Diversity, Phylogeography and Taxonomy of Hard Corals in the genus *Porites*

Thesis submitted by

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Statement of Contribution of Others

This thesis was done under the supervision of Prof. Andrew Baird, Prof. Michael L. Berumen, and Prof. David J. Miller. The samples used were collected by myself, Prof. Andrew H. Baird, Prof. Francesca Benzoni and Dr. Roberto Arrigoni, with small contributions from others as outlined in the chapters.
Contribution to individual chapters can be found in Table I.

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Table I. Statement of contribution to thesis chapters. TT is Tullia Isotta Terraneo, AHB is Andrew H. Baird, MLB is Michael L. Berumen, FB is Francesca Benzoni, RA is Roberto Arrigoni, KM is Kiruthiga G. Mariappan, MF is Marco Fusi.

Chapter	Statement of contribution
Chapter 1: Introduction	TT wrote the chapter with feedback from AHB and MLB
Chapter 2: Phylogenomics and phylogeography of Porites from the Indo-Pacific	TT, AHB, MLB conceived the research. TT, FB, RA collected the samples. TT performed genomic libraries preparation. KM mapped the reads to the coral transcriptome. TT performed genomic, species delimitation, and phylogeographic analyses. TT wrote the chapter with feedback from AHB.
Chapter 3: A quantitative approach to morphological species boundaries in *Porites*	TT, AHB, MLB conceived the study. TT imaged the samples and performed morphometric measurements. FB guided the morphological analyses. MF guided the statistical analyses. TT wrote the chapter with feedback from AHB.
Chapter 4: Reproductive traits as alternative live of evidence for species boundaries in *Porites*	TT, AHB conceived the study. TT and AHB collected the samples and performed reproductive experiments. TT wrote the chapter with feedback from AHB.
Chapter 5: General discussion	TT wrote the chapter with feedback from AHB and MLB.

Thesis abstract

Species are one of the fundamental units of biodiversity. Yet, defining a species remains a challenging task. The current consensus is that an integrative approach, using multiple lines of evidence, such as biology, ecology, morphology and genetics, is most appropriate for species delimitation. In the last two decades, molecular approaches coupled with a re-examination of morphology, have revolutionized our understanding of scleractinian taxonomy and phylogeny. Yet, some of the most abundant and species-rich genera, such *as Acropora, Montipora* and *Porites*, have proved more challenging. The genus *Porites* includes many species that are major contributions to coral reef structure and function. Moreover, species in the genus often serves as models for ecological, physiological and paleoclimate studies. Yet, the taxonomy of the genus *Porites* is notoriously difficult, which undermines both accurate assessments of biodiversity and the interpretation of experiment results. The aim of this thesis was to use an integrated approach that included reduced genome analyses, quantitative and qualitative morphological data, and breeding trials, to clarify the species richness, taxonomy and historical biogeography of *Porites* from 16 localities throughout the Indo-Pacific Ocean. I firstly evaluated the molecular diversity of *Porites* in the Indo-Pacific using high throughput sequencing data (RADseq), supplying a comprehensive hypothesis of the evolutionary history and historical biogeography of 27 nominal species and 12 morphotypes that did not correspond to any of the type material examined. The phylogenetic analyses recovered 16 molecular lineages, 11 of which were composed of only one species, while the remaining five contained unresolved groups of several nominal species plus unknown morphotypes. In most of these groups of species, a recent origin between 1.9 and 0.1 Mya, coupled with clear morphological differences, suggests recent or on-going speciation. Finally, historical distribution analyses suggest an Indian Ocean or Arabian origin for at least eight molecular lineages in the phylogeny reconstruction, while the origin of the remaining lineages remains unclear. I next used multivariate analysis to determine the number of morphological

groups based on 22 skeletal characters. Cluster analyses suggested there were 28 groups. PERMANOVA estimated that 95% of the variance was explained by the *a priori* morphological groupings (based on comparison to type material), while 64% of the variance was explained by the genomic clades. Further morphological analyses within each of the five unresolved groups of species recovered eight of the genetically unresolved nominal species, and also suggested that the status of 10 nominal species should be reconsidered. Finally, I tested barriers to gene flow between two nominal species of *Porites* that were not differentiated by the molecular analyses but have fundamentally distinct morphologies and ecologies: *Porites lutea* and *P. cylindrica*. Cross-fertilization did not occur, suggesting that they are good biological species. In conclusion, the taxonomy and evolutionary history of the genus *Porites* is highly complex and uncertain, with different lines of evidence suggesting different numbers of groups. In addition, there are many specimens that do not correspond to any of the type material, suggesting there are a number of undescribed species in the genus. A great deal of work is required to improve our understanding of the taxonomy and systematics of the genus, including the use of alternative molecular techniques, and sampling a greater proportion of the nominal species in the group

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1. CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 Scleractinian corals

Coral reefs are limestone structures widespread along the world's marine tropical belt. Although occupying only 0.1% of the ocean floor (Spalding & Grenfell, 1997), they host an outstanding biodiversity, comparable to that of rain forests (Connell et al., 1978). According to recent estimates, more than 25% of total marine life is supported by coral reefs, and nearly one third of total fish diversity inhabits reefs ecosystems (Appeltans et al., 2012; Bowen et al., 2013; Fisher et al., 2011). For these reasons, coral reefs are considered one of the most productive and complex ecosystems on the planet (Connell, 1978; Odum & Odum, 1955). Besides their intrinsic biological value, coral reefs are fundamental physical structures that dissipate wave energy and create sheltered environments, such as lagoons for seagrass and mangroves. At the same time, they provide costal protection, and supply food and income to millions of people in coastal communities (Moberg & Folke, 1999; Roberts, 2009). Recent estimates evaluated the asset value of coral reefs close to $1 trillion, with benefits from these ecosystems reaching at least 500 million people from over 90 countries (Gattuso et al., 2015; Hoegh-Guldberg et al., 2015).

Coral reefs are also extremely unstable communities, subject to recurrent natural disturbances (e.g. tropical cyclones, outbreaks of crown of thorns starfish *Acanthaster planci*, El Niño events, and bleaching) and anthropogenic activities (e.g. runoff of pollutants and nutrients, overfishing, oil rigs) (Hughes et al., 1992; Hughes et al., 2003; Munday et al., 2009), that make them one of the most endangered ecosystems on the planet.

The building blocks of coral reefs are stony corals (Cnidaria, Scleractinia), radially symmetrical invertebrates that diverged from near the base of the metazoan tree of life around 240 Ma (Romano & Palumbi, 1997). Within the sub-class Hexacorallia, which comprises five extant orders, *i.e.* Corallimorpharia, Actiniaria, Antipatharia and Zoantharia, the Scleractiania are distinguished by the ability to actively produce continuous aragonitic

skeletons with complex morphologies. Of the approximate 1400 extant coral species, almost 60% are colonial (Cairns, 1999), but solitary corals have evolved in at least six lineages (Barbeitos et al., 2010). Coral colonies are formed by connected units, *i.e.* the polyps, sharing integrated physiologies (Hughes et al., 1992). A total of 865 (55.9%) reef-building Scleractinia species (*i.e.* zooxanthellate corals) host within their endoderm symbiotic unicellular photosynthetic dinoflagellates of the family Symbiodiniaceae (https://www.coraltraits.org). This relationship restricts them to shallow environments in warm tropical regions, where they constitute the major framework builders of reefs. Azoxanthellate corals instead are found in a more diverse range of habitats, from shallow tropical waters, to aphotic regions up to 6300 m deep, as well as in Antarctic waters (Cairns, 1982) and the Arctic Circle (Roberts, 2009).

A healthy state of zooxanthellate corals (*sensu* Wells, 1933) is fundamental to support reef ecosystems. Nevertheless, in the last decades the proportion of threatened corals has increased dramatically (Bellwood et al., 2004; Knowlton, 2001). According to the International Union for Conservation of Nature (IUCN) Red Lists criteria, 35.3% of hermatypic reef coral are at elevated risk of extinction (Carpenter et al., 2008, https://www.coraltraits.org). Nevertheless, the extinction risk faced by individual coral species is still poorly understood. In an era of ongoing biodiversity loss, taxonomy has a direct impact on the designation of biodiversity hotspots, conservation schemes, and informing legislation (Agapow & Bininda-Emonds, 2004; Karl & Bowen, 1999; Mann & Plummer, 1992). Recently it has become clear that we lack basic knowledge of scleractinian taxonomy, especially at lower taxonomic levels, *i.e.* genus and species level. This gap of knowledge further compromises the status of coral reefs, challenging any species extinction-risk assessment (Bridge et al., 2020), and rendering the designation of conservation schemes an almost impossible challenge. This is in fact reflected in outdated species lists used by CITES https://speciesplus.net/. In the context of a flawed taxonomy, making

accurate estimates of the cumulative effects of climate change on coral biodiversity remains unrealistic.

1.2 Traditional taxonomy and systematics in the Scleractinia

The taxonomy and systematics of stony corals have a long and complex history (Esper, 1797; Forsskål, 1775; Lamarck, 1801; Linnaeus, 1758; Pallas, 1766), yet confusion in scleractinian classifications remains at every taxonomic level (Kitahara et al., 2016). Traditional classification of hard corals has been based largely on macro-skeletal characters (*i.e.* corallite level structures such as the calice, the septa, the pali, the columella, the costae) of extant and extinct taxa (see Fig. 1.1 for main coral skeletal features). These macro-features remained the main source of evidence for delimiting species and reconstructing evolutionary relationships among corals until the late 20th century. Starting from 1850, Milne Edwards & Haime (1857), Duncan (1885), and Ogilvie (1896), provided classifications of stony corals based solely on macro-skeletal features. Milne Edwards & Haime (1857, 1860) introduced a uniform terminology for coral morphological structures, and proposed the first comprehensive classification of stony corals. According to their hypothesis, the suborder Madreporaria included extant groups, the Aporosa and Perforata, and fossil taxa (Tabulosa, Tabulata, and Rugosa), together with other non hexacorallians (Vaughan & Wells 1943). Milne Edwards and Haime's subdivision was based on a series of skeletal features, comprising the wall structure (*i.e.* compact or porous), the subdivision of the visceral chamber (completely open or subdivided), and the septal arrangement (rudimentary or well developed). In 1885, Duncan added a sixth category to Milne Edwards and Haime subdivisions, the Fungida, adding as a distinctive morphological feature, the presence or absence of wall granulation. In the 20th century Vaughan & Wells (1943) and Wells (1956), revised the entire order and, on the basis of macro-morphological features, developed the "traditional" hard coral classification system. According to the principle that coral evolution could be explained by the animal skeletal features, Wells (1956) identified five suborders (Astrocoeniina, Fungiina, Faviina, Caryophyllina, Dendrophyllina) and 33

families (20 extant), providing the first hypothesis of evolutionary relationships among coral families (Fig. 1.2) (Budd et al., 2010). Wells' classification of stony corals was primarily based on the septal structural framework, particularly on the arrangement of trabeculae within the septa. Alloiteau (1957) and Chevalier & Beauvais (1987), proposed an alternative classification that used micro-structural data. On the basis of differences in septal ornamentation and the structure of the trabeculae, Alloiteau recognized eight suborders within the Scleractinia, and 71 (30 extant) families. Chevalier and Bauvais (1987) added three new suborders to the eight identified by Alloiteau, bringing the total to 11 suborders and 55 families (a schematic summary of the main classification systems mentioned above is provided in Table 1.1). Phylogenetic Systematics *sensu* Hennig (1999) is an evolutionary approach that was applied to morphological character traits (apomorph vs plesiomorph). This approach was performed for only a short period of time in scleractinian taxonomy (1984-2001), before molecular methods came into fashion. This approach was applied to Fungiidae (Cairns, 1984; Hoeksema, 1989, Hoeksema and Dai 1991), Turbinoliidae (Cairns, 1997), and Dendrophylliidae (Cairns, 2001). The most recent non-molecular phylogeny of corals was provided by Veron (1995), who recognized 13 sub-orders (6 extant) and 61 families (24 extant) (Fig. 1.3).

The reliance on qualitative skeletal morphological characters, and the failure to incorporate any evolutionary theory in these classification schemes was always likely to cause problems. As early as 1886, in a report on the Challenger Expedition, Quelch emphasized that coral morphology varied in response to the environment. With the 70' the importance of ecophenotypic variation on taxonomy started to be recognized (*i.e.* Wijsman-Best 1972). Experiments have since demonstrated that several environmental factors can influence coral morphology, such as light, sedimentation, wave action, depth, and salinity, and the effect that these factors have on coral morphologies varies among and within taxa (Bruno & Edmunds, 1997; Budd, 1993; Miller, 1994; Randall, 1976; Todd et al., 2008). During the past century, the concept of phenotypic plasticity, *i.e.* the capacity of a single genotype to express different

phenotypes in relation to different environments, has been largely regarded as environmental noise obscuring real evolutionary characteristics of organisms (Sultan, 2000). Nowadays, there is general agreement that phenotypic plasticity doesn't involve only morphological responses, but encompasses fundamental aspects of an organism physiology, life-history, and behaviour, that can enhance the organism's fitness in a certain environment. Trying to reconstruct animal evolution based exclusively on their phenotype, thus results in incorrect evolutionary hypotheses.

Morphological based taxonomy is subject to further limitations, such as convergent evolution *i.e.* the independent evolution of similar characters in species belonging to different evolutionary lineages, and homoplasy, *i.e.* the presence of similar features evolved independently in different lineages, that render making inferences about the evolution of corals following a traditional approach particularly challenging (Flot et al., 2011; Huang et al., 2014).

