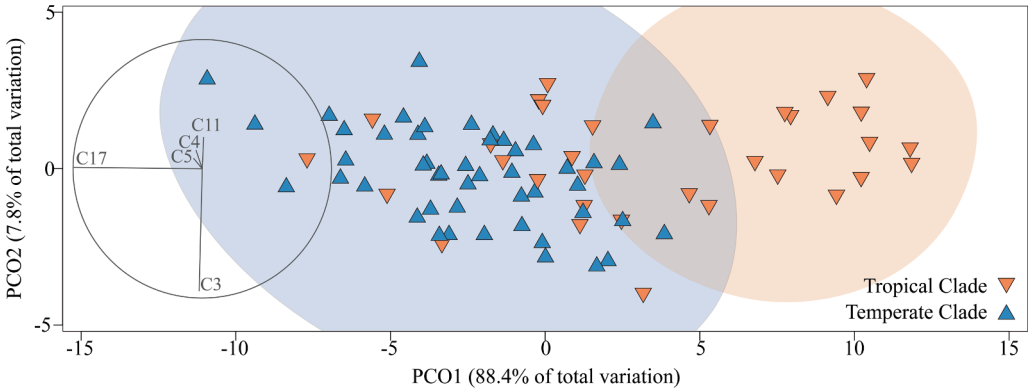

Fig. 7. PCoA based on Euclidean Distance similarity matrix of the morphological characters derived from skeletal sample morphometrics ($n = 80$), with samples coded by tropical (orange▼, $n = 32$) or temperate clade identity (blue▲, $n = 48$) based on the phylogenetic analysis of concatenated mitochondrial markers COI and COIII–COII. Blue and orange shading indicates Euclidean resemblance level $\geq$ 10 of similarity at a Cophenetic correlation of 0.77; Fig. S4.

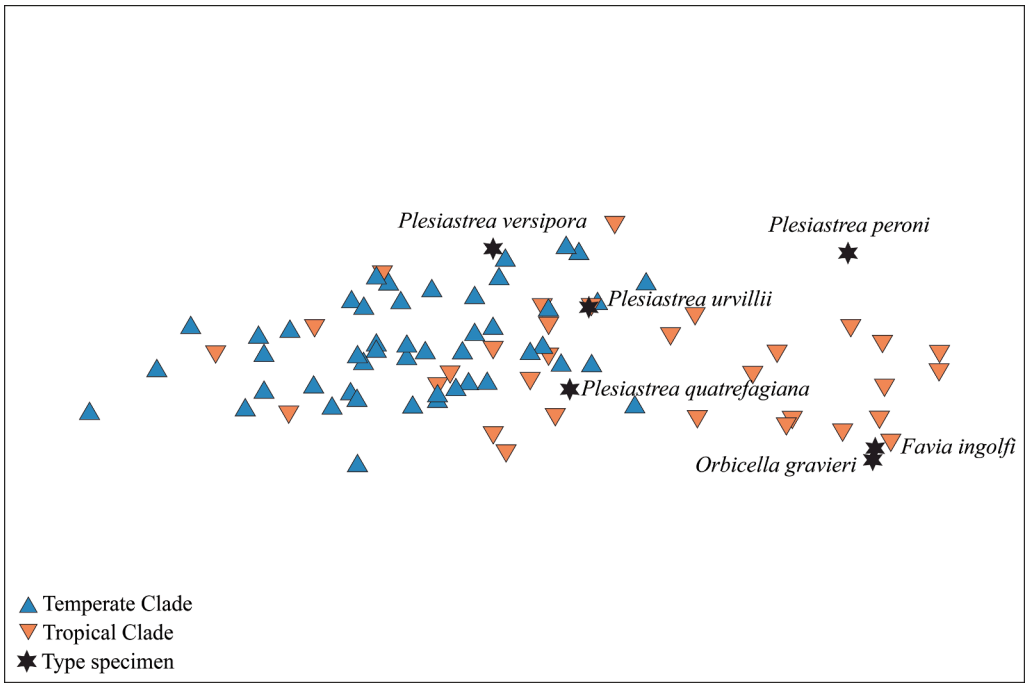

Fig. 8. MDS ordination of specimens based on key distinguishing characters (corallite density [C3] and the total number of septa [C17]; SIMPER). Samples coded by tropical (orange▼, $n = 32$) and temperate clades (blue▲, $n = 48$) based on the phylogenetic analysis of concatenated mitochondrial markers COI; and COIII–COII. Included type specimens were *Favia ingolfi* (type locality Tahiti, French Polynesia); *Orbicella gravieri* (type locality Djibouti, French Somaliland); *Plesiastrea peroni* (type locality Australia); *Plesiastrea quatrefagiana* MNHN IK-2010–476 (type locality unknown); *Plesiastrea urvillii* MNHN IK-2010–691 (type locality Albany, Western Australia); and *Plesiastrea versipora* MNHN IK-2012–10624 (type locality Hamelin Bay, Western Australia) (indicated by stars). Stress = 0.01.

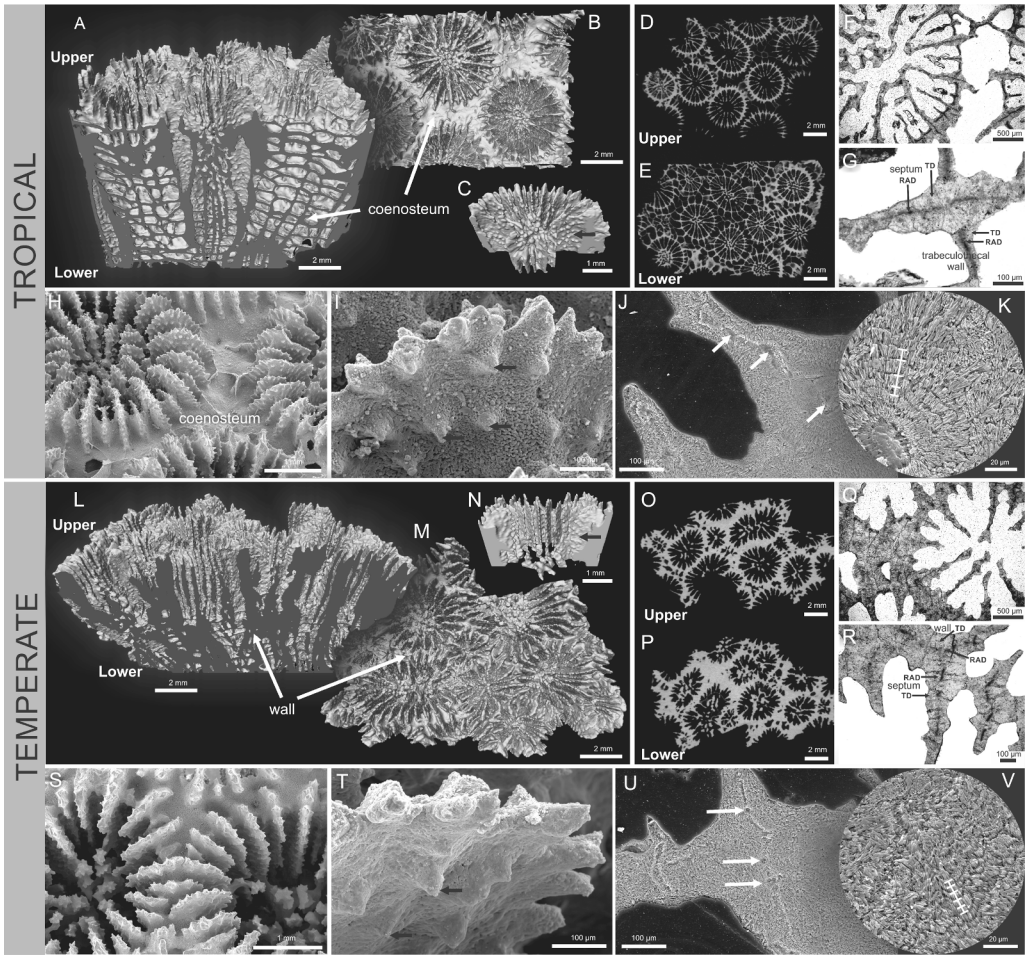

Fig. 9. Direct comparison of skeletal micro-morphological and some microstructural characters of representatives of tropical (A–K) and temperate (L–V) clades of *Plesiastrea versipora* (Lamarck, 1816). A–K. *Plesiastrea* PS 2222 (ZPAL H.25/134: section) Pilbara Shelf, Western Australia; L–V. *Plesiastrea* DI 2137 (ZPAL H.25/126: section) Kent Group, Tasmania, South-East Australia. A–E and L–P Micro-CT images (A, L virtual longitudinal and D, E, O, P transverse section); F, G, Q, R. Transmitted light optical microscopy images; H,I and S,T scanning electron microscopy images of colony (H, S) and septal (I, T) surfaces and transverse polished and slightly etched septa (J, K, U, V). Arrows in J and U point to RADs that correspond to granulations at distal septal edge. Segmented line in K and V indicate regular growth bands within thickening deposits (TDs).

colonies with corallites separated by dissepimental coenosteum (Fig. 9A, B, D, E, H). In contrast, representatives of the temperate clade typically develop cerioid colonies with often polygonal corallites closely packed with no or sparse coenosteum (Fig. 9L, M, O, P, S). The dissepimental coenosteum is porous in topical specimens vs. dense in temperate specimens, whereby the corallite walls are thickened or lacking and sparse coenosteum exists throughout skeletal astogeny (Fig. 9D, E vs. 9O, P, respectively). Individual corallites in colonies of the tropical clade typically show better-developed granulations on septal faces, whereas septal faces of corallites of temperate representatives are smoother (Fig. 9C, I and 9 N, T, respectively). There were no major differences in overall microstructural organization of the skeleton between two clades: septa sectioned transversely, are composed of a centrally located zone composed of rapid accretion deposits (RADs; see Stolarski, 2003) which form a discontinuous zone with individual segments ca. 100 μm in length (Fig. 9F, G, J and 9Q, R, U). Thickening deposits (TDs) which consists of bundles of fibres perpendicular to the septal face develop on both sides of RADs and show regular growth increments typical of zooxanthellate corals (Fig. 9K,V; see also Frankowiak et al., 2016; Stolarski, 2003). Segmental micro-structural organization of septa corresponds to lobate/denticulate septal margins (Fig. 9I, T). Additional transverse section of colonies belonging to tropical and temperate clade representatives across a phylogeographic range can be seen in Fig. S6, S7.

4. Systematic account

Based on the integrated molecular, macro- and micro-morphological results of this study we revise the nomenclature of the genus *Plesiastrea* to clarify that *Plesiastrea versipora* represents the mainly temperate members of the clade (south of the Tropic of Capricorn). We also elevate the name *Plesiastrea peroni* Milne Edwards & Haime, 1857 out of synonymy to distinguish the mainly tropical members (those occurring north of the Tropic of Capricorn). The rationale for elevating *P. peroni* is based on Rules 23.1 and 23.3.5 (Principal of Priority, which state the valid name of a taxon, is the oldest available name applied to it) of the International Commission on Zoological Nomenclature et al. (1999). For further information, see the remainder of the systematic account below and Supplementary file 2.

Order Scleractinia Bourne, 1900.

Family Plesiastreidae Dai and Horng, 2009 (p. 149).

Genus *Plesiastrea* Milne Edwards & Haime, 1848a (p. 494).

Type species. *Astrea versipora* Lamarck, 1816; =*Plesiastrea versipora* (Lamarck, 1816; Fig. 2C) designated by Milne Edwards and Haime (1848a: p. 494).

Species included. *Plesiastrea versipora* (Lamarck, 1816), *Plesiastrea peroni* Milne Edwards & Haime, 1857.

4.1. *Plesiastrea versipora (Lamarck, 1816)*

Plesiastrea versipora (Lamarck, 1816), (Fig. 2A–D, 9L–V, 10A–L, S6E–H, S7A,E,F, Supplementary file 3).

4.1.1. Synonymy

Astraea (Fissicella) versipora Lamarck, 1816 (Dana, 1846: pp. 233–234).

Astraea versipora Lamarck, 1816 (Chevalier, 1954: p. 167; Ehrenberg, 1834: p. 317; Veron et al., 1977: p. 149).

Astrea versipora Lamarck, 1816 (Budd et al., 2012: p. 470; Lamarck, 1816: p. 264).

Favia versipora Lamarck, 1816 (Chevalier, 1954: p. 170; Ehrenberg, 1834: p. 317; Matthai, 1914: p.103, 1924: pp. 16–17; Veron et al., 1977: p. 149).

Orbicella versipora Lamarck, 1816 (Chevalier, 1954: p. 167; Eguchi, 1938: p. 341; Gardiner, 1899: p. 753; Umbgrove, 1940: p. 276; Vaughan, 1918: pp. 85–86; Veron et al., 1977: p. 149).

Plesiastraea urvillei Milne Edwards & Haime, 1848b (Folkeson, 1919: p. 16; Milne Edwards and Haime, 1857: p. 490; Quelch, 1886: p. 104; Tenison-Woods, 1878: p. 323; Verrill, 1866: p. 36).

Plesiastrea urvillei Milne Edwards & Haime, 1848b (Sheppard, 1987: p. 30; Squires, 1966: p. 170; Veron et al., 1977: p. 149).

Plesiastrea urvillii Milne Edwards & Haime, 1848b (Milne Edwards and Haime, 1848b: pl. 9, 1849: pp. 117–118).

Plesiastrea quatrefagesana Milne Edwards & Haime, 1849 (Veron et al., 1977: p. 149).

Plesiastrea quatrefagiana Milne Edwards & Haime, 1849 (Milne Edwards and Haime, 1849: p. 119; Veron et al., 1977: p. 149).

Plesiastraea quatrefagesana Milne Edwards & Haime, 1849 (Milne Edwards and Haime, 1857: p. 491; Veron et al., 1977: p. 149).

Plesiastrea proximans Dennant, 1904 (Dennant, 1904: p. 9; Squires, 1966: p. 170; Veron et al., 1977: p. 150; Wijsman-Best, 1977: pp. 93–94).

For more detailed information see Supplementary file 2 and Table S3.

4.1.2. Type material examined

Plesiastrea versipora (Lamarck, 1816) (holotype MNHN IK-2012-10624; type locality Indian Ocean), *Plesiastrea urvillii* Milne Edwards & Haime, 1848b (holotype MNHN IK-2010-691; type locality Australia), *Plesiastrea quatrefagiana* Milne Edwards & Haime, 1849 (holotype MNHN IK-2010-476; type locality unknown), *Plesiastrea proximans* Dennant, 1904 (holotype examined from illustration; type locality Gulf of St Vincent, South Australia), see Supplementary file 2.