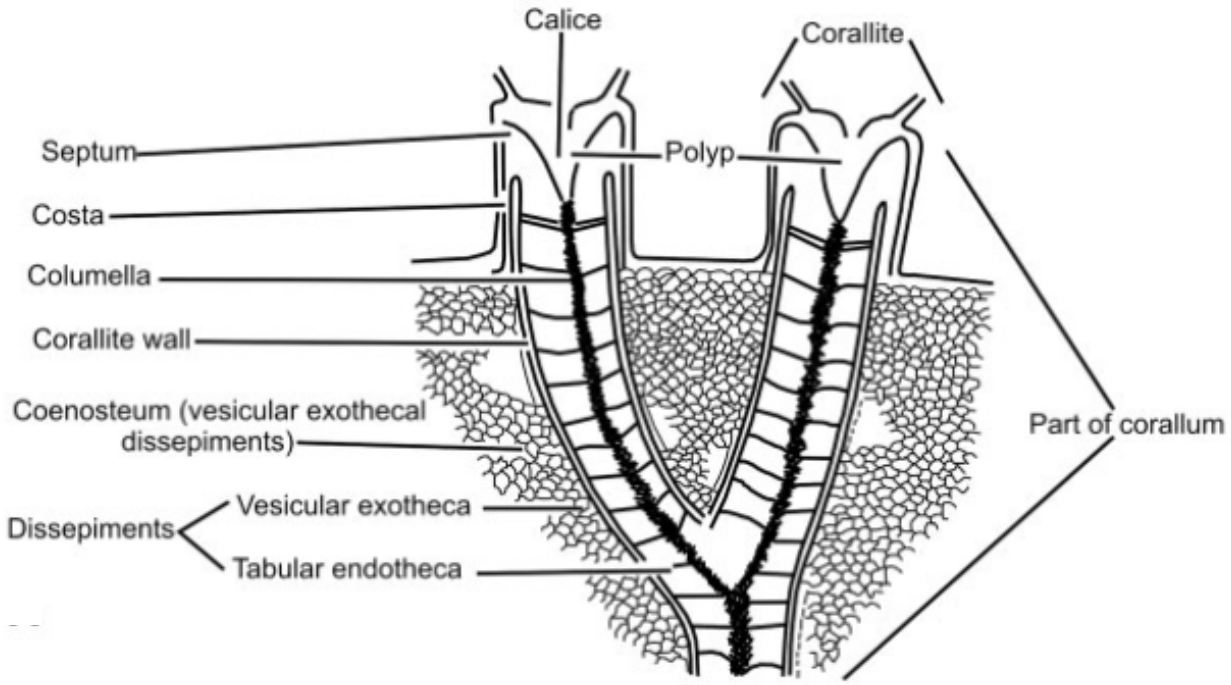


Figure 1.1 The main features of the coral skeletal used in traditional classifications. Modified from Wells (1956).

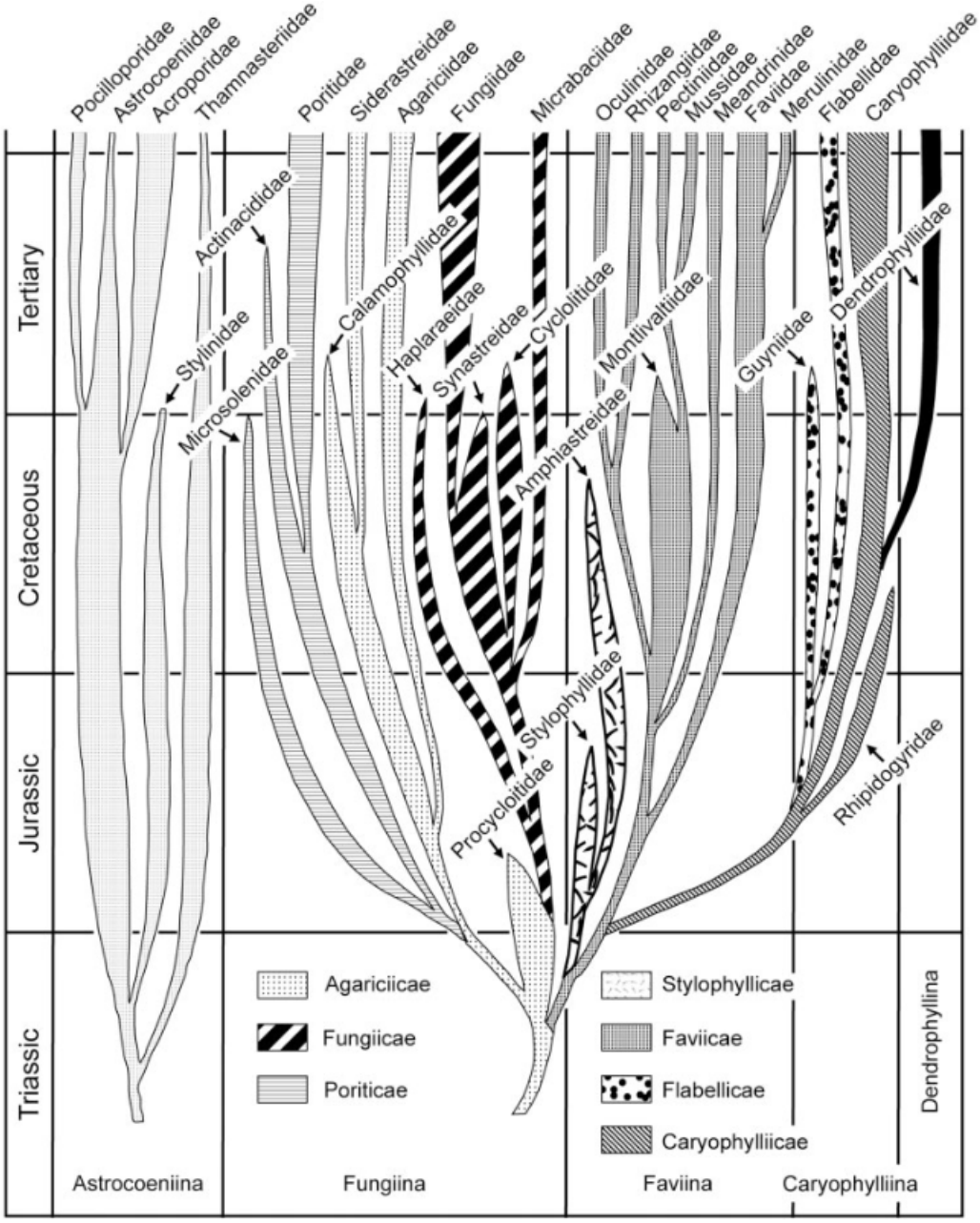


Figure 1.2 The classification system and evolutionary relationships among stony corals proposed by Wells (1956). Branches represent families, patterns represent superfamilies, and columns represent suborders.

Table 1.1 Summary of the main macro- and micro-skeletal features used to distinguish scleractinian suborders in the main classifications proposed during the 19th and 20th centuries (except Veron (1995)). (x) refer to fossil taxa.

Milne Edwards & Haime (1857)	Suborder	Distinctive morphological features
	Aporosa	Visceral chamber: empty or subdivided
		Septa: developed
		Wall: compact
	Perforata	Visceral chamber: empty or subdivided
		Septa: developed
		Wall: porose
	Tabulosa (x)	Visceral chamber: empty or subdivided
		Septa: rudimentary
	Tabulata (x)	Visceral chamber: subdivided
		Septa: rudimentary, exameral
	Rugosa (x)	Visceral chamber: subdivided
		Septa: developed, tetrameral
Wells (1956)		
	Astrocoeniina	Septa: laminar, simple spines
		Trabeculae: single, simple or compound
		Synapticulae: absent
	Fungiina	Septa: fenestrate
		Trabeculae: multiple, simple or compound
		Synapticulae: present
	Faviina	Septa: laminar, isolated spines
		Trabeculae: one or more fan system of multiple simple or compound
		Synapticulae: absent
	Caryophyllina	Septa: laminar

		Trabeculae: one fan system of multiple single
		Synapticulae: absent
	Dendrophyllina	Septa: laminar
		Trabeculae: one fan system of multiple simple
		Synapticulae: present
Alloiteau (1952)		
	Archaeocoeniidae	Synapticulae: absent
		Endotheca: developed
		Symmetry: radial
		Septa: discontinuous
		Trabeaculae: few
	Stylinida	Synapticulae: absent
		Endotheca: developed
		Symmetry: radial
		Septa: continuous
		Trabeaculae: few
		Synapticulae: present
	Fungiida	Endotheca: developed
		Symmetry: bilateral
		Septa: perforata
		Trabeaculae: continuous
		Synapticulae: present
	Astraeoida	Endotheca: developed
		Symmetry: radial
		Septa: continuous
		Septal ornamentation: present
		Trabeaculae: numerous
		Synapticulae: absent

	Meandriida	Endotheca: developed
		Symmetry: radial
		Septa: continuous
		Septal ornamentation: absent
		Trabeaculae: numerous
		Synapticulae: absent
	Amphiastraeida	Endotheca: developed
		Symmetry: bilateral
		Wall: archeotechal
		Synapticulae: absent
	Eupsammiida	Septa: perforata
		Trabeculae: discontinuous
		Synapticulae: present
	Caryophyllida	Septa: perforata
		Endotheca: rare, absent
		Synapticulae: absent
Chevalier and Beauvais (1987)		
	Stylophyllina	Septa: no plane
		Trabeculae: absent
		Sclerenchyma: lamellar
		Radial elements: thecal origin
	Pachytjecalina	Septa: no plane
		Trabeculae: absent
		Theca: fibrous
	Distichophyllina	Septa: mediosеptal plane with lateral axes
		Trabeculae: absent
		Wall: septal or paratechal
	Archaeocaeniina	Septa: no plane

	Trabeculae: present
	Synapticulae: absent
Stylinina	Trabeculae: simple
	Septal granulation: not connected
	Synapticulae: absent
Archeofungiina	Septa: no plane
	Trabeculae: present
	Synapticulae: present
Fungiina	Septa: perforata
	Trabecule: discontinuous
	Synapticulae: present
Faviina	Septa: perforata
	Endotheca: rare, absent
	Synapticulae: absent
Caryophylliina	Septal distal edge: smooth
	Endotheca: absent
	Trabecule: simple and compound
Dendrophylliina	Trabeculae: discontinuous, horizontal and vertical sclerodermites

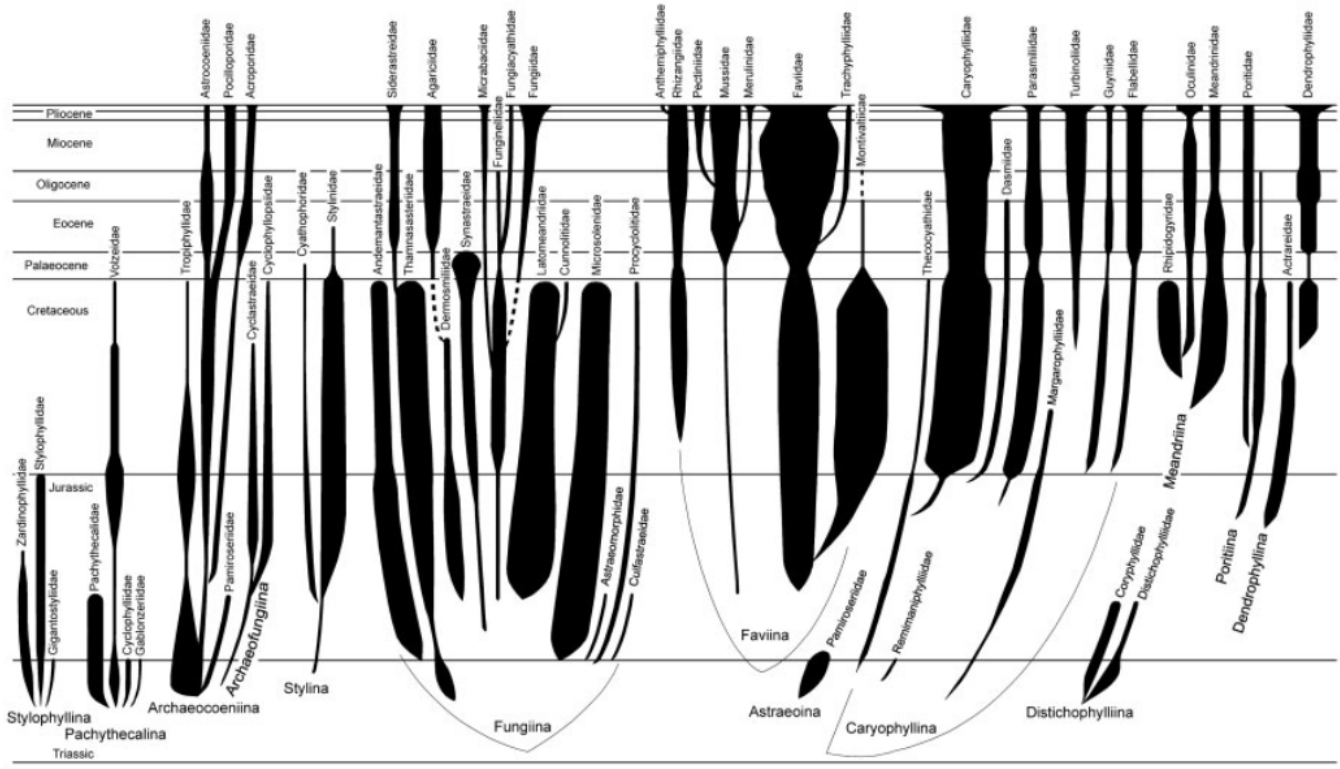


Figure 1.3 The classification system and evolutionary relationships among stony corals proposed by Veron (1995). Branches correspond to families. The width of the branches corresponds to the number of genera in each family.

1.3 The molecular revolution

Towards the end of the 20th century, the inadequacy of these contrasting schemes based on morphological traits was finally exposed with the emergence of molecular approaches to taxonomy (Kerr, 2005). This led to independent hypotheses on coral evolution, prompting revisions at every taxonomic level (Chen et al., 2002; Fukami et al., 2004, 2008; Goff-Vitry et al., 2004; Huang et al., 2011; Kerr, 2005; Romano & Cairns, 2000; Romano & Palumbi, 1996). Molecular phylogenetic reconstructions revealed that extant stony corals fall into three major groups, *i.e.* the Basal, Complex, and Robust clades, instead of the seven suborders recognized by Veron (1995) (Fig. 1.4).

A genetic-based system for systematically cataloguing metazoan biodiversity opened the era of "molecular taxonomy". Comparing

homologous DNA sequences, it became possible to identify species in many groups of organisms and assign them to higher taxonomic levels (Tautz et al., 2003). Generally, diverging lineages acquire different mutations through time, eventually creating unique signatures that can be indicative and distinctive among different taxa (de Queiroz, 1998). In this context, Hebert & Cywinska (2003) proposed a DNA barcoding system for animal life relying upon sequence divergence in the mitochondrial cytochrome c oxidase subunit 1 (COI) gene. Mitochondrial DNA (mtDNA) in animal genomes typically shows evolution rates 10 times higher than in nuclear DNA, is non-recombining, and lacks introns (Brown & George, 1979; Brown et al., 1982). Moreover, as mtDNA is maternally inherited and haploid, it has a smaller effective population size, leading to much faster lineage sorting (Birky et al., 1983). However, while mtDNA proved very useful for species level delineations in many animal taxa, it did not work for corals. As our knowledge of mtDNA increased, unique properties of mtDNA in different classes of cnidarians were identified. In the class Anthozoa, in particular, the mtDNA is characterized by slow evolution rates that render it unsuitable for inferring genus- and species-level relationships (France & Hoover, 2001, 2002; Hellberg, 2006; Huang et al., 2008; McFadden et al., 2006). Notably, Shearer & Coffroth (2008) demonstrated that intraspecific COI variation in Scleractinia, defined as the percentage of single nucleotide mutations in the COI gene among individuals of the same species, is much lower than in other metazoans, making it impossible to discern among hard coral species on the basis of the COI gene. Moreover, other mitochondrial genes commonly used in phylogenetic studies in metazoans, such as 16S rDNA, Cytochrome *b* (cyt*b*), 12S rDNA, ATP synthase 6 (ATP*s*6), and NADH dehydrogenase subunits 2, 3, 4, and 6 (NAD2, NAD3, NAD4L, NAD6) are less divergent between families in anthozoans than between congeneric species in other marine invertebrates (Shearer et al., 2002).

Nonetheless, recent studies have identified highly variable non-coding regions (DNA regions that do not encode for proteins) of the mtDNA containing evolutionary informative sites towards species level resolution in

some genera. The length of these regions in terms of base pairs is highly variable among different taxa so different regions are informative for different organisms, e.g. the putative control region located between ATP8 and COI and an open reading frame located between ATP6 and NAD4 genes can provide high resolution within the Pocilloporidae genera *Pocillopora*, *Seriatopora*, and *Stylophora* (Flot & Tillier, 2007; Flot et al., 2008; Flot et al., 2011; Pinzón et al., 2013; Schmidt-Roach et al., 2013). Meanwhile, the mitochondrial spacer between COI and 16S rRNA has been used to distinguish genera and species in the Agariciidae genera *Pavona* and *Leptoseris* (Luck et al., 2013; Pochon et al., 2015); in the genus *Pachyseris* (Terraneo et al., 2014); in the Merulinidae genera *Goniastrea, Paragoniastrea*, and *Merulina* (Huang et al., 2014); and in the genus *Sclerophyllia* (Arrigoni et al., 2015).

Cnidarian nuclear DNA (nDNA), on the other hand, accumulates mutations at the same rate as in other animals (Hellberg, 2006). The nuclear ribosomal DNA (rDNA) internal transcribed spacers ITS1 and ITS2 (ITS region) are the most commonly used markers to infer species level relationships within corals (Chen et al., 2004; Diekmann et al., 2001; Hunter et al., 1997; Lopez & Knowlton, 1997; Medina et al., 1999; Odorico & Miller, 1997; Van Oppen et al., 2002). rDNA constitutes a multigene family of tandem repeated units. Each unit consists of three highly conserved coding regions, 18S, 5.8S, and 28S, and two internal transcribed spacers (ITS1 and ITS2) located in-between. In many eukaryotic taxa, rDNA evolves via concerted evolution (Arnheim et al., 1980), a mechanism that homogenizes different ITS repeated units through unequal crossing over and gene conversion (Dover, 1982). In many cases, the rate of concerted evolution is enough to homogenize the variation among unit repeats within species, but interspecific divergence can be high (Hillis & Dixon, 1991).

In the past 20 years, a number of other nuclear genetic sequences have been used to infer coral phylogenies, such as the coding genes Calmodulin (CalM), ATPase β (ATPs β), β-Tubulin, mini-collagen, Pax-C 46/ 47 intron (PCI), and the histone cluster h2ab (Arrigoni et al., 2014; Forsman et al., 2009; Fukami

et al., 2004, 2008; Hatta et al., 1999; Márquez et al., 2003; Van Oppen et al., 2004; Vollmer & Palumbi, 2002; Wallace et al., 2007). These advance in molecular phylogenetics helped clarify species relationships for several taxa, yet uncertainty persists, and discrepancies among molecular markers are common. Coral molecular based phylogenies can also be problematic because of 1. hybridization (Veron, 1995), *i.e.* the breeding of individuals of two different species, 2. introgression, *i.e*. the incorporation of alleles from one species into the gene pool of another species following hybridization or backcrossing (Odorico & Miller, 1997; Diekmann et al., 2001; Van Oppen et al., 2000, 2001), and 3. incomplete lineage sorting, *i.e.* the retention of ancestral polymorphism in recent divergent species (Márquez et al., 2003; Queiroz, 2007). With regards to hybridization, synchronized spawning among numerous species of hard corals, *i.e.* mass spawning *sensu* Willis et al. (1985), is a feature of all speciose coral assemblages (Baird et al., 2009). The simultaneous release of large volumes of sperm and egg in a limited period of time creates an opportunity for hybridization and gene introgression (Miller, 1994; Willis et al., 1997; Márquez et al., 2003; Willis et al., 2006). So far, the only taxonomically accepted coral hybrid is the Caribbean *Acropora prolifera* (Lamarck, 1816). Crossing experiments and sequence data for the Caribbean species *A. cervicornis* (Lamarck, 1816), *A. palmata* (Lamarck, 1816), and *A. prolifera* show that, although the first two are genetically distinct species, the morphologically intermediate *A. prolifera* is a F1 hybrid (Van Oppen et al., 2000; Vollmer & Palumbi, 2002).

Although coral hybridization has been reported in *in-vitro* (reviewed by Willis et al., 2006), species boundaries should be established before seeking to hybridize species, and in general, the role of hybridization in driving evolution in corals is not clear (Wallace & Willis, 1994). Although hybridization has often been the answer to otherwise inconsistent reconstructions, the molecular techniques used in the last decades cannot discriminate between introgression and incomplete lineage sorting. In this context, more conservative explanations, such as incorrectly identified specimens, should be

considered, and more in-depth genome analyses are required to add evaluate the role of hybridization as a source of evolutionary novelty in corals.

The definition of species boundaries among species of recent origin remains to date challenging from a molecular point of view. Indeed, recent species divergence can account for low molecular diversity among morphologically distinct entities (Queiroz, 2007). For instance, based on allozymes, Miller & Benzie (1997) proposed that several nominal species of *Platygyra* were not different from a molecular point of view because they have yet to diverge genetically and develop complete reproductive isolation. Finally, ancestral polymorphisms can be hidden by a low rate of molecular evolution, large population size, and long generation time, as well as short generation time with overlap of generations (Van Oppen et al., 2004).

Recently, the proliferation of next-generation sequencing techniques, has offered the possibility to simultaneously investigate thousands of polymorphic markers in the genome, in a relative short amount of time and at a reduced cost. In particular, the development of Restriction site-Associated DNA Sequencing (RADSeq) (Baird et al., 2008) has proved a more powerful tool when resolving evolutionary, biogeographical, and phylogenomic questions than traditional molecular markers in many organisms (Reitzel et al., 2013). The approach consists of the production of short sequences (30-500bp) flanking restriction enzymes recognition sites, producing hundreds of thousands of loci in the genome and allowing the discovery of high-throughput single nucleotide polymorphisms (SNPs) (Andrews et al., 2016). On the basis of the number (one or more) of restriction enzymes used and the frequency of the enzymes activity, several RADSeq protocols have been developed. Some RADSeq methods produce sequence data from all the cut sites of the restriction enzyme (such as the original RADSeq and 2bRAD), while more recent methods rely on analysing sequences produced by two enzyme cut sites, separated by a chosen genomic distance (ddRAD or ezRAD for instance) (Andrews et al., 2016). Unlike other reduced-representation sequencing approaches, RADSeq does not necessary require prior genomic information,

thus it has become widely used for non-model organisms (Cruaud et al., 2014; Emerson et al., 2010; Herrera & Shank, 2016; Herrera et al., 2015; Wagner et al., 2013). With regards to marine invertebrates, RADSeq has been used to disentangle phylogeographic patterns and population genomics of the sea anemone *Nematostella vectensis* Stephenson, 1935 (Reitzel et al., 2013), and to successfully delimit species boundaries and reconstruct evolutionary relationships in the deep-sea octocoral genus *Chrysogorgia* (Pante et al., 2015). RADSeq analyses have recently been used to test for introgressive hybridization in *Pocillopora* in the Eastern Pacific (Combosch & Vollmer, 2015), and to clarify evolutionary relationships in the *Acropora* (Rosser et al., 2017), and *Porites* (Dimond et al., 2017; Forsman et al., 2017). However, as these studies demonstrate, Next Generation Sequencing approaches also have their limits. In Hawaiian *Porites* corals for example, genomic data failed to resolve two nominal species with strikingly different morphologies and ecologies: *P. lobata* Dana, 1846 and *P. compressa* Dana, 1846.

Following the unified species concept proposed by de Queiroz (1998), an integration of different lines of evidence seems necessary to achieve a better understanding of species boundaries and evolutionary relationships in the Scleractinia. According to de Queiroz, species can be considered as independent evolving metapopulation lineages (de Queiroz, 1998), and the plethora of species concepts designed by evolutionary biologist represent arbitrary demarcations imposed on the continuous process of speciation. Following this theory, these concepts should instead be regarded as "operational criteria" and integrated to provide different lines of evidence aimed at distinguishing different stages in the existence of a species. In fact, each species criterion corresponds to a different property that the lineages acquire during their divergence. As lineages diverge, for example they might acquire phenotypic differences, fixed genetic polymorphysms, and differentiate in their breeding systems or ecology. Nevertheless, in the context of a general evolutionary theory, no criterion should be regarded as prominent over the other nor definitive, yet their significance will be related to the

question of interest. Finally, these operational criteria should be regarded as criteria for different stages in the existence of a species (de Queiroz 1998).

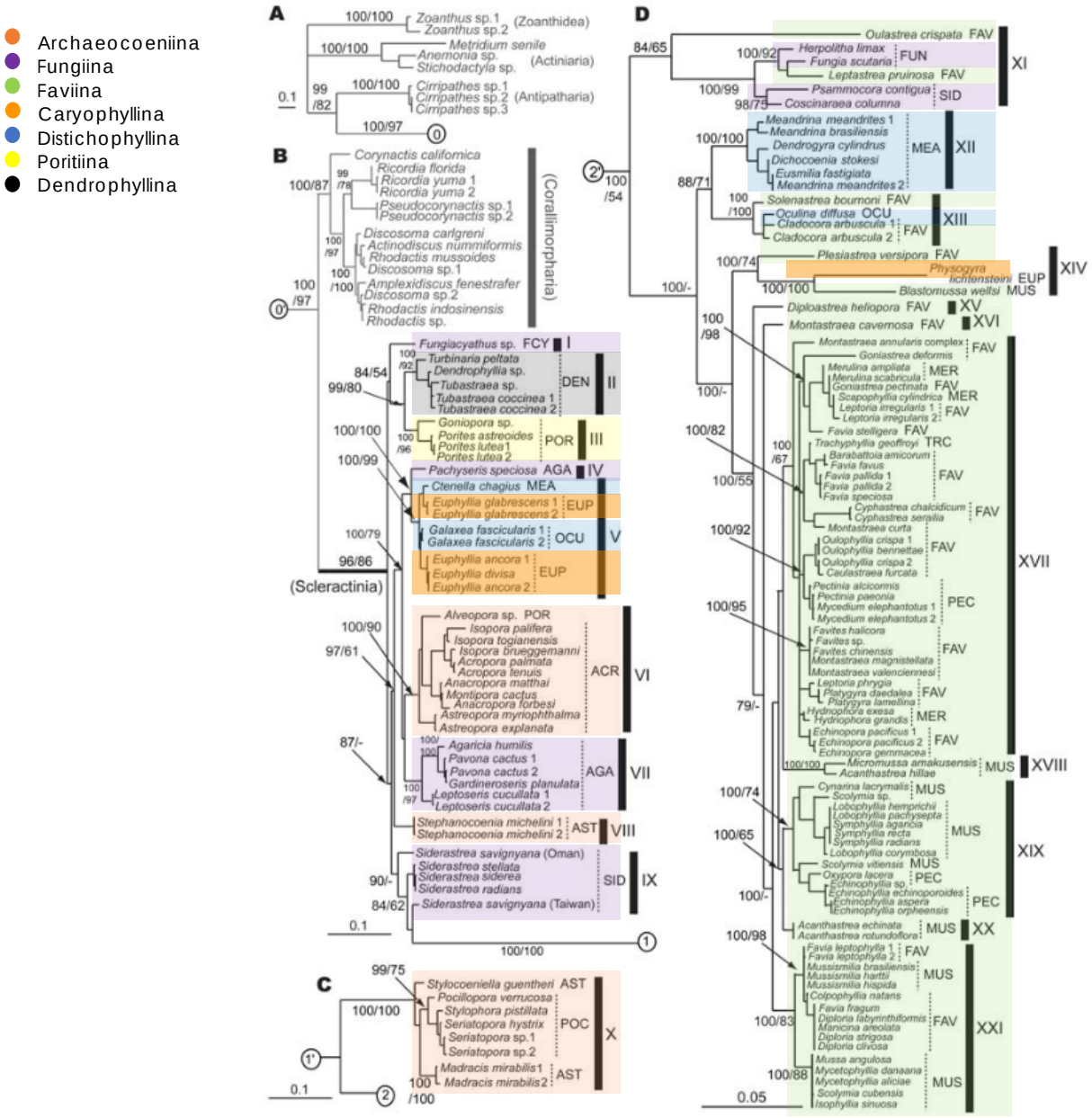


Figure 1.4 Phylogenetic relationships among scleractinian corals based on combined COI and CytB genes. Branch support represent Posterior Bayesian probabilities (>70%), and ML bootstrap values (>50%). Numbers in circles show connections among trees (A to D). Letter codes correspond to traditional coral families. Roman numbers indicate clade subdivisions according to the tree. Colors in the picture refer to coral suborders *sensu* Veron (1995) as outlined in the legend on the left side of the tree. Modified from Fukami et al., (2008).

1.4 The use of alternative characters to clarify coral evolution

The use of alternative line of evidence can prove useful in clarifying evolutionary relationships in corals when morphology and genetic evidence don't make sense or disagree. For example, evidence derived from Symbiodininiaceae associations and different responses to bleaching, helped clarifying boundaries between two morphologically different *Pocillopora* species belonging to the *P. acuta* species complex (Smith et al., 2017). In fact, although 3'179 SNPs failed to differentiate the two morphs, by integrating Symbiodininiaceae ITS2 data with genomic and morphological data, the authors concluded that the two morphs correspond to two lineages currently undergoing speciation (Smith et al., 2017). Further potentially useful lines of evidence for species delimitation include various aspects of coral reproductive biology, such as sexuality, the mode of larval development, the time of reproduction and cross-breeding trials.