4.1.3. Other material examined

Australia: CO 2087 (WAM Z100500), CO 2089 (WAM Z100502), CO 2090 (WAM Z100503), Beagle Anchorage, Western Australia (32°06′18.0″S; 115°45′38.2″E), 14/04/2018 (coll. D. Juszkiewicz); DI 2137 (WAM Z100544), DI 2138 (WAM Z100545), DI 2139 (WAM Z100546), Deal Island, Tasmania (39°29′34.4″S; 147°20′31.6″E), 03/06/2018 (coll. G. Soler); FB 2103 (WAM Z100513), FB 2104 (WAM Z100514), FB 2105 (WAM Z100515), Flinders Bay,Western Australia (34°21′10.1″S; 115°10′07.3″E), 03/08/2018 (coll. D. Juszkiewicz); GB 2148 (WAM Z100555), GB 2149 (WAM Z100556), GB 2150 (WAM Z100557), Busselton, Western Australia (33°37′51.0″S; 115°20′19.3″E), 06/08/2018 (coll. D. Juszkiewicz); GN 2122 (WAM Z100531), GN 2123 (WAM Z100532), GN 2124 (WAM Z100533), GN 2125 (WAM Z100534), GN 2126 (WAM Z100535), GN 2127 (WAM Z100536), Gnaraloo Bay, Western Australia (23°46′05.5″S; 113°32′21.1″E), 20/05/2018 (coll. D. Juszkiewicz); HB 2142 (WAM Z100549), HB 2143 (WAM Z100550), HB 2144 (WAM Z100551), Hamelin Bay, Western Australia (34°13′04.4″S; 115°01′28.6″E), 05/08/2018 (coll. D. Juszkiewicz); HH 2109 (WAM Z100519), HH 2110 (WAM Z100520), HH 2111 (WAM Z100521), Hillarys, Western Australia (31°49′34.7″S; 115°44′13.9″E), 28/07/2018 (coll. D. Juszkiewicz); JS 2494 (WAM Z100594), JS 2495 (WAM Z100595), JS 2496 (WAM Z100596), JS 2497 (WAM Z100597), JS 2498 (WAM Z100598), JS 2499 (WAM Z100599), Joe Smith Island, Western Australia (28°40′55.2″S; 113°51′41.4″E), 28/10/2018 (coll. D. Juszkiewicz); KS 2173 (WAM Z100585), KS 2174 (WAM Z100586), KS 2175 (WAM Z100587), Kingston Reef, Western Australia (31°59′21.1″S; 115°34′35.8″E), 09/09/2018 (coll. D. Juszkiewicz); SI 2197 (WAM Z88634), Vancouver Peninsula, Western Australia (35°03′32.0″S; 117°56′20.0″E), 11/04/2018 (coll. A. Hosie); SI 2199 (WAM Z88636), Shelter Island, Western Australia (35°02′59.0″S; 117°41′37.0″E), 11/04/2018 (coll. A. Hosie); SI 2202 (WAM Z88644), Frenchman Bay, Western Australia (35°05′22.0″S; 117°56′59.0″E), 12/04/2018 (coll. A. Hosie); SM 2092 (WAM Z100505), SM 2093 (WAM Z100506), SM 2094 (WAM Z100507), Bathers Bay, Western Australia (32°03′24.8″S; 115°44′23.6″E), 14/04/2018 (coll. D. Juszkiewicz); SP 2128 (WAM Z100537), SP 2129 (WAM Z100538), SP 2130 (WAM Z100539), Steep Point, Western Australia (26°08′30.5″S; 113°10′06.2″E), 26/06/2018 (coll. D. Juszkiewicz); WE

2483 (WAM Z100591), WE 2484 (WAM Z100592), WE 2485 (WAM Z100593), Cape Vlamingh, Western Australia (32°01′09.5″S; 115°27′08.3″E), 16/10/2018 (coll. D. Juszkiewicz).

4.1.4. Description

Colonies vary from massive to flat encrusting with a range in colony sizes that are frequently lobed (Veron, 2000; Wijsman-Best, 1977). Budding is extra-tentacular, however intratentacular budding has been observed in a few specimens from larger developed corallites. The colony corallite structure exhibits a cerioid to sub-cerioid arrangement (Fig. 2A–D, 10C, G, K, Supplementary file 3 with no or sparse coenosteum. Corallites are 3.9–6.1 mm in diameter (on average 4.5 mm ± 0.4 SD) with a density of 5–11 corallites per 10 mm^2 (on average 8 per 10 mm^2 ± 0.4 SD). There can be 5–7 corallites adjacent to each individual corallite (average 6 ± 0.3 SD). They consist of a developed columella that is small and papillose with a true pali (Benzoni et al., 2011; Veron et al., 1977; Fig. 10D). Average total number of septa amongst corallites is 36 (±3.1 SD). The corallite has three cycles of septa (S_{1-3}) with a well-developed palar structure (Benzoni et al., 2011; Veron, 2002; Fig. 10D, H). In the S_1 (10–16 septa) and S_2 (3–10 septa) can be equal, or the S_2 can be sometimes shorter than S_1. S_3 (14–21 septa) can be observed to be ¼ of the length of S_1 or significantly reduced. S_1 always extends to the columella; S_2 only reaches the columella if it is as developed as the S1 (Benzoni et al., 2011). Septal faces are smooth (Fig. 9T). Living colony colours range from green (Fig. 10A) to brown (Fig. 10I) and blue-grey (Fig. 10E).

4.1.5. Molecular phylogeny

A monophyletic lineage (temperate clade) with high node support values in all phylogeny reconstructions is presented in this study (Figs. 4–6). This species is sister to the lineage *P. peroni*.

4.1.6. Habitat

Occurs in depths of 1 to 17 m though has been observed at depths >20 m (DJJ, pers. obs.). Thrives in most temperate reef environments, especially shaded locations such as overhangs and protected bays. It can be found on rocky foreshores protected from strong wave action (Veron et al., 1977). It can also occur in very muddy and turbid waters (Wijsman-Best, 1977). A high abundance can occur on artificially constructed reefs and limestone seawalls (DJJ, pers. obs.). It has also been observed to grow in other marginal habitats such as macroalgae and attached to rubble (DJJ, pers. obs.).

4.1.7. Distribution

Plesiastrea versipora is found only in Australia. On the west coast of Australia, it is distributed from Gnaraloo Bay (23°45′59.4″S 113°32′49.8″E) on the Ningaloo Reef and extends down to Cape Leeuwin (34°22′33.4″S 115°08′10.9″E) in the south-west of Australia. It is found along the Australian Southern Ocean coastline including north of Tasmania and into the Pacific Ocean as far north as Sydney (33°48′00.4″S, 151°16′30.8″E).

4.1.8. Remarks

The type locality of *P. versipora* (Lamarck, 1816) is Hamelin Bay, Western Australia. This was determined after tracing the collections made on the Baudin Expedition and the type redescription by Milne Edwards and Haime (1849: p. 119; for more information see Supplementary file 2). While the original description of *P. versipora* is rudimentary, results of this study in tandem with results of prior studies (Benzoni et al., 2011; Veron et al., 1977; Veron, 2000) have enabled

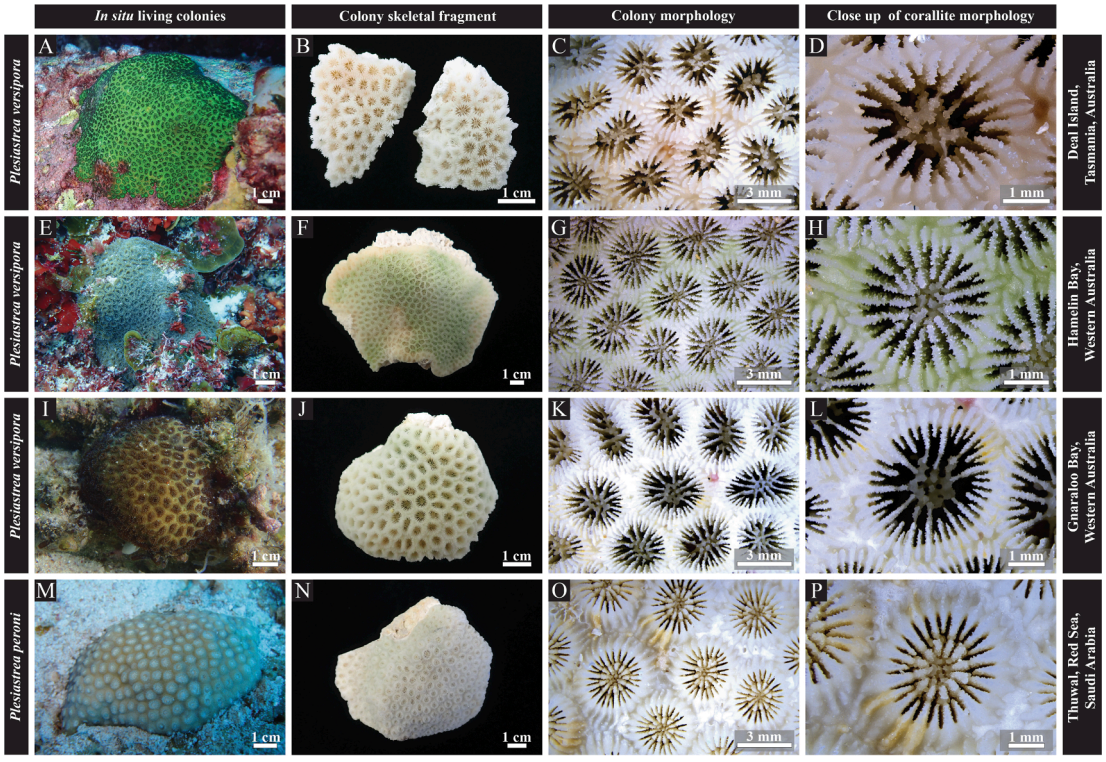

Fig. 10. In situ living and skeletal colonies, including corallite morphology of specimens of *Plesiastrea*. (A–D) *Plesiastrea versipora* DI 2137 at Deal Island, Tasmania, Australia; (A) Encrusting colony with a typical green colouration; (D) Showing 31 septa with a colony average of $\bar{x} = 32$. (E–H) *Plesiastrea versipora* HB 2144 at Hamelin Bay, Western Australia; (E) encrusting colony with a pale green colouration; (H) showing 35 septa with a colony average of $\bar{x} = 35$. (I–L) *Plesiastrea versipora* GN 2124 at Gnaraloo, Western Australia at the intermediate zone distinguishing the two *Plesiastrea* species in this study; (I) massive colony with typical brown colouration; (L) showing 40 septa with a colony average of $\bar{x} = 38$. (M–P) *Plesiastrea peroni* TH 2493 at Thuwal, Red Sea, Saudi Arabia; (M) massive colony with pale brown colouration; (P) Showing 24 septa with a colony average of $\bar{x} = 23$. (C, G, K) colonies are displaying sub-cerioid corallite structure with a density of 9 corallites ± 1 per 10 mm^2; (O) colony displaying plocoid corallite structure with a corallite density of 7 per 10 mm^2.

greater insight into the morphological features that distinguish this species from sister taxa and confirm that *P. versipora*, based on current records, is restricted to temperate latitudes south of 23°26′11.2″S.

The type locality of *Plesiastrea quatrefagiana* Milne Edwards & Haime, 1849 is unknown and assignment as a synonym to either the tropical or temperate localities is useful. Based upon morphological characters (sub-cerioid corallite arrangement and total amount of septa), we assign *P. quatrefagiana* to a temperate locality, thus concluding it is a junior synonym of *P. versipora* (see Table S3 and Supplementary file 2).

4.2. *Plesiastrea peroni* Milne Edwards & Haime, 1857

Plesiastrea peroni Milne Edwards & Haime 1857, (Fig. 2E–H, 9A–K, 10M–P, S6A–D, S7B–D, Supplementary file 4).

4.2.1. Synonymy

Plesiastraea peroni Milne Edwards & Haime, 1857 (Milne Edwards and Haime, 1857: p. 492).

Plesiastrea peronii Milne Edwards & Haime, 1857 (Tenison-Woods, 1878: p. 324).

Orbicella annuligera Vaughan, 1907 (Gravier, 1911: p. 57; Vaughan, 1907: pp. 252–253, 1918: pp. 85–86; Wijsman-Best, 1977, p. 93).

Orbicella gravieri Vaughan, 1918 (Vaughan, 1918: pp. 85–86; Veron et al., 1977: p. 150; Wijsman-Best, 1977: p. 93). Not *Astrea annuligera* Milne Edwards & Haime, 1849 (see Supplementary file 2).

Favia ingolfi Crossland, 1931 (Crossland, 1931: pp. 386–387; Veron et al., 1977: p. 150; Wijsman-Best, 1977: p. 93).

For more detailed information see Table S3 and Supplementary file 2.

4.2.2. Type material examined

Plesiastrea peroni Milne Edwards & Haime, 1857 (holotype examined from illustrations; type locality Australia), *Orbicella gravieri* Vaughan, 1918 (holotype; type locality Djibouti, French Somaliland), *Favia ingolfi* Crossland, 1931 (holotype; type locality Pa'ea Lagoon, Tahiti, French Polynesia), see Supplementary file 2.