Lately, thanks to the increasing number of publications investigating coral reproductive biology, our understanding of scleractinian life-histories has improved dramatically. We now possess knowledge of the sexual system of 1153 coral species (https://www.coraltrais.org), and the geographical range that these studies cover has expanded notably in recent times (Baird et al., 2009). Hard corals have two sexual systems: out-crossing simultaneous hermaphroditism or gonochorism (separate sexes), and two modes of larval development, brooding or broadcast-spawning (Kerr et al., 2011). In brooders, the fertilization phase takes place within the coral polyp that subsequently releases competent larvae; spawning corals instead release gametes, or gamete bundles, into the water column, where external fertilization and pelagic larval development occur. These binary systems offered a unique opportunity for studying corals reproductive traits evolution in a phylogentic framework. Using molecular based phylogenies, Kerr et al. (2011) investigated the systematic patterns of coral sexuality and reproduction, and concluded that, although coral sexuality is highly conserved at different taxonomic levels, the mode of larval development was not. The majority of scleractinian corals

are broadcast-spawning hermaphrodites (62.9%)(Kerr et al., 2011). Hermaphroditism appeared three times during scleractinian evolution, with only few cases of revision to gonochorism; whereas the mode of larval development is far more plastic, evolving independently in different taxa, with an evolution rate four times faster than for sexuality (Barid et al. 2009; Kerr et al., 2011).

Understanding the relationship among life history strategies, and population structures and connectivity is fundamental for clarifying speciation processes in corals. Mayr (1963) first used reproductive criteria to define species. In particular, features of the breeding system, including gamete recognition, and time of reproduction, can provide boundaries to gene flow in potentially interbreeding lineages. Gamete release in broadcast-spawning corals can be temporally restricted on the scale of hours, weeks, or months (Fukami et al., 2003; Willis et al., 2006), but most broadcast-spawning species have highly synchronized breeding events. The majority of spawning species having a single oogenic cycle during the year, therefore synchrony in gametes release is fundamental for successful fertilization by reducing gamete dilution and predation (Levitan et al., 2004). The nature of multi-species spawning events, where gametes belonging to many species get mixed in the water column, infers the existence of isolating mechanisms that maintain species boundaries in corals (Willis et al., 1997). In fact, despite simultaneous spawning, morphologically and genetic distinct corals co-exist in sympatry and coral species diversity is high, suggesting the existence of pre- or post-zygotic barriers that prevent hybridization. For example, fine-scale temporal barriers, gamete aging and incompatibility, gamete dispersal and dilution, ensure reproductive isolation among sympatric *Montastrea* species in the Caribbean (Levitan et al., 2004) and among *Acropora* species of similar morphologies on the Great Barrier Reef (Wolstenholme, 2004). Understanding the presence of mechanisms that prevent hybridization in corals could provide strong evidence for understanding where boundaries among coral species lie.

1.5 The genus *Porites*

The genus *Porites* Link, 1807 is ubiquitous on coral reefs in both the Atlantic and Indo-Pacific Oceans, as well as in the Red Sea (Veron, 2000). Colonies of *Porites* are among the major building blocks in coral reefs and occur in a wide variety of reef habitats, from back reefs and lagoons, to 30m deep or exposed walls (Frost, 1977). The genus consists of species that produce branching, laminar, encrusting and massive structures, up to 10m high and 5m wide that can be hundreds of years old (Veron, 2000).

Porites is morphologically distinct from other Scleractinia. Nevertheless, the high variability in skeletal features within individual corallum, coupled with high levels of geographic variation within the large geographical range of many nominal species, have challenged coral taxonomists since the 19th Century (Veron & Pichon, 1982). in the taxonomy of *Porites* remains one of the most problematic of all the Scleractinia (Veron, 2000).

The first descriptions date back to Pallas (1766), who grouped a number of specimens, now recognized as *Porites*, under the name *Madrepora porites*; this work was followed by Forsskål (1775), who described two variants, (a) and (b), of *Madrepora solida*, (later recognized as *Porites solida* (Forsskål, 1775) and *Porites lutea* Milne Edwards & Haime, 1851 by Klunzinger (1879)). The genus *Porites* was established by Link (1807) with a single species, *Porites polymorphus* (now recognized as *Porites porites* (Pallas, 1776), the type species of the genus. Lamark (1816) described 16 nominal species and provided a more rigorous description of the genus *Porites*: "*fixed, branching, lobate, or obtuse, with the free upper surface everywhere covered with the calices, which are regular, subcontiguous, superficial or excavated"*. Nine of Lamark's nominal species were later removed from the genus by De Blainville (1830). In 1848, Dana grouped the genus *Porites* with *Goniopora*, in the family Poritiidae. In his work, he recognized in *Porites* corallites the presence of 12 septa, a first circle of 5-6 pali surrounding a central point, and a second circle of granules, frequently forming V-shaped pali. Milne Edwards & Haime (1851) in their monograph, attempted to comprehensively describe the variety of different forms within

Porites, classifying 27 extant and one fossil species according to the growth form, the development of the columella, and the thickness of the walls. Interestingly, it was not until Bernard (1903) that the genus-specific pattern of septal fusion (Fig. 1.5) was identified, *i.e.* a total of 12 septa that included four lateral pairs, a dorsal directive, and a ventral triplet opposed to the dorsal directive. On the basis of this arrangement, plus the number of pali and denticles, and the presence or absence of the columella, *Porites* species have been further discriminated. The work of Bernard was a significant advance in the taxonomic history of *Porites*, yet the extreme variability of form and structure in the genus forced Bernard to abandon the Linnean system of nomenclature, and shift to an approach based on geographic location. Talking about all the variety of forms in *Porites* the author states: "*The forms of* Porites *are indeed like the stars in the heavens, which no man can count, but perhaps even harder to deal with than the stars, for they vary not only in position and magnitude, but also in shape and texture*". Veron & Pichon (1982) represents the most substantial and recent taxonomic work on *Porites*. Indeed, in this work, the authors considered 12 species of *Porites* occurring in eastern Australia, and synonymised 32 nominal species. Yet, for the majority of these, a morphological (neither qualitative nor quantitative) or a geographical rationale is lacking, and several species originally described from localities away from eastern Australia are synonymised and thus lost.

According to the World Register of Marine Species (https://www.marinespecies.org/, WoRMS), during the taxonomic history of the genus, 195 nominal extant species have been described, and this does not consider hundreds more subspecies and forms for which type specimens are deposited in museums. At present, 68 species are recognized as valid, 77 have been synonymized and 50 are defined as either *taxon inquirendum* or *nomen nudum* (http://www.marinespecies.org/scleractinia/index.php). For an overview of a *Porites* nomenclature see Appendix 1.1.

In the last decade, several studies have tried to enlighten the intricate taxonomy of *Porites* using a combination of morphological analyses and

molecular techniques. Forsman et al., (2009) first evaluated the evolutionary relationships among several nominal species of *Porites* form both the Pacific and the Atlantic Oceans using the rDNA ITS region, the mitochondrial COI and a mitochondrial putative control region. The work highlighted cryptic patterns of species diversity within *Porites*, and widespread lack of monophyly for both Atlantic and Pacific representatives. Yet the ribosomal reconstruction did discriminate the nominal species *P. astreoides* Lamarck, 1816, *P. lichen* (Dana, 1846), *P. bernardi* Gravier, 1909 (renamed as *P. gabonensis* form Gravier, 1910) and *P. colonensis* Zlatarski, 1990, and allowed the description of one new species *i.e. P. randalli* Forsman & Birkeland, 2009 from American Samoa (Forsman & Birkeland, 2009). Similarly, Benzoni & Stefani (2012) described *P. fontanesii* from the southern Red Sea using both molecular and corallite level analyses. Using 9 single copy nuclear markers, the ITS region, and a mitochondrial control region, Prada et al. (2014) tested species boundaries among three nominal species of branching *Porites* in the Caribbean, but none of the genetic analyses supported *P. divaricata* Le Suer, 1820, *P. furcata* Lamarck, 1816, and *P. porites* as distinct entities. Hellberg et al. (2016), Forsman et al. (2017), and Dimond et al. (2017) are the most recent contributions to the species problem in *Porites*. Hellberg et al. (2016) focused on Eastern and Central Pacific populations of *P. evermanni* Vaughan, 1907 and *P. lobata* Dana,1846, and using five single locus nuclear markers, the ITS region, and COI, the authors investigated species boundaries among 12 nominal Eastern Pacific *Porites.* Confirming the previous findings from Forsman et al. (2009), no corroboration between morphological identification and the genetic reconstructions was achieved for the analysed *Porites* species. Several unresolved groups of species were recovered along with evidence for introgression between *P. evermanni* and *P. lobata* in the eastern Pacific. Forsman et al. (2017) used NGS techniques, *i.e.* RADSeq, to disentangle an unresolved group of species containing *P. lobata* and *P. compressa* Dana, 1846 in Hawaii. These two species are generally considered to be morphologically and ecologically distinct however, molecular work suggests

that they are not genetically isolated (Forsman et al., 2009). Results from 21 ezRAD libraries similarly failed to resolve the two morphs, identifying more structure among geographic locations than between the putative morpho-species. Finally, Dimond et al. (2017), re-evaluated species boundaries among the three branching Atlantic *Porites*, using RADSeq by detecting diversity hidden by single genes approaches, and reconciling morphological and molecular findings.

The above work reveals a deep gap in our understanding of species boundaries and evolutionary relationships in *Porites*, that undermine the designation of conservation status and hence management of biodiversity. The IUCN, classifies 26.6% of *Porites* species as Vulnerable or worse in the Red List of Threatened Animals (for details regarding the meaning of the categories, the criteria adopted by the IUCN council, and the list of threatened species see https://iucnredlist.org). Such designations are meaningless and conservation efforts serious compromised if we cannot identify species. Similarly, this applies to CITES lists, that remain to date outdated (https://speciesplus.net). Clearly, there is an urgent need to improve coral taxonomy and identify the mechanisms shaping coral evolution and diversity.

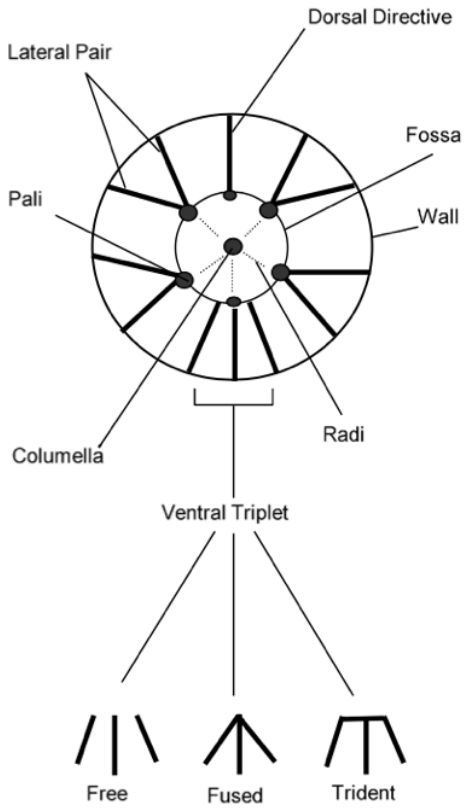


Figure 1.5 Schematic pattern of *Porites* corallites main skeletal features. Modified from Forsman (2015).

1.6 Project summary and objectives

The molecular revolution has revealed that traditional scleractinian taxonomy is flawed at every taxonomic level. The overall aim of this project is to use evidence from different approaches to improve the taxonomy and better understand the evolutionary history of *Porites* in the Indo-Pacific, and provide a framework for a future revision of the genus. As general outline, in Chapter 1, I provided a literature review highlighting the existing gap of knowledge in the understanding of the evolution and systematic of Scleractinia, with a focus on the genus *Porites*. In Chapter 2, I used ezRAD sequencing coupled with species delimitation analyses in order to evaluate the molecular diversity of the genus at several localities in the Indo-Pacific Ocean, and to reconstruct historical and biogeographical patterns of diversity. In Chapter 3, I use

morphological characters and multivariate morphometrics to identify groups and then compare these groups to the nominal species and the molecular clusters recovered in chapter 2. In Chapter 4, I tested for the presence of barriers to reproduction among two nominal species, *P. cylindrica* and *P. lutea*. These two-nominal species are molecularly indistinguishable based on the RADSeq data, yet are morphologically and ecologically distinct. Finally, in Chapter 5 I provided an integrated summary of the achieved results and proposed future research directions, towards a rigorous revision of the genus *Porites*.

2. CHAPTER 2: PHYLOGENOMICS AND PHYLOGEOGRAPHY OF *PORITES* FROM THE INDO-PACIFIC

2.1 Abstract

The advent of high throughput sequencing technologies provides an opportunity to resolve phylogenetic relationships among closely related species. By incorporating hundreds to thousands of unlinked loci and single nucleotide polymorphisms (SNPs), phylogenomic analyses have a far greater potential to resolve species boundaries than approaches that rely on only a few markers. Scleractinian taxa have proved challenging to identify using traditional morphological approaches and many groups lack an adequate set of molecular markers to investigate their phylogenies. In this chapter, I examined the potential of Restriction-site Associated DNA sequencing (RADseq) to investigate phylogenetic relationships and species boundaries within the recalcitrant coral genus *Porites*. In this chapter, I reconstructed phylogenomic relationships of 27 nominal species of *Porites* and 12 unknown morphotypes collected from 16 localities in the Indo-Pacific Ocean and seas around the Arabian Peninsula. Reference mapping was used to retrieve and compare nearly complete mitochondrial genomes, ribosomal DNA locus, and the histone region. Reference mapping to the *P. lobata* coral transcriptome was used to obtain loci and SNPs from coral datasets. Phylogenomic analyses and species delimitation approaches (Bayesian Factor delimitation) recovered 16 molecular lineages, 11 of which were monophyletic and five of which comprised of several nominal species and morphotypes. Of the 11 monophyletic lineages, 8 match the types of nominal species, suggesting these are valid species, and 3 lineages that are endemic to either the Gulf of Aden or New Caledonia likely represent new species awaiting description. The status of the remaining 19 nominal species and 9 morphotypes of *Porites* awaits further research. In the context of the well-supported phylogenetic hypothesis, I then reconstructed a time-calibrated phylogeny, and estimated ancestral

distribution patterns of *Porites* lineages in the Indo-Pacific. These analyses suggested that 8 molecular lineages originated in the western Indian Ocean around 6.8 Mya, an hypothesis that would corroborate the increasing evidence for a Neogene origin of shallow tropical corals, in geologically active regions of the Indian Ocean. Yet the origin of the remaining lineages remains unclear, and this hypothesis can't be confirmed. Finally, the two clades with the highest number of nominal species (clade V- 8 nominal species and clade XIII-12 nominal species) have a relatively recent origin around 1.15 and 1.53 Mya. This recent origin of many nominal species might explain the lack of genomic divergence among taxa with different morphologies.

Keywords: ezRAD, dDocent, species delimitation, systematics, coral

2.2 Introduction

Understanding species boundaries and evolutionary relationships among organisms is a key goal in biology. Recent advances in molecular and computational techniques have revolutionized our understanding of the systematics of numerous organisms (Faircloth et al., 2012; Puritz et al., 2014). Restriction-sites-associated fragmentation of genomic DNA (RADseq) is an effective method for harnessing the power of high throughput sequencing technologies (NGS) (Baird et al., 2008), providing genomic-wide data and a large number of homologous markers for non-model organisms (Pante et al., 2015). RADseq is currently the most widely used genomic approach for high-throughput single nucleotide polymorphism (SNP) discovery and genotyping in non-model organisms (Pante et al., 2015; Forsman et al., 2017). It allows for the simultaneous discovery and genotyping of thousands of polymorphic loci throughout the genome, without requiring any prior genomic resource for the study taxon (Baxter et al., 2011). Closely related species share orthologous restriction sites, thus RADseq is generally used to infer recent evolutionary history (Laché et al., 2015; Harvey et al., 2016; Gottscho et al., 2017). However,

it has also been used to clarify more distant evolutionary relatedness going back to the Paleocene (Rubin et al., 2012; Eaton & Ree, 2013; Cariou et al., 2013; Hipp et al., 2014).

Anthozoans are an ancient and ubiquitous group of benthic marine invertebrates, for which high levels of morphological variation, phenotypic plasticity, and few available orthologous conserved markers, have hindered a clear understanding of their evolutionary history (Prada et al., 2008; Paz-García et al., 2015; Herrera & Shank 2016; Quattrini et al., 2018). The systematics of the class has historically been based primarily on colony morphology, which is known to be highly variable and phenotypically plastic (Todd et al., 2008), and thus misleading towards reconstructing species level relationships. These animals have very simple body plans, with few morphological characters (Daly et al., 2003). Moreover, molecular studies have uncovered widespread homoplasy and convergent evolution of morphological characters within the subclasses Hexacorallia, Octocorallia, and Ceriantharia (Fukami et al., 2004; Stampar et al., 2014; Ament-Velásquez et al., 2016). The use of molecular barcoding has also proved unsuccessful because of a slow rate of evolution of mitochondrial DNA (Hellberg, 2006; Huang et al., 2008), the presence of divergent paralogous copies in the nuclear ribosomal DNA (Odorico & Miller, 1997; Sánchez & Dorado, 2008), and the lack of phylogenetically informative nuclear genes (Conception et al., 2008; McFadden et al., 2010). Incomplete lineage sorting, hybridization, a failure to adequately account for heterozygosity in nuclear genes, and poor taxonomy have combined to create topological discordance between gene and species trees and affect the use of molecular markers to infer meaningful phylogenies (Mcfadden & Hutchinson, 2004; Flot et al., 2010; Ament-Velásquez et al., 2016; Terraneo et al., 2016; Pratlong et al., 2017). Recently, RADseq has been used to untangle the phylogeny of the octocoral genera *Chrysogorgia*, *Paragorgia,* and *Ovabunda* (Pante et al., 2015; Herrera & Shank, 2016; McFadden et al., 2017), and to clarify species boundaries within the scleractinian genera *Pocillopora*, *Porites*, and *Montipora* (Combosch & Vollmer, 2015; Forsman et al., 2017,

Dimond et al., 2017; Johnston et al., 2017; Cunha et al., 2019) with mixed success.

The family Poritidae Gray, 1840 represents a major component of coral communities worldwide (Bellwood & Hughes, 2001), and in particular, the genus *Porites* Link, 1807 is the second-most speciose hermatypic coral genus (Hoeksema & Cairns, 2020). Nevertheless, species boundaries and evolutionary relationships within *Porites* remain largely unresolved (Forsman et al., 2009, 2017; Terraneo et al., 2019a). Several of the morphological traits traditionally used to separate species in *Porites* have proved to be affected by stasis and convergent evolution, and informative morphological synapomorphies have yet to be evaluated for the whole genus (Smith et al., 2007; Forsman et al., 2015; Tisthammer et al., 2018). So far, multi-locus phylogenetic reconstructions have successfully revealed the presence of undescribed species but have also suggest unresolved species complexes (Forsman & Birkeland, 2009; Forsman et al., 2009; Benzoni & Stefani, 2012; Prada et al., 2014; Hellberg et al., 2016; Terraneo et al., 2019a). Moreover, the use of coalescent analyses on seven genes, showed patterns of introgression in two eastern pacific species (Hellberg et al., 2016). Next generation sequencing (RADseq) has been successful in distinguishing three nominal species of *Porites* in the Caribbean (Dimond et al., 2017). Nevertheless, thousands of ezRAD obtained SNPs could not distinguish between morphological variability and hybridization in *P. compressa* Dana, 1846 and *P. evermanni* Vaughan, 1907 in Hawaii, highlighting that this technique has its limits (Forman et al., 2017).

The use of phylogenomic reconstruction, together with the integration of distributional and fossil data, is widely applied to provide hypotheses of species evolution through space and time, and ultimately to inform about the dynamics underlying regional diversity patterns. Hard corals represent good candidates for such reconstructions thanks to their calcium carbonate skeletons, which results in an extensive fossil record. The integration of these methods has been successfully applied to evaluate divergence times of Scleractinia and provide hypotheses of diversification within the order (Storlaski

et a., 2011; Huang et al., 2017; Arrigoni et al., 2018, 2019). Yet, so far there is no reconstruction of the diversification of lineages within the genus *Porites*, or hypotheses of the ancestral distributions.

In this chapter, I reconstructed phylogenomic relationships of 27 nominal species of *Porites* and 12 unknown morphotypes collected from 16 localities in the Indo-Pacific Ocean and seas around the Arabian Peninsula. I reconstructed molecular phylogenies mapping nearly complete nuclear ribosomal DNA and histone regions. I compared these reconstructed trees with the phylogeny obtained from 163,637 genome-wide SNPs data from the coral dataset. I then applied coalescent-based species delimitations to explore relationships and boundaries among the analysed species. Finally, I reconstructed a dated phylogeny of the genus, and provided an hypothesis of ancestral range distribution of *Porites* in the Indo-Pacific.

2.3 Materials and Methods

2.3.1 Collection and identification

A total of 595 *Porites* colonies were collected from 18 localities spanning the Indian and Pacific Oceans, and the seas around the Arabian Peninsula between 2013 and 2018 (Appendix 2.1, Appendix 2.2). Each coral colony was imaged underwater with a Canon G15 camera and a portion of the colony was collected with hammer and chisel. At the surface, a small piece (<1cm) of tissue from each colony was preserved in 98% ethanol or CHAOS solution and stored for genomic analyses, the remainder of the sample was bleached with sodium hypochlorite for 24h and air-dried for morphological examination (see below). Specimens are deposited at James Cook University (JCU, Australia), University of Milano-Bicocca (UNIMIB, Italy), King Abdullah University of Science and Technology (KAUST, Saudi Arabia), Institute de Recherche pour le Développement (IRD, New Caledonia), National University of Singapore (NUS, Singapore), Sultan Qaboos University (Oman) and Qatar University

(Qatar) under unique voucher numbers (Appendix 2.1). Dried skeletons were imaged with a Canon G15 camera. A subset of skeletons was imaged with a Leica M80 microscope equipped with a Leica IC80HD camera at KAUST, and a Leica M80 microscope at UNIMIB, IRD, and at JCU. Nominal species were assigned qualitatively following comparisons with original descriptions and, when available, type material. Table 2.1 summarises the characters derived from *Porites* holotypes, type series or original descriptions that were used to identify the specimens. The references for all the original descriptions are listed in Appendix 1.1 and the images of the available holotypes are listed in Appendix 2.3.

Table 2.1 Morphological characters derived from the *Porites* types and original descriptions, and used to qualitatively match samples with nominal species. For the species highlighted in bold, specimens were identified by comparison with the type material, as referenced in Appendix 1.1. For the species not highlighted, specimens were identified by comparison with the original descriptions, as referenced in Appendix 1.1. The type locality of the nominal species, sampling localities, genomic defined clade, total number of analysed samples, and total number or retained samples for SNPs analyses are also given. SA = Saudi Arabian Red Sea, KA = Kamaran Islands, Yemen, DJ = Djibouti, SO = Socotra Island, Yemen, Y = Yemen, AD = Aden – Yemen, BA = Bir Ali – Yemen, P = Balhaf – Yemen, BU = Burum – Yemen, MA = Mayotte Island, TOM = Oman, QA = Qatar, MD = Madagascar, MY = Mayotte, SI = Singapore, PFB = Papua New Guinea, TAU–GBR = Great Barrier Reef – Australia, TAU–Lord Howe Is = Lord Howe Island – Australia, TAU – Coral Sea = Coral Sae – Australia, AU–GBR = Great Barrier Reef – Australia, AU–Solitary = Solitary Islands – Australia, HS = New Caledonia, MQ = Marquesas Islands.

	Type locality	**Sampling localities**	**Corallum morphology**	**Columns/ Branches tips**	**Corallite dimension**	**Corallite depth**	**Corallite shape**	**Number of pali**	**Coenosteum**	**Coenosteum surface**	**Denticles**	**Ventral triplet**	**Molecular clade**	**Total N of ezRAD samples**	**Total N of ezRAD samples for SNPs**
P. fontanesii	Balhaf, Yemen	SA, DJ, SO, Y	nodular	rounded	0.9-1mm	shallow	rounded	5 to 7	developed	ornamented with spines	1	fused	I	10	5
P. columnaris	Red Sea	AD, BA, DJ, P, PFB, SA, TAU-GBR, Y, MD	columnar	tapered	2 mm	deep	angular	4 to 5	not developed	not developed	1	not fused	II	20	16
***P.* sp 1**	-	HS, TAU-Lord Howe Is	encrusting	0	2 mm	deep	angular	4 to 5	not developed	not developed	1	not fused	II	3	3
***P.* sp 2**	-	HS, TAU-Coral Sea	massive	0	2 mm	deep	angular	4 to 5	not developed	not developed	0	not fused	II	4	2
***P.* sp 3**	-	HS, SO	encrusting	0	1.5 mm	shallow	angular	6	not developed	not developed	1 to 2	fused	II	3	3

P. farasani	Marka, Red Sea	SA	encrusting	0	1-1.06 mm	moderately deep	rounded	6	slightly developed	ornamented with spines	1	fused	III	3	3
P. rus	Red Sea	AD, BA, DJ, HS, MA, MD, MY, SA, SI, TAU-GBR, Y	submassive	rounded	0.6-0.8 mm	shallow	rounded	5 to 6	developed	spongy, papillate	0 to 1	fused	IV	27	15
P. monticulosa	Fiji	HS, MD, MY, PFB, SA, SI, TAU-GBR-Coral Sea,	columnar, lobed	rounded	0.6-0.8 mm	shallow	rounded	5 to 6	developed	spongy, papillate	0 to 1	fused or not fused	IV	20	12
P. hadramauti	South Burum, Yemen	BU	encrusting	0	0.7-0.8 mm	shallow	rounded	5	slightly developed	ornamented with spines	1	fused	VI	1	1
***P.* sp 4**	-	DJ, MD, MY, P, TOM	massive	0	0.9-1 mm	shallow	angular	6	not developed	not developed	1	fused	VII	9	7
P. somaliensis	Marabout, Djibouti	DJ, MD, MY, P, SA	massive	0	0.8-1 mm	shallow	angular	5	slightly developed	smooth, compact	0	not fused	VIII	6	5
P. profundus	Nosy Be, Madagascar	MD, MY	branching	tapered, sometimes bifurcated	2.5 mm	very deep	angular	0	not developed	not developed	0	0	IX	8	6
***P.* sp 5**	Sulu Sea, Philippines	MD, MY	branching	tapered or squared	1.2 mm	moderately deep	angular	4 to 5	not developed	not developed	0 to 1	not fused	IX	4	2
***P.* sp 6**	-	MD, MY	foliouse,	0	1.5 mm	moderately deep	rounded	4 to 5	not developed	not developed	0	0	IX	4	4
***P.* sp 12**	--	HS	encrusting	0	<1 mm	moderately deep	rounded	0 to 5	developed	ridges, spines	2	not fused	X	3	3

P. hawaiiensis	Kalihi Harbour, Oahu, Hawaii	MQ	encrusting	0	0.8 mm	shallow	rounded	6	developed	spines	1 to 3	fused	XI	3	3
***P.* sp 7**	-	HS	lobed	angular	1.5 mm	deep	angular	5	not developed	not developed	0	not fused	XII	8	5
P. flavus	Milne Bay, Papua New Guinea	HS, TAU-GBR-Coral Sea	branching	slightly tapered	0.8 mm	shallow	rounded	4 to 6	developed	granulated	1	fused	XIV	20	7
P. deformis	Pinamungajan, Cebu	HS	nodular	rounded	1.5 mm	shallow	angular	5 to 8	not developed	not developed	1	fused or not fused	XV	5	3
P.* cf *horizontalata	Pago Pago Harbor, Tutuila, Samoa	HS, MD, MY, PFB, SI, TAU-GBR	encrousting, foliouse	0	1 mm	moderately deep	angular	6	developed	ridges	>1	fused or not fused	XVI	15	8
P. annae	Great Barrier Reef, Australia	AD, DJ, KA, SA, TOM, Y, SO	nodular	rounded	1.1-1.5 mm	moderately deep	angular	5 to 6	not developed	not developed	0	fused or not fused	V	13	9
P. arnaudi	Clipperton Atoll	MQ	submassive, tiered plates	0	0.8-1.4 mm	moderately deep	angular	6 to 8	not developed	not developed	1 to 2	fused or not fused	V	14	11
P. australiensis	Murray Island, Australia	HS, TAU-GBR-Coral Sea	massive	0	1-1.5 mm	shallow	angular	5 to 8	not developed	not developed	1 to 2	not fused	V	12	4
P. cylindrica	Fiji	HS, MY, PFB, SI, TAU-GBR-Coral Sea	branching	rounded	1 mm	shallow	rounded	6 to 7	developed	granulated	1	fused	V	31	11
P. harrisoni	Quwait	QA	submassive, columnar	rounded	1-1.5 mm	moderately deep	angualr	6 yo 8	not developed	not developed	1 to 2	fused or not fused	V	8	2