4.2.3. Other material examined

Australia: AR 2097 (WAM Z100510), AR 2098 (WAM Z100511), AR 2100 (WAM Z100512), Arlington Reef, Queensland (16°41′11.8″S; 146°03′50.8″E), 01/05/2018 (coll. Monsoon Aquatics); BU 2232 (WAM Z66116), Mavis Reef, Western Australia (15°30′18.7″S; 123°36′29.7″E), 21/10/2011 (coll. Z. Richards); BU 2233 (WAM Z66150), King and Conway Islands, Western Australia (15°52′17.9″S; 123°39′48.5″E), 24/10/2018 (coll. Z. Richards); DA 2236, DA 2237, DA 2238, Dampier Archipelago (20°27′35″S; 116°43′38″E), 27/03/2017 (coll. Z. Richards); FI 2227 (WAM Z42202), FI 2228 (WAM Z66047), Long Reef, Western Australia (13°51′24.1″S; 125°49′29.3″E), 18/09/2016 (coll. Z. Richards); FI 2229 (WAM Z66080), Champagny Islands, Western Australia (15°19′56.7″S; 124°14′09.5″E), 15/10/2011 (coll. Z. Richards); FI 2230 (WAM Z66235), De Freycinet Island, Western Australia (14°59′19.2″S; 124°31′58.9″E), 13/10/2011 (coll. Z. Richards); FI 2231 (WAM Z66242), Hedley Island, Western Australia (14°56′04.5″S; 124°39′39.6″E), 14/10/2011 (coll. Z. Richards); LH 2179, Gower's Pinnacle, New South Wales (31°27′16.0″S; 159°03′40.2″E), 12/03/2018 (coll. A. Baird); LH 2180, Erscott's Hole, New South Wales (31°32′44.2″S; 159°03′35.0″E), 13/03/2018 (coll. A. Baird); LH 2181, Hogan's Hook, New South Wales (31°32′12.3″S; 159°09′04.3″E), 15/03/2018 (coll. A. Baird); MS 2154 (WAM Z100561), MS 2156 (WAM Z100563), MS 2160 (WAM Z100567), Monck Head, Western Australia (23°09′25.2″S; 113°45′58.0″E), 26/08/2018 (coll. D. Juszkiewicz); PS 2222 (WAM Z981010), Poivre Reef, Western Australia (20°58′52.0″S; 115°16′11.3″E), 17/06/2013 (coll. E. Morello, G. Fry, M. Miller, D. Thomson, and D. Bearham); PS 2224 (WAM Z98093), Rosily Islands, Western Australia (21°15′52.3″S; 115°01′42.4″E), 16/06/2013 (coll. E. Morello, G. Fry, M. Miller, D. Thomson, and D. Bearham); PS 2225 (WAM Z98119), McLennan Bank, Western Australia (20°45′51.0″S; 116°05′22.0″E), 20/06/2013 (coll. E. Morello, G. Fry, M. Miller, D. Thomson, and D. Bearham); SH 2188, SH 2189, SH 2192, Fairlight Pool, New South Wales (33°48′02.9″S; 151°16′31.8″E), 01/09/2017 (coll. A. Baird); VH 2177 (WAM Z100526), VH 2118 (WAM Z100527), VH 2119 (WAM Z100528), Lighthouse Bay Sanctuary, Western Australia (21°47′06.0″S; 114°09′54.0″E), 18/05/2018 (coll. D. Juszkiewicz); VI 2234 (WAM Z66431), Vulcan Shoal, Western Australia (12°47′57.5″S; 124°16′00.1″E), 06/10/2013 (coll. Z. Richards); **Madagascar**: NS 2216 (UNIMIB-MD272), Nosy Sakatia (13°19′01.6″S; 48°08′49.9″E), 18/06/2010 (coll. F. Benzoni); **Maldives**: FA 2203 (UNIMIB-MA0318030), FA 2204 (UNIMIB-MA0318055), FA2210 (UNIMIB-MA0318105), Magoodhoo Island (3°04′37″N; 72°58′23″E), 17/03/2018 (coll. D. Maggioni); **Papua New Guinea**: MI 2217 (UNIMIB-PFB245), Wongat Island (5°08′12.8″S; 145°49′11.8″E), 17/11/2012 (coll. F. Benzoni); **Philippines**: TB 137, Batangas, Talim Point, 29/08/2009 (coll. D. Huang); **Saudi Arabia**: BI 2493, Jazirat Burqan (27°54′21.2″N; 35°03′33.1″E), 28/09/2013 (coll. F. Benzoni); TH 2218 (KAUST-SA0569), Palace Reef, Thuwal (22°18′19.6″N; 38°57′44.0″E), 28/04/2013 (coll. R. Arrigoni); TH 2219 (KAUST-SA0586), Abu Madafi Reef, Thuwal (22°03′43.5″N; 38°45′49.3″E), 29/04/2013 (coll. R. Arrigoni); TH 2220 (KAUST-SA3628), Shi'b Nazar, Thuwal (22°19′51.6″N; 38°51′46.8″E), 15/04/2018 (coll. R Arrigoni); **Singapore**: HD 127 (HQ203307), Pulau Jong, 18/09/2009 (coll. D. Huang); **Yemen**: SO 2215 (UNIMIB SO115), Socotra Island (12°28′35.3″N 53°52′24.8″E), 17/03/2010 (coll. F. Benzoni and M. Pichon); YE 2213 (UNIMIB-MU146), Al Mukallah (12°55′46.9″N; 48°10′15.6″E), 19/03/2007 (coll. F. Benzoni and M. Pichon); YE 2214 (UNIMIB-BA123), Bir Ali (14°00′44.6″N; 48°20′55.0″E), 23/11/2208 (coll. F. Benzoni and S. Montano).

4.2.4. Description

Colonies vary from massive to flat encrusting, with a range in colony sizes that are frequently lobed. Budding is extratentacular, and the colony corallite structure exhibits a plocoid arrangement (Fig. 2E–H) separated by dissepimental coenosteum. Corallites are 3.4–5.3 mm in diameter ($\bar{x} = 4.2$ mm ± 0.4SD) with a density of 5–11 corallites per 10 mm^2 (on average 7 ± 1.5 SD). They consist of a well-developed paliform crown (Fig. 2F, H, 10P) composed of a true pali that is papillose (Fig. 10P). Average total number of septa amongst corallites is 30 ± 5.4 SD. Septa are exert with developed granulation on their faces (Fig. 9H, I). In the S_1 (10–17 septa) and S_2 (2–8 septa) can be equal in length, or the S_2 can be sometimes shorter than S_1. S_3 (9–20 septa) can be observed to be ¼ of the length of S_1 or significantly reduced. S_1 always extends to the columella; S_2 only reaches the columella if it is as developed as the S_1. Living colony colours range from brown to pale yellows and blue-greys with cream derivatives (Fig. 10M).

4.2.5. Molecular phylogeny

A monophyletic lineage (tropical clade) with high node support values in all phylogeny reconstructions is presented in this study (Figs. 4–6). This species is sister to the lineage *P. verispora*.

4.2.6. Habitat

Occurs in depths of 0 to 50 m. Thrives in most reef environments and can be found on lower reef slopes where the current is strong. It has also been observed to grow in other marginal habitats such as macroalgae and mangrove ecosystems (DJJ and ZTR, pers. obs.). It can also occur in the pools of intertidal reef flats (DJJ, pers. obs.).

4.2.7. Distribution

Plesiastrea peroni is distributed from the Red Sea and East Africa as far as the Madagascan coastline to the Ryukyu Archipelago southwest of Japan and across to Tuamotu Archipelago in the Pacific Ocean. In

Australia, it occupies the northern boundaries of continental Australia with Cocos-Keeling and Christmas Islands, stretching from Coral Bay (23°08′32.0″S 113°46′08.2″E), Western Australia, through the north of Australia down to the coast of Queensland and Great Barrier Reef. It is also found at Lord Howe Island (31°33′19.1″S 159°04′55.7″E), eastern Australia.

4.2.8. Remarks

The type locality of *P. peroni* is Australia (Milne Edwards and Haime, 1857: p. 492) however the exact location cannot be determined. Based on morphological features of the type specimen, we assume that *P. peroni* was first collected from a northern Australian locality because of the small number of septa ($\bar{x} = 25$, ± 0.66 SD), plocoid corallite arrangement, and presence of coenosteum between corallites. In accordance with Article Rule 23.1 and 23.3.5. (International Commission on Zoological Nomenclature et al., 1999) we formally elevate *Plesiastrea peroni* out of synonymy because it is the oldest available name relating to taxa that have morphological features matching those occurring in tropical locations (older than *Favia ingolfi* Crossland, 1931; *Orbicella gravieri* Vaughan 1918). *Plesiastrea peroni* is genetically distinct from *P. versipora* based on ITS and mitochondrial genes. Additionally, *P. peroni* shares the same mitochondrial genome architecture as *P. versipora* (Fig. 3). *Plesiastrea peroni* can also be distinguished from *P. versipora* by the significantly smaller number of septa (~30 v 36). *Plesiastrea urvillii* (=*P. versipora* Lamarck, 1816) Milne Edwards & Haime, 1848b (type locality Albany, Western Australia) was initially distinguished from *P. peroni* from the number of septa in the calices (Milne Edwards and Haime, 1857; Squires, 1966) which indicated prior evidence of morphological differentiation between types. *Plesiastrea peroni* has a plocoid corallite arrangement separated by a porous dissepimental coenosteum, whereas *P. versipora* has a sub-ceroid corallite arrangement with minimal dense coenosteum. *Plesiastrea peroni* also displays a granulated septal face whereas *P. versipora* is smoother dense coenosteum. *Plesiastrea peroni* also displays a granulated septal face whereas *P. versipora* is smoother. *Favia ingolfi* Crossland, 1931 and *Orbicella gravieri* Vaughan 1918 are here considered junior synonyms of *P. peroni* because of their tropical type localities (see Table S3). Additionally, *Orbicella annuligera* Vaughan, 1907, is a senior synonym of *O. gravieri* described from the same type specimen from Djibouti, French Somaliland, therefore also a junior synonym of *P. peroni*.

As the holotype of *P. peroni* has been lost, we designate specimen WAM Z981010 (this study *Plesiastrea* PS 2222) as a neotype (Fig. 9A-K, S6B, S8A-C, Supplementary file 4. Specimen WAM Z98101 was collected at Poivre Reef, Pilbara Shelf, Western Australia (20°58′52.0″S 115°16′11.3″E) by collectors E. Morello, G. Fry, M. Miller, D. Thomson, and D. Bearham, on the 17 June 2013, from a depth of 14.3 m. A mitochondrial genome (MT849379) and nuclear ITS (MT946959) sequences have been uploaded to the NCBI GenBank database from this specimen. Specimens WAM Z98093 (this study *Plesiastrea* PS 2224) and WAM Z98119 (*Plesiastrea* PS 2225) are considered additional representatives of *P. peroni* from the Pilbara Shelf, Western Australia (Fig. S8D-I).

5. Discussion

This study explored the phylogeographic structure within *Plesiastrea*, using macro- and micro-morphology and molecular phylogenetics. We provided robust evidence that two reciprocally monophyletic lineages within the genus *Plesiastrea* relate to two distinct species. Multiple lines of evidence substantiate that the phylogeographic structure aligns with a tropical and temperate split around the Tropic of Capricorn (23°26′11.2″S) with a small region of overlap on the east Australian coast (Lord Howe Island). We formally consider that the temperate lineage corresponds to *Plesiastrea versipora* described by Lamarck (1816), and the tropical lineage corresponds to another distinct species, which we designate here as *P. peroni* and subsequently elevate out of synonymy.

5.1. Integrated taxonomy and the characterisation of cryptic species

This study adds to a growing number of scleractinian studies that have detected unexpected patterns of structure and led to a re-evaluation of formally accepted taxonomic entities and formal descriptions of cryptic species (Arrigoni et al., 2017, 2019; Marti-Puig et al., 2014; Mitsuki et al., 2021; Pinzón and Weil, 2011; Stefani et al., 2011). In some of these cases, including the *Plesiastrea* case presented here, debates exist about whether species can be defined as cryptic because the definition of 'cryptic' is controversial (de León and Nadler, 2010; Korshunova et al., 2019; Struck et al., 2018). For example, some consider 'cryptic species' as those classified under one species name due to superficial morphological similarity and erroneous taxonomic conclusions (Bickford et al., 2007; Fišer et al., 2018). Hence, 'cryptic species' have been described as short term taxonomic problems waiting to be resolved (Heethoff, 2018). Jörger and Schrödl (2013) argue that 'fully cryptic species' have no morphological variation between species. Hence, even when all current technology and knowledge are applied, the macro- and micro-morphological characters for an organism (or species complex) overlap (Korshunova et al., 2019; Lajus et al., 2015). In the case of corals, it is increasingly common to find that previously overlooked discrete morphological characters can distinguish between species when micro-morphology is examined (Arrigoni et al., 2019, 2020; Knowlton, 2000; Mitsuki et al., 2021).

Regardless of the semantics, the ability to detect cryptic, or pseudocryptic species is a function of sampling intensity, learning by experience, methodological strength and biogeographic coverage. In this study, an integrated approach using molecular data coupled with macro- and micro-morphological data applied to samples collected from a vast geographic extent has produced a robust result: the existence of two species of *Plesiastrea* with superficially similar morphology that can be distinguished based on two micro-morphological characters and genetic data. Based on these findings, we determine *Plesiastrea peroni* provided a fresh example of a cryptic species, and that the genus *Plesiastrea* is not monotypic.

5.2. Plesiastrea diversity and biogeography

Phylogeographic analyses revealed two distinct lineages of *Plesiastrea*, which occur either north or south of the Tropic of Capricorn. This tropical/temperate clade split was clear for the vast majority of sampling locations, however there were two notable exceptions. Specimens from Lord Howe Island and Gnaraloo Bay occurred in clades opposite to their position relative to the Tropic of Capricorn. *Plesiastrea* specimens collected from Lord Howe Island (located at 31°33′S), were recovered in the tropical clade for both the ITS and mitochondrial sequences. Lord Howe Island lies in the path of the East Australian Current (EAC), a north-to-south flow of warm tropical waters along Australia's east coast (Harriott and Banks, 2002; Ridgway and Godfrey, 1997; Rodriguez-Lanetty and Hoegh-Guldberg, 2002), and is considered to be a region of biogeographic importance because it occurs in a region of overlap where a diverse assemblage of tropical and temperate coral and fish species live side by side (Cameron and Harrison, 2016; Dalton and Roff, 2013; De Vantier and Deacon, 1990; Harriott et al., 1995; Keith et al., 2015; Zann, 2000).

On Australia's west coast, *Plesiastrea* specimens collected from Gnaraloo (23°45′S) also showed discrepancy in clade delineation; ITS reconstruction placed specimens within the tropical clade, however, this is contradicted with the mitogenomic reconstruction, which placed them within the temperate clade. Oceanic currents are also likely responsible for creating this anomaly – the southward flowing Leeuwin Current takes warm waters offshore, whereas the Ningaloo Current draws colder water from the south along the near-coastal regions and is responsible for cooler waters within the inner reef (Feng et al., 2009;

Taylor and Pearce, 1999). Thus, Ningaloo Reef is another zone flushed with waters of mixed origins, meaning both tropical and temperate species inhabit this region (Przeslawski et al., 2013; Schönberg and Fromont, 2012; van Keulen and Langdon, 2011). The action of currents in the vicinity of Ningaloo Reef is likely to explain the northerly occurrence of temperate clade representatives at Gnaraloo, and the discordance between samples collected at Maud Sanctuary (only 70 km away). Altogether, this data concurs with that reported for other groups (Baird et al., 2017; Harriott et al., 1995; Schönberg and Fromont, 2012) and suggests that the region between ~ 29-31°S on both the east and west coasts of Australia is functioning as a transition zone creating a significant biogeographic divide.

Non-congruence between mitochondrial and nuclear reconstructions in corals is not surprising given the lack of intragenomic variation in the ribosomal nuclear DNA, and slow evolving mitochondrial genes in Scleractinia (Hellberg, 2006; Kitahara et al., 2016; Shearer et al., 2002). Genetic differentiation between tropical and temperate populations on the west coast of Australia has also been observed in the coral *Turbinaria reniformis* (Evans et al., 2021), and in *Pocillopora damicornis* (Thomas et al., 2017). The lack of reciprocal monophyly (between mitochondrial and nuclear data) in the intermediary temperate/tropical transition zone (e.g. Gnaraloo, Western Australia) requires further study to explore if this is the result of incomplete lineage sorting, hybrisisation or refugia populations all previously observed in Scleracitina (Cunha et al., 2019; Forsman et al., 2010; Nakabayashi et al., 2019; van Oppen et al., 2004). More thorough sampling is required throughout this dynamic region using integrated phylogenetic and population genetic approaches. Further research into the evolutionary relationships and connectivity patterns of corals living in transition zones is important, given the species composition of these regions are rapidly changing under global warming.