P. lobata	Hawaii	DJ, HS, MD, MY, P, SA, TAU-GBR-Coral Sea	massive	0	1.1-1.2 mm	moderately deep	angular	8	not developed	not developed	0	not fused	V	26	16
P. lutea	Tongatabou	BA, DJ, HS, MD, MY, QA, SA, SI, SO, TAU-GBR-Coral Sea, TOM	massive	0	1 to 1.5 mm	shallow	angular	5 to 6	not developed	not developed	0 to 1	fused	V	58	36
P. cf *reticulum*	Dar es Salaam, Tanzania	MD, SO	branching	rounded or tapared	0.7-0.9 mm	shallow	angular	5 to 6	not developed	not developed	1 to 2	fused or not fused	V	5	5
***P.* sp 9**	-	AD, BA, BU, P, SA	encrusting	0	1-1.5 mm	shallow	angular	5 to 6	not developed	not developed	1	fused	V	7	5
***P.* sp 10**	-	MD, MY	encrusting	0	1.2 mm	moderately deep	rounded	6 to 8	developed	granulated	1	not fused	V	4	4
***P.* sp 11**	-	SI	massive, submassive	0	1 mm	shallow	angular	5 to 8	not developed	not developed	1 to 3	fused or not fused	V	10	7
P. solida	Red Sea	DJ, HS, MY, P, SA, SO, TAU-Coral Sea	massive	0	1.25-1.75 mm	deep	angular	0 to 8	not developed	not developed	0	not fused	V	19	12
P. sillimaniani	Sumilan Island, Philippines	TAU-GBR	branching	tapered	<1 mm	moderately deep	rounded	5 to 8	developed	granulated ridges		fused or not fused	XIII	4	3
P. lichen	Fiji	AU-GBR, HS, MY, PFB, TAU-GBR, TAU-Lord Howe Is	encrusting	0	0.8-1.2 mm	moderately deep	angular	5 to 8	not developed	not developed	0	fused or not fused	XIII	60	37
P. negrosensis	Negros Island, Philippines	PFB, TAU-GBR	branching	flat	0.8-1.2 mm	moderately deep	rounded	6 t 8	developed	granulated ridges	2	fused or not fused	XIII	14	4

P. vaughani	-	TAU-GBR	encrusting	0	1-1.1 mm	shallow	rounded	5 to 7	developed	spiked ridges	0	fused or not fused	XIII	10	7
***P.* sp 8**	-	AU-Solitary-TAU-GBR-Lord Howe Is	encrusting, plate like	0	1-1.5 mm	shallow	rounded	5 to 8	not developed	not developed	0	fused or not fused	XIII	17	12
P. heronensis	Heron Island, Queensland, Australia	TAU-Lord Howe Is	encrusting, nodular	0	1.1.-1.5 mm	shallow	rounded	5	not developed	not developed	1	fused or not fused	XIII	12	3
P. tuberculosus	Flores, Indonesia	MY, HS, PFB, TAU-GBR-Coral Sea	branching	tapered or squared	1.6-2 mm	moderately deep	rounded	5 to 8	developed	granulated ridges	0	not fused	XIII	15	7

2.3.2 DNA extraction and quantification

Genomic DNA was extracted using DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) for samples stored in ethanol or using a phenol-chloroform-based method for samples stored in CHAOS solution. Extracted DNA was quantified with the Qubit dsDNA High Sensitivity Assay kit (Thermo Fisher Scientific, Waltham, MA, USA) using Qubit® fluorometer (Thermo Fisher Scientific, Waltham, MA, USA).

R*estriction enzyme digestion and ezRAD libraries preparation*

Samples were first analysed using traditional molecular tools (mtCR Sanger sequencing) following Terraneo et al., 2019a, b. Based on these first results, samples were selected for Next Generation Sequencing and analyses (results not shown).

I followed protocols by Toonen et al., (2013) and Knapp et al., (2016) for DNA digestion and ezRAD library preparation. Each sample was digested using frequent cutter restriction enzymes MboI and Sau3AI (New England BioLabs, Ipswich, MA, USA) to cleave sequences at GATC cut sites (Toonen et al., 2013). Digestions were performed in a 50 µl reaction volume consisting of 43 µl dsDNA (about 1.2-1.3 µg), 5 µl of Cutsmart Buffer (New England BioLabs, Ipswich, MA, USA), and 1 µl of each undiluted restriction enzyme, under the following thermocycler profile: 37° C for 3 hours followed by 65° C for 20 minutes. Digested samples were cleaned using Agencourt AMPure XP beads (Beckmann Coulter, Danvers, MA, USA) at a 1:1.8 (DNA:beads) ratio following the standard protocol. The concentration of cleaned digests was checked with Qubit® Fluorometer 3.0 (Thermo Fisher Scientific, Waltham, MA, USA). A total amount of 200 ng of each digested DNA sample was used for the library preparation using the TruSeq® Nano DNA Library prep kit (Illumina, San Diego, CA, USA), following the manufacture protocol. Libraries were size-selected at 350 bp and passed through two quality control steps, *i.e.* bioanalyzer and qPCR, to check size and concentration, respectively. Finally, ezRAD libraries were normalized and combined. Each library pool was run in a single 150 bp

paired-end lane on Illumina HiSeq 4000 System at KAUST Genomics Core Lab (Thuwal, Saudi Arabia). Sample information with sequenced lengths and number of reads are available upon request.

2.3.3 ezRAD data processing

The Illumina raw data consisted of 2,876,144,069 - 150 bp reads. Samples were de-multiplexed using their unique barcode and adapter sequences, effectively removing reads that lacked identifiable barcode pairs. An average of 4,899 million reads per individual (N = 587) were trimmed, assembled, and genotyped using dDocent v.2.25 (Puritz et al., 2014).

The trimmed reads were first assembled to the transcriptome of *P. lobata* obtained from Forsman et al., (2017) using Bowtie v.2 2.3.4 (Langmead and Salzberg 2012). Later, the aligned reads were converted to bam format using SAMtools v.1.6 (Li et al., 2009) and then converted to fastq using BEDtools v.2.26.0 (Quinlan and Hall 2010). These binned files were then copied to a separate folder and genotyped using dDocent v.2.25 (Puritz et al., 2014). In short, the reads were trimmed using Trimmomatic v.0.36 (Bolger et al., 2014), merged using PEAR v.0.9.6 (Zhang et al., 2013) and aligned to the reference transcriptome again using BWA v.0.7.15 (Li and Durbin 2009) under the settings -t 16 -a -M -T 10 –R. SNPs were finally identified using FreeBayes (Garrison and Marth 2012), as mentioned in Forsman et al., (2017).

The coral VCF file was further filtered using VCFtools v.0.1.16 (Danecek et al., 2011). A total of 65 samples were removed from the analyses because of low quality. A first supermatrix was generated with 522 samples using the following filtering options: mean depth = 3, max missing data = 50%, and minimum distance between SNPs = 5. A total of 312 of the 587 samples were furthered sub-selected and filtered in order to maximize the number of SNPs available for phylogenomic reconstructions, maintaining the same number of geographic localities and nominal species. To examine the sensitivity of the phylogenetic inference to the filtering process, I generated three filtered supermatrices for this dataset. I obtained the “coral-max” supermatrix using

the following filter options: mean depth = 3, max missing data = 50%, and minimum distance between SNPs = 5. Conversely, I generated the "coral-min" supermatrix under mean depth = 10, max missing data = 10%, and minimum distance between SNPs = 150. Finally, intermediate filters were used to generate the "coral-med" supermatrix under mean depth = 5, max missing data = 25%, and minimum distance between SNPs = 75. Haplotypes were then called and filtered for complex loci, potential paralogs, missing data, and sequencing errors using the rad_haplotyper v.1.1.8 pipeline (https://github.com/chollenbeck/rad_haplotyper; Willis et al., 2017). Contigs were collapsed into genotypes for final analyses. PGDspider v.2.1.1.5 (Lischer and Excoffier 2011) was used to convert the dataset to the required file types for further analysis. The "coral-max" supermatrix contained 163,637 SNPs, the "coral-min" 1,937 SNPs, the "coral-med" 9,499 SNPs. Each of the resulting three concatenated loci supermatrices was analysed in RAxML-HPC2 v.8.0 (Stamatakis 2014) for maximum likelihood (ML) phylogenetic inference. I applied the GTR + GAMMA substitution model and the branch support was assessed by 1000 bootstrap replicates. ML analyses were run on the CIPRES Science Gateway (Miller et al., 2010).

Following Terraneo et al., submitted, Johnston et al., 2017 and Forsman et al., 2017, the holobiont matrix was not included. In fact, in these works the high concordance between the coral and holobiont reconstructions highlighted that non-coding regions or other components in the coral holobiont (coral, algae, bacteria, fungi, microbes, and other organisms) either do not impair the detection of the phylogenetic signal of the coral protein coding genes and/or, to some extent, exhibit a similar pattern (Terraneo et al., submitted; Johnston et al., 2017; Forsman et al., 2019).

2.3.4 Reference assemblies and phylogenetic analyses of histone, and rDNA regions

One of the main benefits of ezRAD among the other RADseq techniques is that ezRAD provides a mix of breadth and depth of coverage (Toonen et al., 2013; Stobie et al., 2019). While depth of coverage is important to accurately

genotype SNPs, breadth of coverage can result in very long contigs, resulting in the resolution of the complete or a large percentage of the mitochondrial genomes (mtGenomes) and other multicopy gene regions such as histones and ribosomes. Therefore, I used reference mapping against previously published reference sequences to acquire and compare from each library histone region (histone), and nuclear ribosomal DNA array (rDNA, including the complete 18S, ITS1, 5.8S, ITS2, and 28S regions). I used the nearly complete histone (5,301 bp) and rDNA (6,629 bp) sequences of *Porites superfusa* Gardiner, 1898 obtained by Forsman et al., (2017) as reference. Trimmed reads were aligned to the three reference sequences using Bowtie v.2.3.4 (Langmead and Salzberg 2012) in --fast-local mode. Aligned reads were converted to bam and indexed using SAMtools v.1.6 (Li et al., 2009), and the consensus sequences were identified using SAMtools mpileup combined with Vcfutils.pl.

I aligned histone, and rDNA sequences using MAFFT v.7 (Katoh & Standley, 2013) (all alignment data are available upon request). I determined the optimal among-gene partitioning scheme and model choice in PartitionFinder v.2 (Lanfear et al., 2012) under the Bayesian Information Criterion (BIC). The rDNA dataset was partitioned in five partitions (18S, ITS1, 5.8S, ITS2, and 28S), the histone dataset was partitioned by genes and codon position. Phylogenetic relationships based on these two datasets were inferred using two phylogeny reconstruction methods, *i.e.* bayesian inference (BI) and ML. Bayesian phylogenetic inference was performed with MrBayes v.3.2.6 (Ronquist et al., 2012) using two independent runs of four chains. Chains were started from random trees and run for 10 million generations each, being sampled every 1000 generations. Stationarity from each independent run was assessed in Tracer v.1.6 (Rambaut & Drummond, 2007) by checking that the effective sample sizes (ESS) of all parameters were greater than 200 and the first 10% of trees were discarded as burn-in before generating the consensus tree. ML trees were inferred with RAxML-HPC2 v.8.0 (Stamatakis, 2014), using the GTR + GAMMA model of nucleotide substitution. Node support was

assessed using 1000 bootstrap replicates. Analyses were run on the CIPRES Science Gateway (Miller et al., 2010).

2.3.5 Species delimitation analysis

I used Bayes Factor Delimitation (BFD*) to rank species delimitation models in a multispecies coalescent framework (Leaché et al., 2014). Briefly, BFD* consists of running SNAPP analyses (Bryant et al., 2012) on models with different numbers of species and assignments of individuals to species, estimating the marginal likelihood of each model, and ranking model fit among runs by comparing Bayes factors (BF). The BFD* approach uses path sampling to estimate the marginal likelihood (MLE) of a population divergence model directly from SNPs data (without integrating over gene trees) and is robust to a relatively large amount of missing data (Leaché et al., 2014), being especially suited for RADseq data. I tested the following three models: (A) one single species; (B) assigning individuals according to the 16 molecular clades recovered in the concatenation-based phylogenies (a total of 16 species); (C) traditional taxonomy (a total of 39 species). I performed the BFD* analysis using the SNAPP package (Bryant et al., 2012) implemented in BEAST v.2.5.2 (Bouckaert et al., 2014). I estimated MLE of each model by running path sampling with 48 independent steps (chain length of 100,000 MCMCs with a pre-burnin of 10,000 steps). Model convergence was assessed by monitoring the ESS for the likelihoods of each path using Tracer v.1.6 (Rambaut & Drummond, 2007). I ranked the alternative species delimitation models by their MLE and calculated the corresponding BF to compare the models. The strength of support from BF ($2 * [MLE_{best} - MLE_{alternative}]$) comparisons of competing models was evaluated using the framework of Kass & Raftery (1995).

2.3.6 Divergence time analysis

In order to provide estimates of the divergence time of each *Porites* molecular clade, morphotype, and nominal species, a time-calibrated phylogenetic hypothesis was inferred based on a concatenated matrix of all protein-coding genes of the mtGenomes. I used reference mapping of one sample for each nominal species, morphology, and molecular clades (N=39), against the complete mtGenome of *Porites lobata* Dana, 1846 (NC030186, 18,647 bp). Trimmed reads were aligned to the reference sequence using Bowtie v.2.3.4 (Langmead & Salzberg, 2012) in --fast-local mode. Aligned reads were converted to bam and indexed using SAMtools v.1.6 (Li et al., 2009), and the consensus sequences were identified using SAMtools mpileup combined with Vcfutils.pl. Three additional mtGenomes were downloaded from NCBI: the outgroup *Goniopora columna* (NC015643), *P. panamensis* Verrill, 1866 (NC024182), and *P. porites* (Pallas, 1766) (NC008166). *Porites panamensis* occurs along the western coasts of Central America (Eastern Pacific), while *P. porites* in the Caribbean and in the Cape Verde islands in the East Atlantic. Given the sister relationships between these two *Porites* species (Terraneo et al., 2018a, b), I hypothesised that the closure of the Isthmus of Panama caused the vicariance between *P. panamensis* and *P. porites*. Therefore, I used the split between them as the calibration point for the timetree. Although an earlier and complex emergence of the Isthmus of Panama between 23 and 7 million years ago (Ma) has been proposed (Bacon et al., 2015; Montes et al., 2012), it is now largely accepted that Isthmus formation and complete separation occurred around 3 Mya (O'Dea et al., 2016). In order to narrow the confidence intervals of the analyses, and increase overall confidence of the timing, a second calibration point around 37 Mya at the end of the Eocene was included in the analyses. This calibration point corresponds to the oldest fossil occurrence of *Porites* recovered to date (Simpson et al., 2011, http://paleodb.org/).

Alignment and model selection were done as described above. The analysis was carried out under a Bayesian framework using BEAST v.2.5.2 (Bouckaert et al., 2014), with an uncorrelated (lognormal) clock model, and a

birth-death prior process with incomplete sampling. I ran two analyses of 100 million generations each, with sampling every 10,000 generation. I used Tracer v.1.6 (Rambaut & Drummond, 2007) to inspect the log files. I removed the first 10% of the trees from each analysis as burn-in, used LogCombiner v.2.5.2 (Bouckaert et al., 2014) to merge the files with the remaining trees, and a maximum clade credibility chronogram with mean node heights was computed using TreeAnnotator v.2.5.2 (Bouckaert et al., 2014). The mtGenome of the closely related *G. columna* Dana, 1846, together with four representatives of the sister family Dendrophyllidae (*Tubastrea coccinea* Lesson, 1830 – KX024566, *Turbinaria peltate* (Esper, 1794) – NC024671, *Dendrophyllia arbuscula* van der Horst, 1922 – NC030352 and *D. cribrosa* Blanville, 1830 – NC027590), were used to root the phylogeny (Terraneo et al., 2018a).

2.3.7 Historical biogeographical analyses

The maximum clade credibility tree was obtained using BEAST2 and was used as the dated input tree to study the historical biogeography of *Porites* in the Indo-Pacific with the R (R Core Team, 2018) package BioGeoBEARS v.1.1 (Matzke, 2013). The tree was pruned to exclude all outgroup sequences and to include only a single representative of each extant species.

Based on the current distribution patterns of *Porites* species derived from this work and previous literature (Veron, 2000; Veron et al., 2015), five biogeographical areas were defined for the ancestral range analyses: (A) Arabian seas, (I) Indian Ocean, (P) Pacific Ocean, (E) East Pacific Ocean, (C) and the Caribbean. The range of a taxon corresponds to the entire geographic distribution of that taxon, while areas are geographic units. Finally, the range might comprise one or more areas. The maximum number of areas in the distribution range of each species was set at three since all the extant species occur in a maximum of three areas. The AIC was used to select the model that best fits the data among the four analysed BioGeoBEARS models: DEC, DEC+J, DIVALIKE, DIVALIKE+J (Ronquist 1997; Ree & Smith, 2008; Matzke,

2014). DEC is the likelihood-based Dispersal-Extinction Cladogenesis model implemented in the LAGRANGE software package (Ree & Smith, 2008). DIVALIKE is a likelihood version of the parsimony-based Dispersal-Vicariance Analysis model (Ronquist, 1997). The '+J' versions of these models include a founder-effect speciation parameter and this allows a descendant to occupy a different area than its immediate ancestor (Matzke, 2013). Likelihood Ratio Tests (LRT) were used to compare the two pairs of nested models (DEC vs. DEC+J, DIVALIKE vs. DIVALIKE+J). Ancestral ranges were then estimated under the best-fit model.

2.4 Results

2.4.1 Morphological identification of Porites

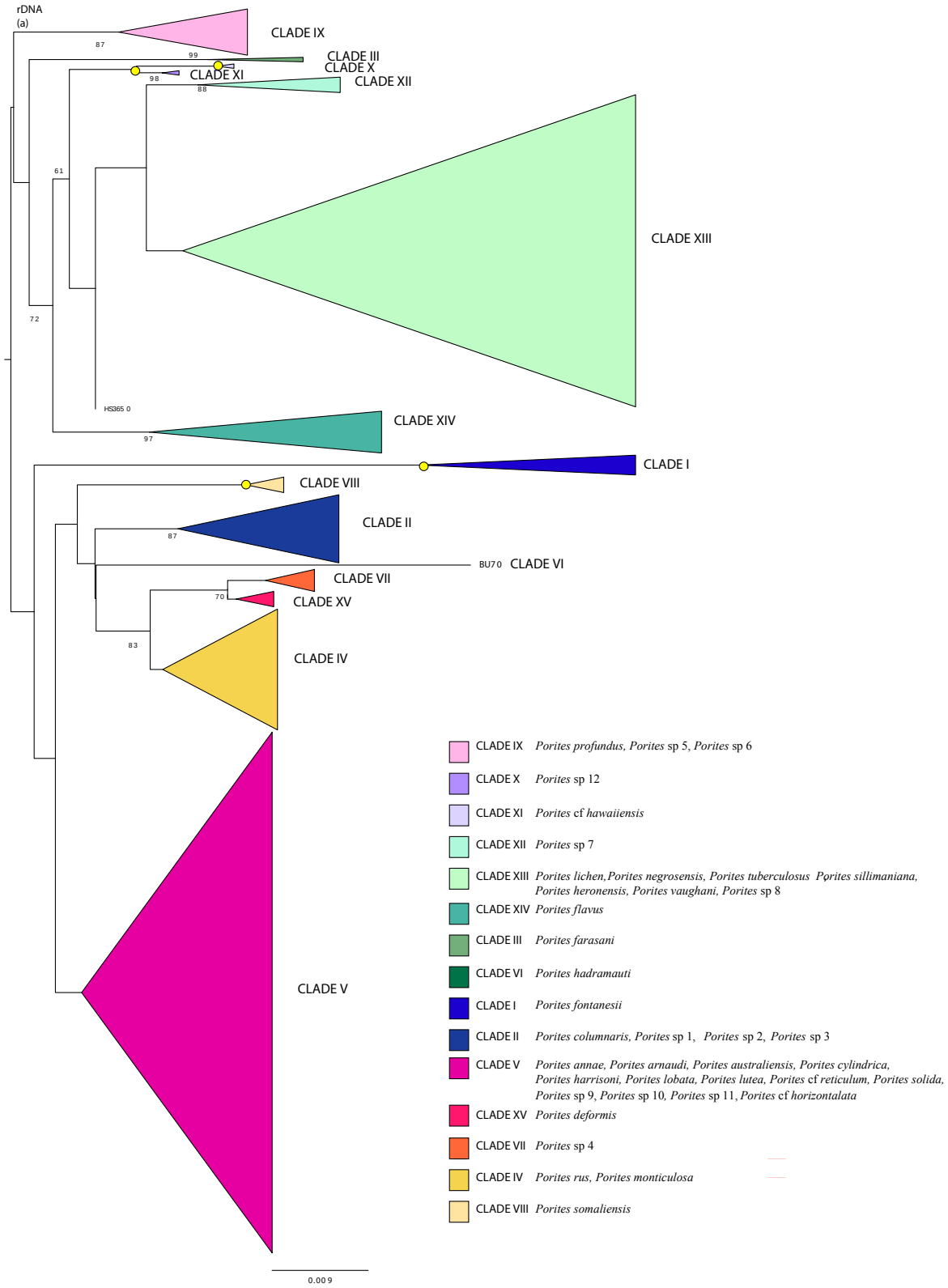
The 595 collected colonies were assigned to 27 nominal species and 12 unknown morphotypes (hereafter *Porites* sp 1 to 12) as summarized in Table 2.1 and Appendix 2.1.

2.4.2 Histone, and rDNA phylogenetic analyses

Mapping paired end reads to the *P. superfusa* histone and rDNA resulted in coverage of 94% (mean depth 376 ± 371 s.d) and 96% (mean depth 795 ± 854 s.d) of the reference sequences. The histone (n=547) and rDNA (n=567) alignments were 5,371 bp and 7,252 bp long, respectively. The histone alignment contained 1,232 variable sites, of which 394 were singleton sites and 838 were parsimony informative sites, while a total of 745 variable sites, with 209 singleton and 536 parsimony informative sites were present in the rDNA. The BI and ML topologies from the two datasets were mostly congruent, and clustered *Porites* samples into 15 (rDNA) and 13 (histone) highly supported molecular clades (clades I to XVI – clade number is consistent with Terraneo et al., 2019a, b– Fig. 2.1 a, b, Appendix 2.4). The reconstructions differed in the position of *Porites* sp 4 and *Porites deformis* Nemenzo, 1955, as well as the lack

of *Porites fontanesii* Benzoni & Stefani, 2012 data in the histone reconstruction, as outlined below. In the rDNA reconstruction, 11 clades were comprised of samples belonging to a single nominal species or morphology, and their monophyly was highly supported: clade I = *P. fontanesii*; clade III = *Porites farasani* Benzoni & Terraneo, 2019; clade VI = *Porites hadramauti* Benzoni & Terraneo, 2019; clade VII = *P.* sp 4; clade VIII = *Porites somaliensis* Gravier, 1910; clade X = *Porites* sp 12; clade XI = *Porites* cf *hawaiiensis* Vaughan, 1907; clade XII = *Porites* sp 7; clade XIV = *Porites flavus* Veron, 2000; clade XV = *P. deformis.* In the histone reconstruction the number of clades nesting a single nominal species or morphotype was nine. These corresponded to the same clades identified in the rDNA reconstruction, with the exception of *P. sp* 4 (clade VII in the rDNA phylogeny) and *P. deformis* (clade XV in the rDNA phylogeny). According to the histone reconstruction, these nested into a single clade, while *P. fontanesii* samples (clade I in the rDNA phylogeny), could not be aligned with the remaining data. Moreover, in the histone topology an additional monophyletic clade (clade XVI) was recovered, clustering *Porites* cf *horizontalata* Hoffmeister, 1925 specimens, otherwise nested within clade V in the rDNA topology. In both reconstructions, specimens of *Porites columnaris* Klunzinger, 1879, *Porites sp* 1, *Porites sp* 2, *Porites sp* 3 clustered within clade II. *Porites rus* (Forskål, 1775) and *Porites monticulosa* Dana, 1846 clustered within clade IV. Specimens of *P. annae* Crossland, 1952*, Porites arnaudi* Reyes-Bonilla & Carricart-Ganivet, 2000*, Porites australiensis* Vaughan, 1918*, P.* cf *horizontalata* (rDNA only), *Porites cylindrica* Dana, 1846*, Porites harrisoni* Veron 2000*, P. lobata, Porites lutea* Milne Edwards & Haime, 1851*, Porites* cf *reticulum* Ortman, 1892 and *Porites solida* (Forskål, 1775) clustered within clade V, together with *Porites* sp 9, *Porites* sp 10, *P*orites sp 11. Clade IX included samples of *Porites profundus* Rehnber, 1892, together with *Porites* sp 5 and *Porites* sp 6. Finally, clade XIII was comprised of *Porites lichen* (Dana, 1846)*, Porites tuberculosus* Veron, 2000*, Porites negrosensis* Veron, 1990*, Porites sillimaniana* Nemenzo, 1976*, Porites heronensis* Veron, 1985*, Porites vaughani* Crossland, 1952*,* and *Porites* sp 8. The topologies highlighted the presence of a deep

divergence in the phylogeny, with one group (A) comprising clades I (rDNA only), II, IV, V, VI, VII, VIII, XV (clade VII/ XV in the histone reconstruction), and XVI (histone only). Group (B) comprised clades III, IX, X, XI, XII, XIII, and XIV.


rDNA
(a)
CLADE IX
CLADE III
CLADE X
CLADE XI
CLADE XII
CLADE XIII
CLADE XIV
CLADE I
CLADE VIII
CLADE II
CLADE VI
CLADE VII
CLADE XV
CLADE IV
CLADE V
87
99
98
88
61
72
HS365 0
97
87
BU70
70
83
0.009
CLADE IX Porites profundus, Porites sp 5, Porites sp 6
CLADE X Porites sp 12
CLADE XI Porites cf hawaiiensis
CLADE XII Porites sp 7
CLADE XIII Porites lichen,Porites negrosensis, Porites tuberculosus Porites sillimaniana, Porites heronensis, Porites vaughani, Porites sp 8
CLADE XIV Porites flavus
CLADE III Porites farasani
CLADE VI Porites hadramauti
CLADE I Porites fontanesii
CLADE II Porites columnaris, Porites sp 1, Porites sp 2, Porites sp 3
CLADE V Porites annae, Porites arnaudi, Porites australiensis, Porites cylindrica, Porites harrisoni, Porites lobata, Porites lutea, Porites cf reticulum, Porites solida, Porites sp 9, Porites sp 10, Porites sp 11, Porites cf horizontalata
CLADE XV Porites deformis
CLADE VII Porites sp 4
CLADE IV Porites rus, Porites monticulosa
CLADE VIII Porites somaliensis