5.3. Additional evidence of phylogeographic structure in Plesiastrea

The hypothesis that there may be more than one lineage of *Plesiastrea* was first proposed by Squires (1966) and later by Veron et al. (1977). Veron et al. (1977) mention that *P. versipora* colonies from the Great Barrier Reef belonged to a single species but purported that the southern forms were a separate species, *P. urvillii* (including its synonym *P. proximans* Dennant, 1904) due to wide morphological variation (Squires, 1966; Veron et al., 1977). Despite this, Veron et al. (1977) synonymised *P. urvillii* with *P. versipora*. Further evidence of the possibility of multiple lineages arose after the finding that two distinct genotypes of Symbiodiniaceae exist on the East Coast of Australia. The genus *Breviolum* was present in high latitude temperate *P. versipora* populations (Gulf of St Vincent, South Australia; Batemans Bay and Port Jackson, New South Wales), and the genus *Cladocopium* was detected in tropical and subtropical waters (Moreton Bay and Orpheus Island, Queensland) (Rodriguez-Lanetty et al., 2001; Rodriguez-Lanetty and Hoegh-Guldberg, 2002). For the most part, Symbiodiniaceae genera are associated with specific host genera or species (Keshavmurthy et al., 2017; LaJeunesse et al., 2004, 2018), and future investigation of symbiont type may provide further support for a temperate/tropical split.

Although reproductive biology was not examined, the deep divergence suggests different spawning times are likely. It has been observed that spawning events in temperate localities such as Sydney Harbour, Australia occur in January and February (Madsen et al., 2014) like Rottnest Island, Western Australia (Dee, 2016; Gilmour et al., 2015). Interestingly, *P. versipora* populations did not spawn with other subtropical corals on the central east coast of Australia during summer (Fellegara et al., 2013). Further investigation of reproductive patterns (including hybridisation) is required, especially at Gnaraloo Bay, Western Australia (Fig. 10. I–L) where contrasting clade groupings were recovered.

5.4. The value of types in resolving complex taxonomic problems

This study has provided a valuable case study demonstrating the importance of type material for making robust taxonomic decisions. While finding of cryptic diversity within the extensive range of *Plesiastrea* is not unusual, in many prior studies, putatively new cryptic species have been left undescribed due to taxonomic uncertainty (e.g. Ladner and Palumbi, 2012; Suzuki et al., 2016; Taninaka et al., 2021; Underwood et al., 2020; Warner et al., 2015; Wepfer et al., 2020). Taxonomic uncertainty can relate to insufficient spatial and statistical sampling but often broadly relate to inadequately described, missing, lost or misplaced type specimens that prevent robust taxonomic interpretations.

In this study, we were presented the challenge of not knowing the type locality of *Plesiastrea versipora* and by the fact that 18 other species were placed in its synonymy. To resolve this problem, we referred to the original descriptions and holotypes of the seven junior synonyms currently synonymised with *Plesiastrea versipora* (Hoeksema and Cairns, 2022). Details about the type locality of *P. versipora* are vague and were reported in the taxonomic literature as Indian Ocean (*Habite l'Océan indien*; Lamarck, 1816). Further exploration of historic taxonomic records revealed that the holotype (Fig. 2C; MNHN IK-2012-10624) was collected during the Baudin expedition (See Supplementary file 2). Later, taxonomic descriptions of *P. versipora* by Milne Edwards and Haime (1849) provided a reference to the collectors, François. A. Péron and Charles. A. Lesueur. Both men were part of the crew on the Géographe during the Baudin Expedition (Baudin et al., 1807; Jones, 2017; Péron et al., 2006). Unlike Péron, Lesueur only joined the Baudin Expedition (Baudin et al., 1807; Chinard, 1949; Hansen, 2013; Péron et al., 2006), confirming that the *P. versipora* holotype was collected during the Baudin Expedition.

During the Baudin Expedition marine specimens were collected at Shark Bay, Western Australia (W.A.) and north of Cape Naturaliste, W. A., where sampling took place using a dredge designed for coral (Baudin et al., 1807; Christensen, 2008; Jones, 2017; Péron et al., 2006). At Shark Bay, W.A., only specimens of Mollusca, Asteroidea and one branched *Madrepora* (*Pocillopora*) coral were collected (Baudin et al., 1807; Christensen, 2008; Jones, 2017; Péron et al., 2006) and well documented in illustrations by Lesueur housed in the National Museum of Natural History in Paris (Jones, 2017). Illustrations of specimens collected during dredging at Cape Naturaliste, W.A., are unaccounted for despite personal diary entries from Péron, that he and Lesueur spent countless hours drawing specimens collected from dredging north of Cape Leeuwin around Hamelin Bay, W.A. (Baudin et al., 1807; Péron et al., 2006; see Supplementary file 2). With no provenance information, the exact collection location of *Astrea versipora* Lamarck, 1816 *(Plesiastrea versipora*) cannot be confirmed unless the drawings of Lesueur are located. Hence based on the available information, we hereby restrict the type locality of *Plesiastrea versipora* to Hamelin Bay, W.A. This new information also suggests that the *P. versipora* specimen was collected in 1801 (Baudin et al., 1807; Péron et al., 2006).

Examination of the holotype of *P. peroni* (Milne Edwards and Haime, 1857) revealed that it was morphologically similar to the tropical samples in this study (i.e. total amount of septa and corallite density). The exact type locality of *P. peroni* is not known however it was collected from Australia (*Habite l'Australie*; Milne Edwards and Haime, 1857). Based on the morphological similarity to the tropical specimens, we infer the tropical clade is *Plesiastrea peroni* (Fig. 4E) based on Article 23 Principle of Priority (International Commission on Zoological Nomenclature et al., 1999) because all other junior synonyms of *P. versipora* relate to specimens collected in temperate waters. See Table S1 and Supplementary file 2 for further discussion of nomenclatural decision-making.

5.5. Promising prospects for the use of newly developed mitochondrial markers and the challenges of ITS

Exploring phylogenetic patterns within scleractinians can present challenges because of slow evolutionary rates within their mitochondrial genes (Hellberg, 2006; Huang et al., 2008; Shearer and Coffroth, 2008) and elevated intraspecific and intraindividual variation in the nuclear ITS DNA region (Chen et al., 2004; van Oppen et al., 2002; Vollmer and Palumbi, 2004). Studies using the first section of the COI barcode have discouraged its use for scleractinian species delineation, finding it uninformative in resolving phylogenies (Benzoni et al., 2011; Fukami et al., 2007; Huang et al., 2011; Shearer et al., 2002). However, our study demonstrates the potential of the second upper end of the COI to function as a more informative barcode region to aid species delineation in *Plesiastrea,* and we recommend this part of the gene to be further explored in other genera.

The challenges of using nuclear ITS barcodes for species delineation has been well documented in previous scleractinian coral studies (Alidoost Salimi et al., 2021; Benzoni et al., 2011; Huang et al., 2014). In this study, the ITS region provides moderate support for a tropical/temperate *Plesiastrea* split (albeit with mitochondrial and nuclear discordance within Indo-Pacific localities of Lord Howe Island, Gnaraloo and Madagascar). Sanger-based methods for ITS barcode sequencing can be unfavourable because ITS sequence variation in an individual may differ as much as 30% depending on the coral species (Lam and Morton, 2003; Márquez et al., 2003; Odorico and Miller, 1997; van Oppen et al., 2001; Vollmer and Palumbi, 2004) and the results will only produce one sequence copy per individual. Nevertheless, the traditional use of ITS1 and ITS2 barcodes for phylogeographic studies in scleractinians have been proven to be informative (van Oppen et al., 2002;Yiu et al., 2021), and methods combining nuclear and mitochondrial loci have been adequate for defining coral species boundaries (Arrigoni et al., 2014, 2016, 2021; Kitahara et al., 2010; Mitsuki et al., 2021).

5.6. Alternative hypotheses for biogeographic differences in morphology

The split between tropical/temperate clades is partly supported by the results of macro- and micro-morphological skeletal analyses. Scleractinia evolved 400Mya and in that time the macro-morphological characters that make up colonial growth forms are homeomorphic in nature and have remained relatively constant between genera (Drake et al., 2020; Stolarski, 2003; Stolarski et al., 2011). Previous integrative approaches of coral genera have indicated that morphology can in some cases, be uninformative when compared to molecular phylogenies (Arrigoni et al., 2016; Kitahara et al., 2016; Terraneo et al., 2016). Nevertheless, our study demonstrated two morphological characters had sufficient power to support the temperate/tropical clade split. Representatives of the tropical clade typically develop plocoid colonies with corallites separated by dissepimental coenosteum, whereas representatives of the temperate clade typically develop cerioid colonies with no or sparse coenosteum. Considering that dissepiments are the skeletal elements growing rapidly (Brahmi et al., 2012), more extensive development of these structures in tropical clade representatives may point to their faster growth in comparison to temperate clade forms. Such an interpretation is consistent with generally thicker walls in temperate forms, whose slower vertical extension would be compensated by skeletal thickening (thus also masking of sharp granulations on septal faces); this hypothesis needs to be supported by in-situ growth rate measurements. Mixed tropical-temperate morphological features of some representatives of the tropical clade may suggest that separation of biomineralisation strategies within these lineages is not sharp.

5.7. Future directions and conclusions

This study provides robust morphological and molecular support for a previously undetected cryptic species within the currently accepted concept of *Plesiastrea versipora*. In addition, the results presented here indicate further population structuring within the tropical and temperate clades, and we recommend that future studies further examine this hypothesis within both the southern and northern hemispheres. Modern advancements in high throughput sequencing such as RAD-seq and exon capture can explore the within-clade spatial structure and has proven useful in species delimitation and phylogenies within recently and rapidly diverged groups (Arrigoni et al., 2020; Cowman et al., 2020; Grinblat et al., 2021; Wepfer et al., 2020). Concurrent research on symbionts and reproductive biology may also provide additional valuable lines of evidence to help understand the level of diversity within *Plesiastrea*. This study highlights the importance of using an integrated taxonomic approach in phylogeographic studies exploring species complexes. By grounding future phylogeographic studies with sound taxonomy, museum-vouchered specimens and type specimens, there is a greater likelihood that taxonomic problems in other cosmopolitan species or species complexes can be solved. This integrated approach will strengthen inferences about species relationships and their relation to ecological niches, assisting coral biodiversity conservation to prevent the loss of phylogenetic diversity.

Declaration of Competing Interest

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

Acknowledgements

This project was funded by an ARC linkage Grant LP160101508, Australian Biological Resources Grant and an Australian Academy of Science Thomas Davies Grant awarded to Z.T. Richards. We thank D. Maggioni (UNIMIB) for collecting samples in the Maldives; M.L. Berumen (KAUST) and D. Huang (NUS) for collection in the Red Sea; G. Soler and the staff from University of Tasmania (UTAS) for collection in the Kent Group, Tasmania, Australia; A. Hara, A. Hosie and O. Gomez for collection in Albany, Western Australia (W.A.); A. Andrews, D. Kimberley and the staff from Monsoon Aquatics for collection in Arlington Reef, Queensland, Australia; and E. Fenny and the staff from W.A. Ocean Park for assistance with collections at Shark Bay, W.A. We thank Z.K. and Z.B. Juszkiewicz for funding the W.A., Gnaraloo Bay sampling trip. We thank A. Adam, K. Savill, M. Rossen-Abercromby, M. Thiele and R. Hofmann, for assistance with field work. We thank Z. Wysokowska for her illustrations of *Plesiastrea* based on skeletal samples. From Curtin University; we thank the TrEnD Lab and CORE Group, for their assistance with laboratory work, figure recommendations and moral support; C. Boisvert for her assistance with French translations and microscopy; B. Saunders for his assistance with multivariate data analyses. We thank K. Janiszewska (Institute of Paleobiology, Polish Academy of Sciences) for your help with computed micro-tomography visualization, it is greatly appreciated. We thank N. Carey for her assistance with multivariate analyses and field sampling. We thank T. James for his assistance with morphological data entry. We thank M. Castelin and C. Chambard from the Muséum National d'Histoire Naturelle in Paris, France for photographing the *Plesiastrea* holotypes. M. Pichon for his help with historical French translations. We thank D. Jones from the Western Australian Museum for her consultation regarding the Baudin Expeditions. We thank I. van Riemsdijk from the Naturalis Biodiversity Centre in the Netherlands and A. Dornburg from the University of North Carolina at Charlotte, for their assistance with the phylogenetic analyses. We thank A.H. Baird for edits and collection of samples in Sydney Harbour and Lord Howe Island, New South Wales, Australia. We thank the following expeditions that resulted in their collection; For the specimens from Yemen: E. Dutrieux (CREOCEAN), C.H. Chaineau (Total SA), R. Hirst and M. AbdulAziz (YLNG) for allowing and supporting our research in Yemen. Thanks to S. Basheen (Professional Divers Yemen),

M.A. Ahmad and F.N. Saeed (EPA Socotra). For the material from PNG: The Niugini Biodiversity Expedition, P. Bouchet (MNHN) and B. Dreyfus (IRD) are acknowledged for collections in Papua New Guinea (https://doi.org/10.17600/12100070). The Madang expedition specimens were obtained during the 'Our Planet Reviewed' Papua Niugini expedition organized by Museum National d'Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le Développement (IRD) and University of Papua New Guinea (UPNG), Principal Investigators P. Bouchet, C. Payri and S. Samadi. The organizers acknowledge funding from the Total Foundation, Prince Albert II of Monaco Foundation, Foundation EDF, Stavros Niarchos Foundation and Entrepose Contracting, and in-kind support from the Divine Word University (DWU). The expedition operated under a permit delivered by the Papua New Guinea Department of Environment and Conservation. For the specimen from Madagascar: Material from Madagascar was collected during the MAD (https://doi.org/10.17600/16004700) expedition on the RV Antea. We are grateful to the captain and crew; to the chief scientist H. Magalon (ULR). Lastly, the author D.J. Juszkiewicz would like to acknowledge and dedicate his work to his babcia (grandmother) K.Z. Wysokowska, who passed away during the writing of this manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2022.107469.

References

Adjeroud, M., Andréfouët, S., Payri, C., Orempüller, J., 2000. Physical factors of differentiation in macrobenthic communities between atoll lagoons in the Central Tuamotu Archipelago (French Polynesia). Mar. Ecol. Prog. Ser. 196, 25–38. http://www.jstor.org/stable/24855090.

Agapow, P.-M., Bininda-Emonds, O.R., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C., Purvis, A., 2004. The impact of species concept on biodiversity studies. Q. Rev. Biol. 79, 161–179. https://doi.org/10.1086/383542.

Alidoost Salimi, P., Ghavam Mostafavi, P., Chen, C.A., Pichon, M., Alidoost Salimi, M., 2021. Molecular phylogeny of some coral species from the Persian Gulf. Mol. Biol. Rep. 48, 2993–2999. https://doi.org/10.1007/s11033-021-06251-x.

Appeltans, W., Ahyong, S.T., Anderson, G., Angel, M.V., Artois, T., Bailly, N., Bamber, R., Barber, A., Bartsch, I., Berta, A., Błażewicz-Paszkowycz, M., Bock, P., Boxshall, G., Boyko, C.B., Brandão, S.N., Bray, R.A., Bruce, N.L., Cairns, S.D., Chan, T.-Y., Cheng, L., Collins, A.G., Cribb, T., Curini-Galletti, M., Dahdouh-Guebas, F., Davie, P. J.F., Dawson, M.N., De Clerck, O., Decock, W., De Grave, S., de Voogd, N.J., Domning, D.P., Emig, C.C., Erséus, C., Eschmeyer, W., Fauchald, K., Fautin, D.G., Feist, S.W., Fransen, C.H.J.M., Furuya, H., Garcia-Alvarez, O., Gerken, S., Gibson, D., Gittenberger, A., Gofas, S., Gómez-Daglio, L., Gordon, D.P., Guiry, M.D., Hernandez, F., Hoeksema, B.W., Hopcroft, R.R., Jaume, D., Kirk, P., Koedam, N., Koenemann, S., Kolb, J.B., Kristensen, R.M., Kroh, A., Lambert, G., Lazarus, D.B., Lemaitre, R., Longshaw, M., Lowry, J., Macpherson, E., Madin, L.P., Mah, C., Mapstone, G., McLaughlin, P.A., Mees, J., Meland, K., Messing, C.G., Mills, C.E., Molodtsova, T.N., Mooi, R., Neuhaus, B., Ng, P.K.L., Nielsen, C., Norenburg, J., Opresko, D.M., Osawa, M., Paulay, G., Perrin, W., Pilger, J.F., Poore, G.C.B., Pugh, P., Read, G.B., Reimer, J.D., Rius, M., Rocha, R.M., Saiz-Salinas, J.I., Scarabino, V., Schierwater, B., Schmidt-Rhaesa, A., Schnabel, K.E., Schotte, M., Schuchert, P., Schwabe, E., Segers, H., Self-Sullivan, C., Shenkar, N., Siegel, V., Sterrer, W., Stöhr, S., Swalla, B., Tasker, M.L., Thuesen, E.V., Timm, T., Todaro, M. A., Turon, X., Tyler, S., Uetz, P., van der Land, J., Vanhoorne, B., van Ofwegen, L.P., van Soest, R.W.M., Vanaverbeke, J., Walker-Smith, G., Walter, T.C., Warren, A., Williams, G.C., Wilson, S.P., Costello, M.J., 2012. The magnitude of global marine species diversity. Curr. Biol. 22, 2189–2202. https://doi.org/10.1016/j.cub.2012.09.036.

Arrigoni, R., Benzoni, F., Huang, D., Fukami, H., Chen, C.A., Berumen, M.L., Hoogenboom, M., Thomson, D.P., Hoeksema, B.W., Budd, A.F., Zayasu, Y., Terraneo, T.I., Kitano, Y.F., Baird, A.H., 2016. When forms meet genes: revision of the scleractinian genera *Micromussa* and *Homophyllia* (Lobophylliidae) with a description of two new species and one new genus. Contrib. Zool. 85, 387–422. https://doi.org/10.1163/18759866-08504002.

Arrigoni, R., Berumen, M.L., Huang, D., Terraneo, T.I., Benzoni, F., 2017. *Cyphastrea* (Cnidaria: Scleractinia: Merulinidae) in the Red Sea: phylogeny and a new reef coral species. Invertebr. Syst. 31, 141–156. https://doi.org/10.1071/IS16035.

Arrigoni, R., Berumen, M.L., Mariappan, K.G., Beck, P.S.A., Hulver, A.M., Montano, S., Pichon, M., Strona, G., Terraneo, T.I., Benzoni, F., 2020. Towards a rigorous species delimitation framework for scleractinian corals based on RAD sequencing: the case study of *Leptastrea* from the Indo-Pacific. Coral Reefs 39, 1001–1025. https://doi.org/10.1007/s00338-020-01924-8.

Arrigoni, R., Berumen, M.L., Stolarski, J., Terraneo, T.I., Benzoni, F., 2019. Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. Cladistics 35, 301–328. https://doi.org/10.1111/cla.12346.

Arrigoni, R., Huang, D., Berumen, M.L., Budd, A.F., Montano, S., Richards, Z.T., Terraneo, T.I., Benzoni, F., 2021. Integrative systematics of the scleractinian coral genera *Caulastraea*, *Erythrastrea* and *Oulophyllia*. Zool. Scr. 50, 509–527. https://doi.org/10.1111/zsc.12481.

Arrigoni, R., Kitano, Y.F., Stolarski, J., Hoeksema, B.W., Fukami, H., Stefani, F., Galli, P., Montano, S., Castoldi, E., Benzoni, F., 2014. A phylogeny reconstruction of the Dendrophylliidae (Cnidaria, Scleractinia) based on molecular and micromorphological criteria, and its ecological implications. Zool. Scr. 43, 661–688. https://doi.org/10.1111/zsc.12072.

Baird, A.H., Hoogenboom, M.O., Huang, D., 2017. *Cyphastrea salae*, a new species of hard coral from Lord Howe Island, Australia (Scleractinia, Merulinidae). ZooKeys 662, 49–66. https://doi.org/10.3897/zookeys.662.11454.

Baudin, N., de Freycinet, L.C.D., Lesueur, C.A., Péron, F., Péron, F., Petit, N.-M., 1807. Voyage de découvertes aux terres australes: exécuté par ordre de Sa Majesté l'empereur et roi, sur les corvettes le Géographe, le Naturaliste, et la goëlette le Casuarina, pendent les années 1800, 1801, 1802, 1803 et 1804; [Historique] publié p. De l'Imprimerie impériale, Paris. https://doi.org/10.5962/bhl.title.44096.

Benzoni, F., Arrigoni, R., Stefani, F., Pichon, M., 2011. Phylogeny of the coral genus *Plesiastrea* (Cnidaria, Scleractinia). Contrib. Zool. 80, 231–249. https://doi.org/10.1163/18759866-08004002.

Benzoni, F., Arrigoni, R., Stefani, F., Reijnen, B.T., Montano, S., Hoeksema, B.W., 2012. Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsi* (Scleractinia: Fungiidae): lost mushroom corals find their way home. Contrib. Zool. 81, 125–146. https://doi.org/10.1163/18759866-08103001.

Benzoni, F., Stefani, F., Pichon, M., Galli, P., 2010. The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). Zool. J. Linn. Soc. 160, 421–456. https://doi.org/10.1111/j.1096-3642.2010.00622.x.

Bernt, M., Donath, A., Jühling, F., Externbrink, F., Florentz, C., Fritzsch, G., Pütz, J., Middendorf, M., Stadler, P.F., 2013. MITOS: Improved de novo metazoan mitochondrial genome annotation. Mol. Phylogenet. Evol. 69, 313–319. https://doi.org/10.1016/j.ympev.2012.08.023.

Best, M.B., Hoeksema, B.W., Moka, W., Moll, H., Suharsono, S., I.n.,, 1989. Recent scleractinian coral species collected during the Snellius-II expedition in eastern Indonesia. Neth. J. Sea Res. 23, 107–115. https://doi.org/10.1016/0077-7579(89)90005-7.

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K., Das, I., 2007. Cryptic species as a window on diversity and conservation. Trends Ecol. Evol. 22, 148–155. https://doi.org/10.1016/j.tree.2006.11.004.

Bouckaert, R.R., Drummond, A.J., 2017. bModelTest: Bayesian phylogenetic site model averaging and model comparison. BMC Evol. Biol. 17, 42. https://doi.org/10.1186/s12862-017-0890-6.

Bouckaert, R.R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10, e1003537 https://doi.org/10.1371/journal.pcbi.1003537.

Bourne, G.C., 1900. The Anthozoa. In: Lankester, E.R. (Ed.), A Treatise on Zoology. Part II. The Porifera and Coelenterata, Chap. 6. Adam & Charles Black, London, pp. 1–84. https://doi.org/10.5962/bhl.title.26654.

Brahmi, C., Kopp, C., Domart-Coulon, I., Stolarski, J., Meibom, A., 2012. Skeletal growth dynamics linked to trace-element composition in the scleractinian coral *Pocillopora damicornis*. Geochim. Cosmochim. Acta 99, 146–158. https://doi.org/10.1016/j.gca.2012.09.031.

Bromfield, K., Pandolfi, J.M., 2012. Regional patterns of evolutionary turnover in Neogene coral reefs from the central Indo-West Pacific Ocean. Evol. Ecol. 26, 375–391. https://doi.org/10.1007/s10682-011-9483-9.

Budd, A.F., Fukami, H., Smith, N.D., Knowlton, N., 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool. J. Linn. Soc. 166, 465–529. https://doi.org/10.1111/j.1096-3642.2012.00855.x.

Budd, A.F., Stolarski, J., 2011. Corallite wall and septal microstructure in scleractinian reef corals: Comparison of molecular clades within the family Faviidae. J. Morphol. 272, 66–88. https://doi.org/10.1002/jmor.10899.

Burgess, S.N., McCulloch, M.T., Mortimer, G.E., Ward, T.M., 2009. Structure and growth rates of the high-latitude coral: *Plesiastrea versipora*. Coral Reefs 28, 1005–1015. https://doi.org/10.1007/s00338-009-0533-5.

Bustin, S., Huggett, J., 2017. qPCR primer design revisited. Biomol. Detect. Quantif. 14, 19–28. https://doi.org/10.1016/j.bdq.2017.11.001.

Cairns, S.D., Kitahara, M.V., 2012. An illustrated key to the genera and subgenera of the Recent azooxanthellate Scleractinia (Cnidaria, Anthozoa), with an attached glossary. ZooKeys 227, 1–47. https://doi.org/10.3897/zookeys.227.3612.

Cairns, S.D., Parker, S.A., 1992. Review of the recent Scleractinia (stony corals) of South Australia, Victoria and Tasmania. Rec. South Aust. Mus. Monogr. Ser. 3, 1–82. https://repository.si.edu/handle/10088/7228.

Cameron, K.A., Harrison, P.L., 2016. Patterns of scleractinian coral recruitment at Lord Howe Island, an isolated subtropical reef off eastern Australia. Coral Reefs 35, 555–564. https://doi.org/10.1007/s00338-016-1414-3.

Chen, C.A., Chang, C.-C., Wei, N.V., Chen, C.-H., Lein, Y.-T., Lin, H.-E., Dai, C.-F., Wallace, C.C., 2004. Secondary structure and phylogenetic utility of the Ribosomal Internal Transcribed Spacer 2 (ITS2) in scleractinian corals. Zool. Stud. 43, 759–771. http://ntur.lib.ntu.edu.tw/bitstream/246246/174420/1/24.pdf.

Chenuil, A., Cahill, A.E., Délémontey, N., Salliant, Du, du Luc, E., Fanton, H., 2019. Problems and questions posed by cryptic species. A framework to guide future studies. In: Casetta, E., Marques da Silva, J., Vecchi, D. (Eds.), From assessing to

conserving biodiversity: Conceptual and practical challenges. Springer International Publishing, Cham, pp. 77–106. https://doi.org/10.1007/978-3-030-10991-2_4.
Chevalier, J.-P., 1954. Contribution à la révision de polypiers du genre Heliastraea. Ann. Hébert Haug Trav. Lab. Géologie Fac. Sci. Univ, Paris.
Chinard, G., 1949. The American sketchbooks of Charles-Alexandre Lesueur. Proc. Am. Philos. Soc. 93, 114–118.
Christensen, J., 2008. Shark Bay 1616–1991: the spread of science and the emergence of ecology in a World Heritage Area. The University of Western Australia, Perth. Ph. D. Thesis.
Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: An approach to statistical analysis and interpretation, 2nd ed. PRIMER-E, Plymouth.
Cowman, P.F., Quattrini, A.M., Bridge, T.C.L., Watkins-Colwell, G.J., Fadli, N., Grinblat, M., Roberts, T.E., McFadden, C.S., Miller, D.J., Baird, A.H., 2020. An enhanced target-enrichment bait set for Hexacorallia provides phylogenomic resolution of the staghorn corals (Acroporidae) and close relatives. Mol. Phylogenet. Evol. 153, 106944 https://doi.org/10.1016/j.ympev.2020.106944.
Cracraft, J., 2002. The seven great questions of systematic biology: an essential foundation for conservation and the sustainable use of biodiversity. Ann. Mo. Bot. Gard. 89, 127–144. https://doi.org/10.2307/3298558.
Crossland, C., 1931. 17. The Reduced Building-power and other Variation in the Astrean Corals of Tahiti, with a Note on *Herpetolitha limax* and *Fungia* spp. Proc. Zool. Soc. Lond. 101, 351–392. https://doi.org/10.1111/j.1096-3642.1931.tb01017.x.
Cunha, R.L., Forsman, Z.H., Belderok, R., Knapp, I.S.S., Castilho, R., Toonen, R.J., 2019. Rare coral under the genomic microscope: timing and relationships among Hawaiian *Montipora*. BMC Evol. Biol. 19, 153. https://doi.org/10.1186/s12862-019-1476-2.
Dai, C.F., Horng, S., 2009. Scleractinia fauna of Taiwan II. The robust group. Taipei National Taiwan University, pp. 1–162.
Dalton, S.J., Roff, G., 2013. Spatial and temporal patterns of Eastern Australia subtropical coral communities. PLoS ONE 8, e75873. https://doi.org/10.1371/journal.pone.0075873.
Dana, J.D., 1846. Zoophytes. United States Exploring Expedition during the years 1838-1842. Lea Blanchard Phila. 7, 1–740, 61 pls. (1846: 1–120, 709–720; 1848: 121–708, 721–740; 1849: atlas pls. 1–61). http://www.sil.si.edu/digitalcollections/usexex/navigation/ScientificText/USExEx19_08select.cfm.
Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods 9, 772. https://doi.org/10.1038/nmeth.2109.
Dayrat, B., 2005. Towards integrative taxonomy. Biol. J. Linn. Soc. 85, 407–415. https://doi.org/10.1111/j.1095-8312.2005.00503.x.
de León, G.-P.-P., Nadler, S.A., 2010. What we don't recognize can hurt us: A plea for awareness about cryptic species. J. Parasitol. 96, 453–464. https://doi.org/10.1645/GE-2260.1.
De Vantier, L.M., Deacon, G., 1990. Distribution of *Acanthaster planci* at Lord Howe Island, the southern-most Indo-Pacific reef. Coral Reefs 9, 145–148. https://doi.org/10.1007/BF00258226.
Dee, S., 2016. Reproductive activity of temperate coral species *Plesiastrea versipora* in Marmion Marine Park. The University of Western Australia, Perth. Ph. D. Thesis.
Dennant, J., 1904. Recent corals from the South Australian and Victorian coasts. Trans. Proc. R. Soc. S. Aust. 28, 1–11 pls. 1–2.
Drake, J.L., Mass, T., Stolarski, J., Von Euw, S., Schootbrugge, B., Falkowski, P.G., 2020. How corals made rocks through the ages. Glob. Change Biol. 26, 31–53. https://doi.org/10.1111/gcb.14912.
Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4, e88 https://doi.org/10.1371/journal.pbio.0040088.
Drummond, A.J., Rambaut, A., Shapiro, B., Pybus, O.G., 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. Mol. Biol. Evol. 22, 1185–1192. https://doi.org/10.1093/molbev/msi103.
Eguchi, M., 1938. A systematic study of the reef-building corals of the Palao Islands. Palao Trop. Biol. Stn. Stud. 1, 326–390.
Ehrenberg, C.G., 1834. Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. Phys. Math. Abh. K. Akad. Wiss. Berlin (for 1832). 1, 225–380.
Ellis, J., Solander, D., 1786. The Natural History of many curious and uncommon Zoophytes, collected from various parts of the Globe. In: Systematically arranged and described by the late Daniel Solander. London, 1786. Benjamin White & Son, London, pp. 1–206 pls 1–63. 10.5962/bhl.title.64985.
Evans, R.D., Thomas, L., Kennington, W.J., Ryan, N.M., Wilson, N.G., Richards, Z., Lowe, R.J., Tuckett, C., 2021. Population genetic structure of a broadcast-spawning coral across a tropical–temperate transition zone reveals regional differentiation and high-latitude reef isolation. J. Biogeogr. 48, 3185–3195. https://doi.org/10.1111/jbi.14280.
Fellegara, I., Baird, A.H., Ward, S., 2013. Coral reproduction in a high-latitude, marginal reef environment (Moreton Bay, south-east Queensland, Australia). Invertebr. Reprod. Dev. 57, 219–223. https://doi.org/10.1080/07924259.2012.752766.
Feng, M., Waite, A.M., Thompson, P.A., 2009. Climate variability and ocean production in the Leeuwin Current system off the west coast of Western Australia. J. R. Soc. West. Aust. 92, 67–81 https://www.rswa.org.au/publications/Journal/92(2)/ROY%20SOC%2092.2%20LEEUWIN%2067-81.pdf.
Fišer, C., Robinson, C.T., Malard, F., 2018. Cryptic species as a window into the paradigm shift of the species concept. Mol. Ecol. 27, 613–635. https://doi.org/10.1111/mec.14486.
Fisher, B.L., Smith, M.A., 2008. A Revision of Malagasy Species of *Anochetus* Mayr and *Odontomachus Latreille* (Hymenoptera: Formicidae). PLoS ONE 3, e1787. https://doi.org/10.1371/journal.pone.0001787.
Flot, J.-F., Blanchot, J., Charpy, L., Cruaud, C., Licuanan, W.Y., Nakano, Y., Payri, C., Tillier, S., 2011. Incongruence between morphotypes and genetically delimited species in the coral genus *Stylophora*: phenotypic plasticity, morphological convergence, morphological stasis or interspecific hybridization? BMC Ecol. 11, 22. https://doi.org/10.1186/1472-6785-11-22.
Folkeson, F., 1919. Madreporaria. Results of Dr. E. Mjoberg's Swedish Scientific Expeditions to Australia, 1910–1913. XXII. Kungliga Svenska Vetenskapsakademiens Handlingar (4 Ser.). 59, 1–23, pl. l.
Forsman, Z.H., Barshis, D.J., Hunter, C.L., Toonen, R.J., 2009. Shape-shifting corals: Molecular markers show morphology is evolutionarily plastic in *Porites*. BMC Evol. Biol. 9, 45. https://doi.org/10.1186/1471-2148-9-45.
Forsman, Z.H., Concepcion, G.T., Haverkort, R.D., Shaw, R.W., Maragos, J.E., Toonen, R. J., 2010. Ecomorph or endangered coral? DNA and microstructure reveal Hawaiian species complexes: *Montipora dilatata/flabellata/turgescens* & *M. patula/verrilli*. PLoS ONE 5, e15021. https://doi.org/10.1371/journal.pone.0015021.
Fouquet, A., Vences, M., Salducci, M.-D., Meyer, A., Marty, C., Blanc, M., Gilles, A., 2007. Revealing cryptic diversity using molecular phylogenetics and phylogeography in frogs of the *Scinax ruber* and *Rhinella margaritifera* species groups. Mol. Phylogenet. Evol. 43, 567–582. https://doi.org/10.1016/j.ympev.2006.12.006.
Frankowiak, K., Kret, S., Mazur, M., Meibom, A., Kitahara, M.V., Stolarski, J., 2016. Fine-scale skeletal banding can distinguish symbiotic from asymbiotic species among modern and fossil scleractinian corals. PLoS ONE 11, e0147066. https://doi.org/10.1371/journal.pone.0147066.
Fukami, H., Budd, A.F., Paulay, G., Solé-Cava, A., Chen, C.A., Iwao, K., Knowlton, N., 2004. Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. Nature 427, 832–835. https://doi.org/10.1038/nature02339.
Fukami, H., Chen, C.A., Chiou, C.-Y., Knowlton, N., 2007. Novel group I introns encoding a putative homing endonuclease in the mitochondrial cox1 gene of scleractinian corals. J. Mol. Evol. 64, 591–600. https://doi.org/10.1007/s00239-006-0279-4.
Fukami, H., Knowlton, N., 2005. Analysis of complete mitochondrial DNA sequences of three members of the *Montastraea annularis* coral species complex (Cnidaria, Anthozoa, Scleractinia). Coral Reefs 24, 410–417. https://doi.org/10.1007/s00338-005-0023-3.
Gardiner, J.S., 1899. On the astraeid corals collected by the author in the South Pacific. Proc. Zool. Soc. Lond. 1899, 734–764.
Gattuso, J.-P., Pichon, M., Jaubert, J., 1991. Physiology and taxonomy of scleractinian corals: a case study in the genus *Stylophora*. Coral Reefs 9, 173–182. https://doi.org/10.1007/BF00290419.
Gilmour, J., Speed, C.W., Babcock, R., 2015. Coral reproduction in Western Australia. PeerJ PrePrints 3, e1462v2. https://doi.org/10.7287/peerj.preprints.1462v2.
Gittenberger, A., Reijnen, B.T., Hoeksema, B.W., 2011. A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. Contrib. Zool. 80, 107–132. https://doi.org/10.1163/18759866-08002002.
Glynn, P.W., Wellington, G.M., Riegl, B., Olson, D.B., Borneman, E., Wieters, E.A., 2007. Diversity and biogeography of the scleractinian coral fauna of Easter Island (Rapa Nui). Pac. Sci. 61, 67–90. http://hdl.handle.net/10125/22599.
González, A.M., Prada, C.A., Ávila, V., Medina, M., 2018. Ecological speciation in corals. In: Oleksiak, M., Rajora, O. (Eds.), Population genomics: Marine organisms. Population Genomics. Springer, Cham. https://doi.org/10.1007/13836_2018_35.
González-Castellano, I., González-López, J., González-Tizón, A.M., Martínez-Lage, A., 2020. Genetic diversity and population structure of the rockpool shrimp *Palaemon elegans* based on microsatellites: evidence for a cryptic species and differentiation across the Atlantic-Mediterranean transition. Sci. Rep. 10, 10784. https://doi.org/10.1038/s41598-020-67824-7.
Gravier, C., 1911. Les récifs de coraux et les Madréporaires de la baie de Tadjourah (Golfe d'Aden). Ann. Inst. Océan. 2, 1–99.
Griffiths, A.M., Sims, D.W., Cotterell, S.P., El Nagar, A., Ellis, J.R., Lynghammar, A., McHugh, M., Neat, F.C., Pade, N.G., Queiroz, N., Serra-Pereira, B., Rapp, T., Wearmouth, V.J., Genner, M.J., 2010. Molecular markers reveal spatially segregated cryptic species in a critically endangered fish, the common skate (*Dipturus* batis). Proc. R. Soc. B Biol. Sci. 277, 1497–1503. https://doi.org/10.1098/rspb.2009.2111.
Grinblat, M., Cooke, I., Shlesinger, T., Ben-Zvi, O., Loya, Y., Miller, D.J., Cowman, P.F., 2021. Biogeography, reproductive biology and phylogenetic divergence within the Fungiidae (mushroom corals). Mol. Phylogenet. Evol. 164, 107265 https://doi.org/10.1016/j.ympev.2021.107265.
Hansen, A., 2013. Nineteenth Century natural history art and belonging in Tasmania. University of Tasmania. Ph. D. Thesis.
Harriott, V., Banks, S., 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. Coral Reefs 21, 83–94. https://doi.org/10.1007/s00338-001-0201-x.
Harriott, V., Harrison, P., Banks, S., 1995. The coral communities of Lord Howe Island. Mar. Freshw. Res. 46, 457–465. https://doi.org/10.1071/MF9950457.
Heethoff, M., 2018. Cryptic, species – conceptual or terminological chaos? A response to Struck et al. Trends Ecol. Evol. 33, 310. https://doi.org/10.1016/j.tree.2018.02.006.
Heled, J., Drummond, A.J., 2012. Calibrated tree priors for relaxed phylogenetics and divergence time estimation. Syst. Biol. 61, 138–149. http://www.jstor.org/stable/41515182.
Hellberg, M.E., 2006. No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. BMC Evol. Biol. 6, 24. https://doi.org/10.1186/1471-2148-6-24.
Hobbs, J.-P.-A., Richards, Z.T., Popovic, I., Lei, C., Staeudle, T.M., Montanari, S.R., DiBattista, J.D., 2021. Hybridisation and the evolution of coral reef biodiversity. Coral Reefs. https://doi.org/10.1007/s00338-021-02193-9.

Hoeksema, B.W., Cairns, S., 2022. World List of Scleractinia. *Plesiastrea versipora* (Lamarck, 1816). Accessed at: ttp://www.marinespecies.org/scleractinia/aphia.php?p=taxdetails&id=207494 on 2022-02-12.

Huang, D., 2012. Systematics of Merulinidae (Scleractinia) and conservation phylogenetics of reef corals. University of California, San Diego. Ph. D. Thesis.

Huang, D., Benzoni, F., Arrigoni, R., Baird, A.H., Berumen, M.L., Bouwmeester, J., Chou, L.M., Fukami, H., Licuanan, W.Y., Lovell, E.R., 2014. Towards a phylogenetic classification of reef corals: the Indo-Pacific genera *Merulina*, *Goniastrea* and *Scapophyllia* (Scleractinia, Merulinidae). Zool. Scr. 43, 531–548. https://doi.org/10.1111/zsc.12061.

Huang, D., Licuanan, W.Y., Baird, A.H., Fukami, H., 2011. Cleaning up the'Bigmessidae': Molecular phylogeny of scleractinian corals from Faviidae, Merulinidae. Pectiniidae and Trachyphylliidae. BMC Evol. Biol. 11, 37. https://doi.org/10.1186/1471-2148-11-37.

Huang, D., Licuanan, W.Y., Hoeksema, B.W., Chen, C.A., Ang, P.O., Huang, H., Lane, D.J. W., Vo, S.T., Waheed, Z., Affendi, Y.A., Yeemin, T., Chou, L.M., 2015. Extraordinary diversity of reef corals in the South China Sea. Mar. Biodivers. 45, 157–168. https://doi.org/10.1007/s12526-014-0236-1.

Huang, D., Meier, R., Todd, P.A., Chou, L.M., 2008. Slow mitochondrial COI sequence evolution at the base of the metazoan tree and its implications for DNA barcoding. J. Mol. Evol. 66, 167–174. https://doi.org/10.1007/s00239-008-9069-5.

International Commission on Zoological Nomenclature, Ride, W.D.L., International Trust for Zoological Nomenclature, Natural History Museum (London, England), International Union of Biological Sciences (Eds.), 1999. International code of zoological nomenclature, fourth ed. International Trust for Zoological Nomenclature, c/o Natural History Museum, London. https://www.iczn.org/the-code/the-code-online/.

Isaac, N.J., Mallet, J., Mace, G.M., 2004. Taxonomic inflation: its influence on macroecology and conservation. Trends Ecol. Evol. 19, 464–469. https://doi.org/10.1016/j.tree.2004.06.004.

Jones, D.S., 2017. A lasting legacy: the Baudin Expedition in Australian waters (1801-1803). Gt. Circ. 39, 56–85. https://www.jstor.org/stable/26381273.

Jonker, L., Johan, O., 1999. Checklist of the scleractinian coral species from the waters of Padang (West Sumatra, Indonesia) held in the coral collection of Bung Hatta University. Beagle Rec. Mus. Art Galleries North. Territ. 15, 47–54.

Jörger, K.M., Schrödl, M., 2013. How to describe a cryptic species? Practical challenges of molecular taxonomy. Front. Zool. 10, 59. https://doi.org/10.1186/1742-9994-10-59.

Kadane, J.B., Lazar, N.A., 2004. Methods and criteria for model selection. J. Am. Stat. Assoc. 99, 279–290. https://doi.org/10.1198/016214504000000269.

Keith, S.A., Woolsey, E.S., Madin, J.S., Byrne, M., Baird, A.H., 2015. Differential establishment potential of species predicts a shift in coral assemblage structure across a biogeographic barrier. Ecography 38, 1225–1234. https://doi.org/10.1111/ecog.01437.

Keshavmurthy, S., Tang, K.-H., Hsu, C.-M., Gan, C.-H., Kuo, C.-Y., Soong, K., Chou, H.-N., Chen, C.A., 2017. *Symbiodinium* spp. associated with scleractinian corals from Dongsha Atoll (Pratas), Taiwan, in the South China Sea. PeerJ 5, e2871. https://doi.org/10.7717/peerj.2871.

Kitahara, M.V., Cairns, S.D., Stolarski, J., Blair, D., Miller, D.J., 2010. A comprehensive phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) Based on mitochondrial CO1 sequence data. PLoS ONE 5, e11490. https://doi.org/10.1371/journal.pone.0011490.

Kitahara, M.V., Fukami, H., Benzoni, F., Huang, D., 2016. The new systematics of Scleractinia: Integrating molecular and morphological evidence. In: Goffredo, S., Dubinsky, Z. (Eds.), The Cnidaria, past, present and future: The world of Medusa and her sisters. Springer International Publishing, Cham, pp. 41–59. 10.1007/978-3-319-31305-4_4.

Kitano, Y.F., Benzoni, F., Arrigoni, R., Shirayama, Y., Wallace, C.C., Fukami, H., 2014. A Phylogeny of the family Poritidae (Cnidaria, Scleractinia) based on molecular and morphological analyses. PLoS One 9, e98406. https://doi.org/10.1371/journal.pone.0098406.

Knowlton, N., 1993. Sibling species in the sea. Annu. Rev. Ecol. Syst. 24, 189–216. https://doi.org/10.1146/annurev.es.24.110193.001201.

Knowlton, N., 2000. Molecular genetic analyses of species boundaries in the sea, in: Marine Genetics. Springer, pp. 73–90. 10.1007/978-94-017-2184-4_8.

Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32, 1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009.

Korshunova, T., Picton, B., Furfaro, G., Mariottini, P., Pontes, M., Prkić, J., Fletcher, K., Malmberg, K., Lundin, K., Martynov, A., 2019. Multilevel fine-scale diversity challenges the 'cryptic species' concept. Sci. Rep. 9, 6732. https://doi.org/10.1038/s41598-019-42297-5.

Ladner, J.T., Palumbi, S.R., 2012. Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. Mol. Ecol. 21, 2224–2238. https://doi.org/10.1111/j.1365-294X.2012.05528.x.

LaJeunesse, T.C., Bhagooli, R., Hidaka, M., deVantier, L., Done, T., Schmidt, G.W., Fitt, W.K., Hoegh-Guldberg, O., 2004. Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. Mar. Ecol. Prog. Ser. 284, 147–161. https://doi.org/10.3354/meps284147.

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R., 2018. Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Curr. Biol. 28, 2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008.

Lajus, D., Sukhikh, N., Alekseev, V., 2015. Cryptic or pseudocryptic: can morphological methods inform copepod taxonomy? An analysis of publications and a case study of the *Eurytemora affinis* species complex. Ecol. Evol. 5, 2374–2385. https://doi.org/10.1002/ece3.1521.

Lam, K., Morton, B., 2003. Morphological and ITS1, 5.8S, and partial ITS2 ribosomal DNA sequence distinctions between two species *Platygyra* (Cnidaria: Scleractinia) from Hong Kong. Mar. Biotechnol. 5, 555–567. https://doi.org/10.1007/s10126-002-0114-x.

Lamarck, J.-B.M. de, 1816. Histoire naturelle des animaux sans vertèbres. Tome second. 10.5962/bhl.title.12712.

Lin, M.-F., Kitahara, M.V., Luo, H., Tracey, D., Geller, J., Fukami, H., Miller, D.J., Chen, C.A., 2014. Mitochondrial Genome Rearrangements in the Scleractinia/Corallimorpharia Complex: Implications for Coral Phylogeny. Genome Biol. Evol. 6, 1086–1095. https://doi.org/10.1093/gbe/evu084.

Ling, S.D., Barrett, N.S., Edgar, G.J., 2018. Facilitation of Australia's southernmost reef-building coral by sea urchin herbivory. Coral Reefs 37, 1053–1073. https://doi.org/10.1007/s00338-018-1728-4.

Losos, J.B., 2011. Convergence, adaptation, and constraint. Evolution 65, 1827–1840. https://doi.org/10.1111/j.1558-5646.2011.01289.x.

Lucas, C., Fresneau, D., Kolmer, K., Heinze, J., Delabie, J.H., Pho, D.B., 2002. A multidisciplinary approach to discriminating different taxa in the species complex *Pachycondyla villosa* (Formicidae). Biol. J. Linn. Soc. 75, 249–259. https://doi.org/10.1046/j.1095-8312.2002.00017.x.

Luck, D.G., Forsman, Z.H., Toonen, R.J., Leicht, S.J., Kahng, S.E., 2013. Polyphyly and hidden species among Hawai'i's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agariciidae). PeerJ 1, e132. https://doi.org/10.7717/peerj.132.

Luckett, W., 2012. Phylogeny of the Primates: A Multidisciplinary Approach. Springer Science & Business Media. https://doi.org/10.1007/978-1-4684-2166-8.

Luo, A., Qiao, H., Zhang, Y., Shi, W., Ho, S.Y., Xu, W., Zhang, A., Zhu, C., 2010. Performance of criteria for selecting evolutionary models in phylogenetics: a comprehensive study based on simulated datasets. BMC Evol. Biol. 10, 242. https://doi.org/10.1186/1471-2148-10-242.

Luzon, K.S., Lin, M.-F., Lagman, M.C.A.A., Licuanan, W.R.Y., Chen, C.A., 2017. Resurrecting a subgenus to genus: molecular phylogeny of *Euphyllia* and *Fimbriaphyllia* (order Scleractinia; family Euphyllidae; clade V). PeerJ 5. https://doi.org/10.7717/peerj.4074.

Mace, G.M., 2004. The role of taxonomy in species conservation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 359, 711–719. https://doi.org/10.1098/rstb.2003.1454.

Madsen, A., Madin, J.S., Tan, C.-H., Baird, A.H., 2014. The reproductive biology of the scleractinian coral *Plesiastrea versipora* in Sydney Harbour. Australia. Sex. Early Dev. Aquat. Org. 1, 25–33. https://doi.org/10.3354/sedao00004.

Malhotra, A., Thorpe, R.S., 2004. Maximizing information in systematic revisions: a combined molecular and morphological analysis of a cryptic green pitviper complex (*Trimeresurus stejnegeri*). Biol. J. Linn. Soc. 82, 219–235. https://doi.org/10.1111/j.1095-8312.2004.00354.x.

Mao, Y., Economo, E.P., Satoh, N., 2018. The roles of introgression and climate change in the rise to dominance of *Acropora* corals. Curr. Biol. 28, 3373–3382. https://doi.org/10.1016/j.cub.2018.08.061.

Márquez, L.M., Miller, D.J., MacKenzie, J.B., Van Oppen, M.J.H., 2003. Pseudogenes contribute to the extreme diversity of nuclear ribosomal DNA in the hard coral *Acropora*. Mol. Biol. Evol. 20, 1077–1086. https://doi.org/10.1093/molbev/msg122.

Marti-Puig, P., Forsman, Z.H., Haverkort-Yeh, R.D., Knapp, I.S., Maragos, J.E., Toonen, R.J., 2014. Extreme phenotypic polymorphism in the coral genus *Pocillopora*; micro-morphology corresponds to mitochondrial groups, while colony morphology does not. Bull. Mar. Sci. 90, 211–231. https://doi.org/10.5343/bms.2012.1080.

Matthai, G., 1914. A revision of the recent colonial Astraeidae possessing distinct corallites. Trans. Linn. Soc. Lond. 2nd Ser. Zool. 17, 1–38. https://doi.org/10.1111/j.1096-3642.1914.tb00590.x.

Matthai, G., 1924. Report on the Madreporarian corals in the collection of the Indian Museum, Calcutta. Mem. Indian Mus. 8, 1–59. http://faunaofindia.nic.in/PDFVolumes/memoirs/008/01/0001-0059.pdf.

McKeown, N.J., Gwilliam, M.P., Healey, A.J.E., Skujina, I., Potts, W.M., Sauer, W.H.H., Shaw, P.W., 2020. Deep phylogeographic structure may indicate cryptic species within the Sparid genus *Spondyliosoma*. J. Fish Biol. 96, 1434–1443. https://doi.org/10.1111/jfb.14316.

Milne Edwards, H., Haime, J., 1848a. Note sur la classification de la deuxième tribu de la famille des Astréides. Comptes Rendus Hebd. Séances Académie Sci. 27, 490–497. https://doi.org/10.5962/bhl.part.29692.

Milne Edwards, H., Haime, J., 1848b. Recherches sur les polypiers. Mémoire 4. Monographie des Astréides. Ann. Sci. Nat. Zool. Ser. 3. 10, 209–320, pls. 5–9.

Milne Edwards, H., Haime, J., 1849. Recherches sur les polypiers. Mémoire 4. Monographie des Astréides. Ann. Sci. Nat. Zool. Ser. 3. 12, 95–197.

Milne Edwards, H., Haime, J., 1857. Histoire naturelle des coralliaires ou polypes proprement dits 2. Librairie Encyclopédique de Roret, Paris. https://doi.org/10.5962/bhl.title.11574.

Mitsuki, Y., Isomura, N., Nozawa, Y., Tachikawa, H., Huang, D., Fukami, H., 2021. Distinct species hidden in the widely distributed coral *Coelastrea aspera* (Cnidaria, Anthozoa, Scleractinia). Invertebr. Syst. 35, 876–891. https://doi.org/10.1071/IS21025.

Moll, H., Borel-Best, M., 1984. New scleractinian corals (Anthozoa: Scleractinia) from the Spermonde Archipelago. South Sulawesi Indones. Zool. Meded. Leiden 58, 47–58. https://repository.naturalis.nl/pub/318035.

Nakabayashi, A., Yamakita, T., Nakamura, T., Aizawa, H., Kitano, Y.F., Iguchi, A., Yamano, H., Nagai, S., Agostini, S., Teshima, K.M., Yasuda, N., 2019. The potential role of temperate Japanese regions as refugia for the coral *Acropora hyacinthus* in the face of climate change. Sci. Rep. 9, 1892. https://doi.org/10.1038/s41598-018-38333-5.

Niu, W., Xiao, J., Tian, P., Guo, F., 2020. The complete mitochondrial genome of *Plesiastrea versipora* (Scleractinia, Plesiastreidae) sheds light on its phylogeny and taxonomy of the family Plesiastreidae. Saudi J. Biol. Sci. 27, 1830–1834. https://doi.org/10.1016/j.sjbs.2020.04.041.

Nguyen, J.M.T., Ho, S.Y.W., 2020. Calibrations from the fossil record, in: Ho, S.Y.W. (Ed.), The Molecular Evolutionary Clock. Springer International Publishing, Cham, pp. 117–133. 10.1007/978-3-030-60181-2_8.

Odorico, D.M., Miller, D.J., 1997. Variation in the ribosomal internal transcribed spacers and 5.8S rDNA among five species of *Acropora* (Cnidaria; Scleractinia): patterns of variation consistent with reticulate evolution. Mol. Biol. Evol. 14, 465–473. https://doi.org/10.1093/oxfordjournals.molbev.a025783.

Ow, Y.X., Todd, P.A., 2010. Light-induced morphological plasticity in the scleractinian coral *Goniastrea pectinata* and its functional significance. Coral Reefs 29, 797–808. https://doi.org/10.1007/s00338-010-0631-4.

Padial, J.M., De la Riva, I., 2009. Integrative taxonomy reveals cryptic Amazonian species of *Pristimantis* (Anura: Strabomantidae). Zool. J. Linn. Soc. 155, 97–122. https://doi.org/10.1111/j.1096-3642.2008.00424.x.

Pante, E., Schoelinck, C., Puillandre, N., 2015. From integrative taxonomy to species description: One step beyond. Syst. Biol. 64, 152–160. https://doi.org/10.1093/sysbio/syu083.

Pérez-Ponce de León, G., Poulin, R., 2016. Taxonomic distribution of cryptic diversity among metazoans: not so homogeneous after all. Biol. Lett. 12, 20160371. https://doi.org/10.1098/rsbl.2016.0371.

Péron, F., Cornell, C., de Freycinet, L.C.D., 2006. Voyage of discovery to the southern lands. Friends of the State Library of South Australia, Adelaide.

Pfennig, D.W., Wund, M.A., Snell-Rood, E.C., Cruickshank, T., Schlichting, C.D., Moczek, A.P., 2010. Phenotypic plasticity's impacts on diversification and speciation. Trends Ecol. Evol. 25, 459–467. https://doi.org/10.1016/j.tree.2010.05.006.

Pfenninger, M., Schwenk, K., 2007. Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. BMC Evol. Biol. 7, 121. https://doi.org/10.1186/1471-2148-7-121.

Pinzón, J.H.C., Weil, E., 2011. Cryptic species within the Atlantic-Caribbean genus *Meandrina* (Scleractinia): A multidisciplinary approach and description of the new species *Meandrina jacksoni*. Bull. Mar. Sci. 87, 823–853. https://doi.org/10.5343/bms.2010.1085.

Posada, D., Crandall, K.A., 2001. Selecting the best-fit model of nucleotide substitution. Syst. Biol. 50, 580–601. https://doi.org/10.1080/10635150118469.

Precoda, K., Baird, A., Madsen, A., Mizerek, T., Sommer, B., Su, S., Madin, J., 2018. How does a widespread reef coral maintain a population in an isolated environment? Mar. Ecol. Prog. Ser. 594, 85–94. https://doi.org/10.3354/meps12537.

Przeslawski, R., McArthur, M.A., Anderson, T.J., 2013. Infaunal biodiversity patterns from Carnarvon Shelf (Ningaloo Reef). Western Australia. Mar. Freshw. Res. 64, 573. https://doi.org/10.1071/MF12240.

Quelch, J., 1886. Report on the Reef-corals collected by H.M.S. Challenger during the years 1873–76. Rep. Sci. Results Voyage HMS Chall. Years 1873–1876 Zool. https://doi.org/10.5962/bhl.title.6513.

Rambaut, A., 2012. Figtree 1.4.0. Available from: http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut, A., Suchard, M.A., Xie, D. & Drummond, A.J., 2014. Tracer v1.6. Available from: http://beast.bio.ed.ac.uk/Tracer.

Reaka-Kudla, M.L., 2005. Biodiversity of Caribbean coral reefs. In: Miloslavich, P., Klein, E. (Eds.), Caribbean Marine Biodiversity. DesTech Publishers, Lancaster, PA, pp. 259–276.

Richards, Z.T., Berry, O., van Oppen, M.J., 2016. Cryptic genetic divergence within threatened species of *Acropora* coral from the Indian and Pacific Oceans. Conserv. Genet. 17, 577–591. https://doi.org/10.1007/s10592-015-0807-0.

Richards, Z.T., Hobbs, J.-P.-A., 2015. Hybridisation on coral reefs and the conservation of evolutionary novelty. Curr. Zool. 61, 132–145. https://doi.org/10.1093/czoolo/61.1.132.

Richards, Z.T., Miller, D.J., Wallace, C.C., 2013. Molecular phylogenetics of geographically restricted *Acropora* species: implications for threatened species conservation. Mol. Phylogenet. Evol. 69, 837–851. https://doi.org/10.1016/j.ympev.2013.06.020.

Richards, Z.T., Wallace, C.C., Miller, D.J., 2010. Archetypal 'elkhorn' coral discovered in the Pacific Ocean. Syst. Biodivers. 8, 281–288. https://doi.org/10.1080/14772001003758278.

Ridgway, K.R., Godfrey, J.S., 1997. Seasonal cycle of the East Australian Current. J. Geophys. Res. Oceans 102, 22921–22936. https://doi.org/10.1029/97JC00227.

Rocha, R.J.M., Silva, A.M.B., Fernandes, M.H.V., Cruz, I.C.S., Rosa, R., Calado, R., 2014. Contrasting light spectra constrain the macro and microstructures of scleractinian corals. PLoS ONE 9, e105863. https://doi.org/10.1371/journal.pone.0105863.

Rodriguez-Lanetty, M., Hoegh-Guldberg, O., 2002. The phylogeography and connectivity of the latitudinally widespread scleractinian coral *Plesiastrea versipo*ra in the Western Pacific. Mol. Ecol. 11, 1177–1189. https://doi.org/10.1046/j.1365-294X.2002.01511.x.

Rodriguez-Lanetty, M., Hoegh-Guldberg, O., 2003. Symbiont diversity within the widespread scleractinian coral *Plesiastrea versipora*, across the northwestern Pacific. Mar. Biol. 143, 501–509. https://doi.org/10.1007/s00227-003-1105-9.

Rodriguez-Lanetty, M., Loh, W., Hoegh-Guldberg, O., 2001. Latitudinal variability in symbiont specificity within the widespread scleractinian coral *Plesiastrea versipora*. Mar. Biol. 138, 1175–1181. https://doi.org/10.1007/s002270100536.

Sáez, A.G., Lozano, E., 2005. Body doubles. Nature 433, 111. https://doi.org/10.1038/433111a.

Sauquet, H., 2013. A practical guide to molecular dating. Syst. Phylogenetics Systématique Au-Delà Phylogénétique 12, 355–367. https://doi.org/10.1016/j.crpv.2013.07.003.

Sbordoni, V., Allegrucci, G., Cesaroni, D., 1991. A multidimensional approach to the evolution and systematics of *Dolichopoda* cave crickets. In: Hewitt, G.M., Johnston, A.W.B., Young, J.P.W. (Eds.), Molecular techniques in taxonomy. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 171–199. https://doi.org/10.1007/978-3-642-83962-7_12.

Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E., Crozier, R.H., 2010. Integrative taxonomy: A multisource approach to exploring biodiversity. Annu. Rev. Entomol. 55, 421–438. https://doi.org/10.1146/annurev-ento-112408-085432.

Schmidt-Roach, S., Miller, K.J., Lundgren, P., Andreakis, N., 2014. With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. Zool. J. Linn. Soc. 170, 1–33. https://doi.org/10.1111/zoj.12092.

Schönberg, C.H.L., Fromont, J., 2012. Sponge gardens of Ningaloo Reef (Carnarvon Shelf, Western Australia) are biodiversity hotspots. Hydrobiologia 687, 143–161. https://doi.org/10.1007/s10750-011-0863-5.

Schöne, B.R., Dunca, E., Fiebig, J., Pfeiffer, M., 2005. Mutvei's solution: An ideal agent for resolving microgrowth structures of biogenic carbonates. Palaeogeogr. Palaeoclimatol. Palaeoecol. 228, 149–166. https://doi.org/10.1016/j.palaeo.2005.03.054.

Shearer, T.L., Coffroth, M.A., 2008. DNA barcoding: Barcoding corals: limited by interspecific divergence, not intraspecific variation. Mol. Ecol. Resour. 8, 247–255. https://doi.org/10.1111/j.1471-8286.2007.01996.x.

Shearer, T.L., van Oppen, M.J.H., Romano, S.L., Wörheide, G., 2002. Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). Mol. Ecol. 11, 2475–2487. https://doi.org/10.1046/j.1365-294X.2002.01652.x.

Sheppard, C.R.C., 1987. Coral species of the Indian Ocean and adjacent seas: a synonymised compilation and some regional distribution patterns. Atoll Res. Bull. 307, 1–32. https://doi.org/10.5479/si.00775630.307.1.

Simpson, C., Kiessling, W., Mewis, H., Baron-Szabo, R.C., Müller, J., 2011. Evolutionary diversification of reef corals: a comparison of the molecular and fossil records. Evolution 65, 3274–3284. https://doi.org/10.1111/j.1558-5646.2011.01365.x.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., Robertson, J., 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. BioScience 57, 573–583. https://doi.org/10.1641/B570707.

Squires, D.F., 1966. Port Phillip Survey 1957-1963. Scleractinia. Memoirs of the Natural History Museum of Victoria 27: 167-174. Mem. Nat. Hist. Mus. Vic., 27 167–174. 10.24199/j.mmv.1966.27.09.

Stefani, F., Benzoni, F., Pichon, M., Cancelliere, C., Galli, P., 2008. A multidisciplinary approach to the definition of species boundaries in branching species of the coral genus *Psammocora* (Cnidaria, Scleractinia). Zool. Scr. 37, 71–91. https://doi.org/10.1111/j.1463-6409.2007.00309.x.

Stefani, F., Benzoni, F., Yang, S.-Y., Pichon, M., Galli, P., Chen, C.A., 2011. Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in Stylophora (Cnidaria, Scleractinia). Coral Reefs 30, 1033–1049. https://doi.org/10.1007/s00338-011-0797-4.

Stern, D.L., 2013. The genetic causes of convergent evolution. Nat. Rev. Genet. 14, 751–764. https://doi.org/10.1038/nrg3483.

Stolarski, J., 2003. Three-dimensional micro- and nanostructural characteristics of the scleractinian coral skeleton: a biocalcification proxy. Acta Palaeontol. Pol. 48. https://www.app.pan.pl/archive/published/app48/app48-497.pdf.

Stolarski, J., Kitahara, M.V., Miller, D.J., Cairns, S.D., Mazur, M., Meibom, A., 2011. The ancient evolutionary origins of Scleractinia revealed by azooxanthellate corals. BMC Evol. Biol. 11, 316. https://doi.org/10.1186/1471-2148-11-316.

Struck, T.H., Feder, J.L., Bendiksby, M., Birkeland, S., Cerca, J., Gusarov, V.I., Kistenich, S., Larsson, K.-H., Liow, L.H., Nowak, M.D., Stedje, B., Bachmann, L., Dimitrov, D., 2018. Finding evolutionary processes hidden in cryptic species. Trends Ecol. Evol. 33, 153–163. https://doi.org/10.1016/j.tree.2017.11.007.

Suzuki, G., Keshavmurthy, S., Hayashibara, T., Wallace, C.C., Shirayama, Y., Chen, C.A., Fukami, H., 2016. Genetic evidence of peripheral isolation and low diversity in marginal populations of the *Acropora hyacinthus* complex. Coral Reefs 35, 1419–1432. https://doi.org/10.1007/s00338-016-1484-2.

Tahseen, Q., 2014. Taxonomy-the crucial yet misunderstood and disregarded tool for studying biodiversity. J. Biodivers. Endanger. Species 2, 128. https://doi.org/10.4172/2332-2543.1000128.

Tan, D.S.H., Ang, Y., Lim, G.S., Ismail, M.R.B., Meier, R., 2010. From 'cryptic species' to integrative taxonomy: an iterative process involving DNA sequences, morphology, and behaviour leads to the resurrection of *Sepsis pyrrhosoma* (Sepsidae: Diptera). Zool. Scr. 39, 51–61. https://doi.org/10.1111/j.1463-6409.2009.00408.x.

Taninaka, H., Maggioni, D., Seveso, D., Huang, D., Townsend, A., Richards, Z.T., Tang, S.-L., Wada, N., Kikuchi, T., Yuasa, H., Kanai, M., De Palmas, S., Phongsuwan, N., Yasuda, N., 2021. Phylogeography of blue corals (Genus *Heliopora*) across the Indo-West Pacific. Front. Mar. Sci. 8, 714662 https://doi.org/10.3389/fmars.2021.714662.

Taylor, J.G., Pearce, A.F., 1999. Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. J. R. Soc. West. Aust. 82, 57–65. https://www.rswa.org.au/publications/Journal/82(2)/82(2)taylor.pdf.

Tenison-Woods, J., 1878. On the extra tropical corals of Australia. Proceedings of the Linnean Society of New South Wales 2, 292–341, pls. 4–6.

Terraneo, T.I., Benzoni, F., Arrigoni, R., Berumen, M.L., 2016. Species delimitation in the coral genus *Goniopora* (Scleractinia, Poritidae) from the Saudi Arabian Red Sea. Mol. Phylogenet. Evol. 102, 278–294. https://doi.org/10.1016/j.ympev.2016.06.003.

Thomas, L., Kennington, W.J., Evans, R.D., Kendrick, G.A., Stat, M., 2017. Restricted gene flow and local adaptation highlight the vulnerability of high-latitude reefs to rapid environmental change. Glob. Change Biol. 23, 2197–2205. https://doi.org/10.1111/gcb.13639.

Todd, P.A., 2008. Morphological plasticity in scleractinian corals. Biol. Rev. 83, 315–337. https://doi.org/10.1111/j.1469-185X.2008.00045.x.

Umbgrove, J., 1940. Madreporaria from the Togian Reefs (Gulf of Tomini, North-Celebes. Zool. Meded. Leiden 22, 265–310. https://repository.naturalis.nl/pub/318138.

Underwood, J.N., Richards, Z., Berry, O., Oades, D., Howard, A., Gilmour, J.P., 2020. Extreme seascape drives local recruitment and genetic divergence in brooding and spawning corals in remote north-west Australia. Evol. Appl. 13, 2404–2421. https://doi.org/10.1111/eva.13033.

van der Meij, S.E.T., Suharsono, Hoeksema, B.W., 2010. Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920–2005). Mar. Pollut. Bull. 60, 1442–1454. 10.1016/j.marpolbul.2010.05.011.

van Keulen, M., Langdon, M.W., 2011. Ningaloo Collaboration Cluster: biodiversity and ecology of the Ningaloo Reef lagoon. CSIRO National Research Flagships. http://researchrepository.murdoch.edu.au/id/eprint/6174.

van Oppen, M.J.H., Koolmees, E.M., Veron, J.E.N., 2004. Patterns of evolution in the scleractinian coral genus *Montipora* (Acroporidae). Mar. Biol. 144, 9–18. https://doi.org/10.1007/s00227-003-1188-3.

van Oppen, M.J.H., McDonald, B.J., Willis, B., Miller, D.J., 2001. The evolutionary history of the coral genus *Acropora* (Scleractinia, Cnidaria) based on a mitochondrial and a nuclear marker: reticulation, incomplete lineage sorting, or morphological convergence? Mol. Biol. Evol. 18, 1315–1329. https://doi.org/10.1093/oxfordjournals.molbev.a003916.

van Oppen, M.J.H., Wörheide, G., Takabayashi, M., 2002. Nuclear markers in evolutionary and population genetic studies of scleractinian corals and sponges. In: Proc 9th Int Coral Reef Symp 1, 131–138. http://coremap.or.id/downloads/ICRS9th-vanoppen.pdf.

Vaughan, T.W., 1907. Some madreporarian corals from French Somaliland, East Africa, collected by Dr. Charles Gravier. Proc. U. S. Natl. Mus. 32, 249–266. https://doi.org/10.5479/si.00963801.32-1526.249.

Vaughan, T.W., 1918. Some shallow-water corals from Murray Island (Australia), Cocos-Keeling Island, and Fanning Island. Pap. Dep. Mar. Biol. Carnegie Inst. Washington 9, 49–234.

Veron, J.E.N., 1993. Corals of Australia and the Indo-Pacific. University of Hawaii Press edition, Honolulu.

Veron, J.E.N., 2000. Corals of the World, Volumes 1–3. Australian Institute of Marine Science, Townsville.

Veron, J.E.N., 2013. Overview of the taxonomy of zooxanthellate Scleractinia. Zool. J. Linn. Soc. 169, 485–508. https://doi.org/10.1111/zoj.12076.

Veron, J.E.N., 2002. New species described in *Corals of the World*. Volume 11. Australian Institute of Marine Science, Townsville. https://www.aims.gov.au/sites/default/files/New%20species%20described%20in%20Corals%20of%20the%20World.pdf.

Veron, J.E.N., Pichon, M., 1976. Scleractinia of Eastern Australia. Part I: Families Thamnasteriidae, Astrocoeniidae. Pocilloporidae. Aust. Inst. Mar. Sci. Monogr. Ser. 1, 1–86. https://doi.org/10.5962/bhl.title.60617.

Veron, J.E.N., Pichon, M., Wijsman-Best, M., 1977. Scleractinia of Eastern Australia – Part II. Families Faviidae. Trachyphylliidae. Aust. Inst. Mar. Sci. Monogr. Ser. 3, 1–233. https://doi.org/10.5962/bhl.title.60631.

Veron J.E.N., Stafford-Smith M.G., Turak E. and DeVantier L.M., 2016. Corals of the World. http://www.coralsoftheworld.org/species_factsheets/species_factsheet_summary/plesiastrea-versipora/?version=0.01. Accessed 2021-11-08.

Verrill, A.E., 1866. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853 to 1856. Collected by Dr. Wm. Stimpson, Naturalist to the Expedition. With descriptions of some additional species from the west coast of North America. Part III. Madreporaria. With two plates. Commun. Essex Inst. Salem. 5, 17–50, pls. 1–2. https://www.biodiversitylibrary.org/page/33204514#page/255/mode/1up.

Vollmer, S.V., Palumbi, S.R., 2004. Testing the utility of internally transcribed spacer sequences in coral phylogenetics. Mol. Ecol. 13, 2763–2772. https://doi.org/10.1111/j.1365-294X.2004.02265.x.

Vollmer, S.V., Palumbi, S.R., 2002. Hybridization and the evolution of reef coral diversity. Science 296, 2023–2025. https://doi.org/10.1126/science.1069524.

Wallace, C., 1999. Staghorn corals of the world: a revision of the genus *Acropora* (Scleractinia; Astrocoeniina; Acroporidae) worldwide, with emphasis on morphology, phylogeny and biogeography. Vic, CSIRO publishing, Collingwood.

Warner, P.A., van Oppen, M.J.H., Willis, B.L., 2015. Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. Mol. Ecol. 24, 2993–3008. https://doi.org/10.1111/mec.13225.

Wepfer, P.H., Nakajima, Y., Sutthacheep, M., Radice, V.Z., Richards, Z., Ang, P., Terraneo, T.I., Sudek, M., Fujimura, A., Toonen, R.J., Mikheyev, A.S., Economo, E.P., Mitarai, S., 2020. Evolutionary biogeography of the reef-building coral genus *Galaxea* across the Indo-Pacific ocean. Mol. Phylogenet. Evol. 151, 106905 https://doi.org/10.1016/j.ympev.2020.106905.

Wijsman-Best, M., 1972. Systematics and Ecology of New Caledonian Faviinae (Coelenterata - Scleractinia). Bijdr. Dierkd. 42, 3–90. https://doi.org/10.1163/26660644-04201001.

Wijsman-Best, M., 1974. Habitat-induced modification of reef corals (Faviidae) and its consequences for taxonomy. Proc. Second Int. Coral Reef Symp. 2, 217–228.

Wijsman-Best, M., 1977. Indo-Pacific coral species belonging to the subfamily Montastreinae Vaughan and Wells, 1943 (Scleractinia-Coelenterata): Part I. The genera *Montastrea* and *Plesiastrea*. Zool. Meded. 52, 81–97. https://repository.naturalis.nl/pub/318749.

Williams, H.C., Ormerod, S.J., Bruford, M.W., 2006. Molecular systematics and phylogeography of the cryptic species complex *Baetis rhodani* (Ephemeroptera, Baetidae). Mol. Phylogenet. Evol. 40, 370–382. https://doi.org/10.1016/j.ympev.2006.03.004.

Willis, B.L., van Oppen, M.J.H., Miller, D.J., Vollmer, S.V., Ayre, D.J., 2006. The Role of Hybridization in the evolution of reef corals. Annu. Rev. Ecol. Evol. Syst. 37, 489–517. https://doi.org/10.1146/annurev.ecolsys.37.091305.110136.

Witt, J.D.S., Threloff, D.L., Hebert, P.D.N., 2006. DNA barcoding reveals extraordinary cryptic diversity in an amphipod genus: implications for desert spring conservation. Mol. Ecol. 15, 3073–3082. https://doi.org/10.1111/j.1365-294X.2006.02999.x.

WoRMS Editorial Board, 2021. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2022-02-19. 10.14284/170.

Yiu, S.K.F., Chung, S.S.W., Qiu, J.W., 2021. A new species of the sun coral genus *Tubastraea* (Scleractinia: Dendrophylliidae) from Hong Kong. Zootaxa 5047, 1–16. https://doi.org/10.11646/zootaxa.5047.1.1.

Zann, L.P., 2000. The Eastern Australian region: a dynamic tropical/temperate biotone. Mar. Pollut. Bull. 41, 188–203. https://doi.org/10.1016/S0025-326X(00)00110-7.

Zar, J.H., 2010. Biostatistical analysis, fifth ed. Pearson Prentice Hal, Upper Saddle River, N.J.