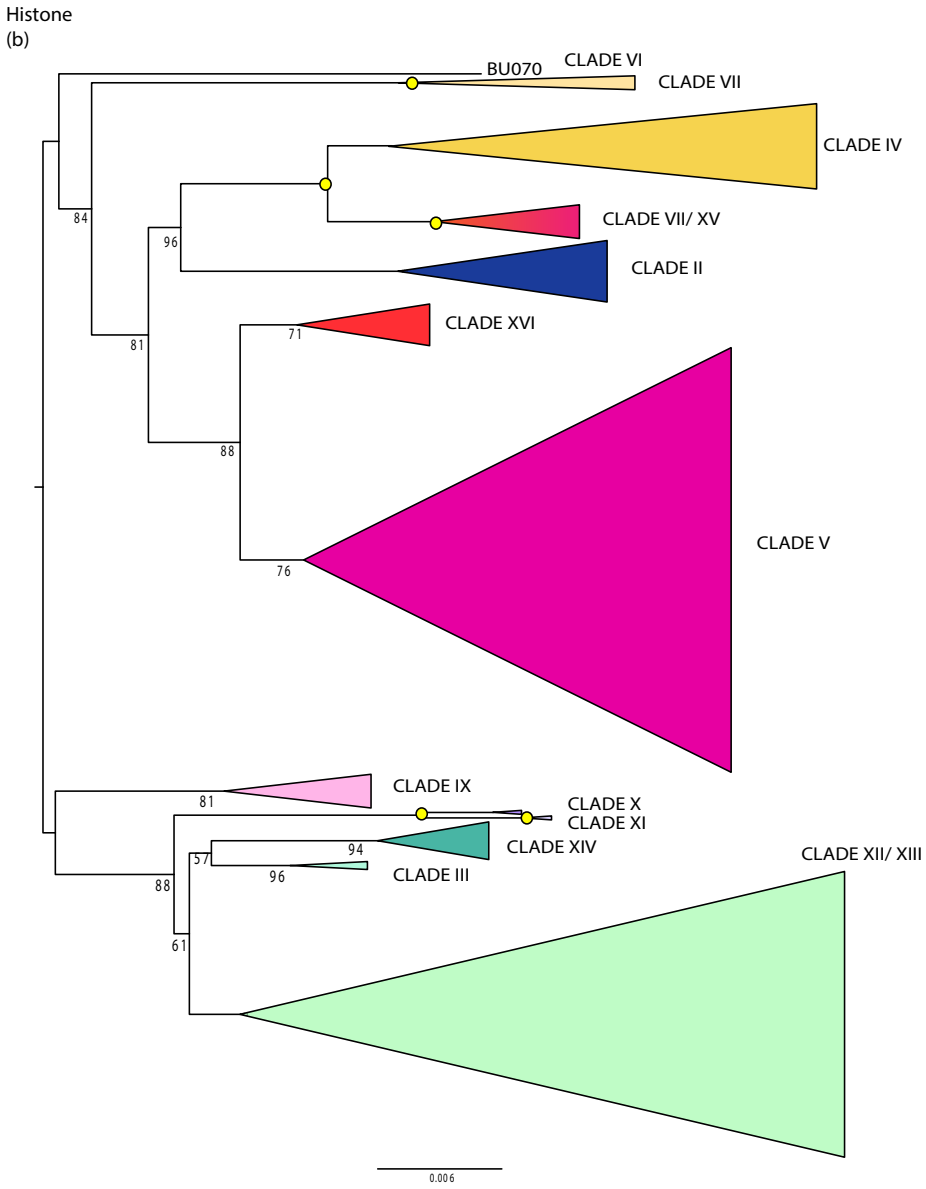
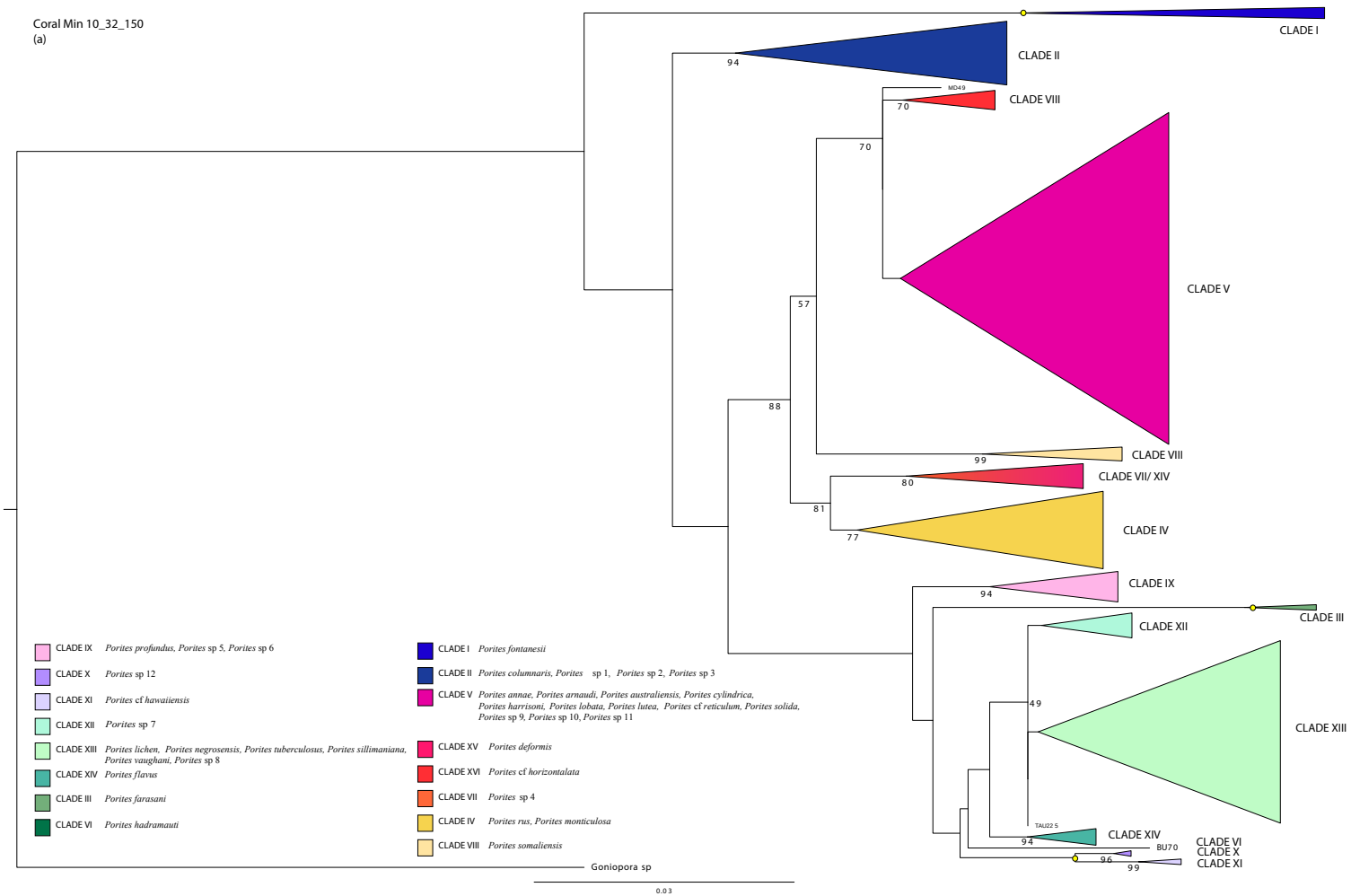


Figure 2.1 Comparison of reconstructed species trees. a) coral rDNA, b) coral histone region. Node values represent BI posterior probabilities and ML bootstrap supports. Roman numbers from I to XVI refer to the assigned clade numbers. Colour codes are explained in the legend.

2.4.3 Phylogenomic analyses

The "coral-max", "coral-min", and "coral-med" topologies resulted in well-supported trees, with high bootstrap values at every node. Only the "coral-max" and "coral-min" reconstructions are shown here (Fig. 2.2 a, b, Appendix 2.5, 2.6). Samples were clustered in 16 genetic clades in the three topologies, in agreement with the rDNA phylogeny reconstruction illustrated in Fig. 2.1 a. A partial geographical and/or morphological structuring emerged within clades II, IV, V, VII, VIII, XIII, and XVI with the SNPs analyses, particularly when considering the "coral-max' dataset where the number of SNPs considered was maximized (163,637 SNPs) (Fig. 2.2 a, b). Geographic structuring in clade II included one sub-cluster of samples of *P. columnaris* from the seas around the Arabian Peninsula, one sub-cluster from Madagascar, and one third sub-cluster of samples from the Pacific Ocean. Within clade IV, samples of both *P. rus* and *P. monticulosa* were structured in one sub-cluster exclusive from the Arabian Peninsula, and one comprising both the Indian Ocean (Madagascar and Mayotte) and the samples from the Pacific Ocean. Geographic sub-clusters of nominal species within clade V included: *P. arnaudi* from the Marquesas Islands, *P. harrisoni* from the Persian Arabian Gulf, *P.* sp 10 from Madagascar and Mayotte, *P.* sp 11 from Singapore, *P. reticulum* from Madagascar, *P. cylindrica* from the Indian Ocean and finally *P. cylindrica* from the Pacific Ocean. In clades VII and VIII samples were structured within two sub-clusters: one comprising samples from Madagascar and Mayotte, and one comprising samples from the seas around the Arabian Peninsula. Within clade XIII, the geographic and morphological structuring included samples *of P.* sp 8 from the Solitary Islands – Australia, *P. vaughani* from Australia, and finally *P. sillimaniana* and *P. negrosensis* from Australia. Finally, in clade XVI samples of *P.* cf *horizontalata* were structured within a Madagascar and Mayotte sub-cluster, alongside a Pacific sub-cluster (Appendix 2.6)


Coral Min 10_32_150
(a)
CLADE I
CLADE II
MD49
CLADE VIII
CLADE V
CLADE VIII
CLADE VII/ XIV
CLADE IV
CLADE IX
CLADE III
CLADE XII
CLADE XIII
TAU22 5
CLADE XIV
BU70
CLADE VI
CLADE X
CLADE XI
94
70
70
57
88
99
80
81
77
94
49
94
96
99
CLADE IX Porites profundus, Porites sp 5, Porites sp 6
CLADE X Porites sp 12
CLADE XI Porites cf hawaiiensis
CLADE XII Porites sp 7
CLADE XIII Porites lichen, Porites negrosensis, Porites tuberculosus, Porites sillimaniana, Porites vaughani, Porites sp 8
CLADE XIV Porites flavus
CLADE III Porites farasani
CLADE VI Porites hadramauti
CLADE I Porites fontanesii
CLADE II Porites columnaris, Porites sp 1, Porites sp 2, Porites sp 3
CLADE V Porites annae, Porites arnaudi, Porites australiensis, Porites cylindrica, Porites harrisoni, Porites lobata, Porites lutea, Porites cf reticulum, Porites solida, Porites sp 9, Porites sp 10, Porites sp 11
CLADE XV Porites deformis
CLADE XVI Porites cf horizontalata
CLADE VII Porites sp 4
CLADE IV Porites rus, Porites monticulosa
CLADE VIII Porites somaliensis
Goniopora sp
0.03

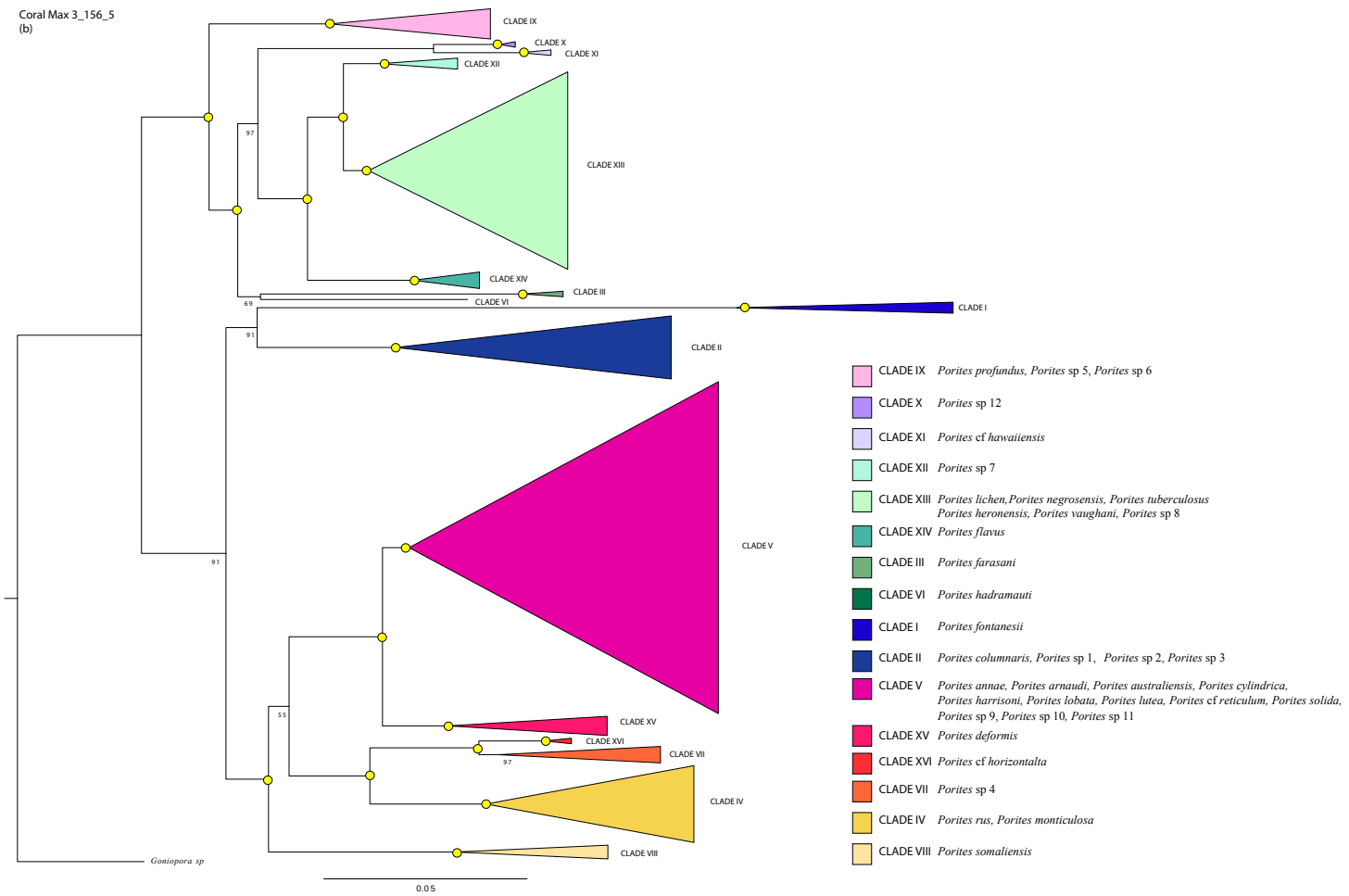


Figure 2.2 Comparison of RAxML tree based on (a) "coral-min" dataset, that allowed for 50% missing data, and consisted of 1,637 SNPs b) "coral-max" dataset, that allowed for 50% missing data and consisted of 163,637 SNPs. Values at nodes represent ML bootstrap supports. Roman numbers from I to XVI refer to the assigned molecular clade numbers. Colour codes are explained in the legend.

2.4.4 Species delimitation analyses

The BFD* analysis best supported model B that assigned the samples according to the 16 molecular clades recovered by the phylogenomic reconstructions (MLE = -3.881; BF = 0). The second-best model assigned the samples using the specimens identified based on comparison to type material (model C, MLE = -8990; BF = 10,218). The third best model, Model A, considered all specimens as belonging to a single species (MLE = -9644; BF = 11,526) (Table 2.2).

Table 2.2 Bayes Factor delimitation (BFD*) results for each analysis using path sampling (PS) with SNAPP. The number of lineages represents the number of putative species included in each analysis. BF values are used to rank species models, relative to the species model with the lowest marginal likelihood. The model B with 16 lineages corresponding to the 16 molecular clades recovered in Figure 2.2 was supported as the best fit model.

Model name	Model specifications	Number of lineages	MLE	BF	Rank
A	One single species	1	-9,644	11,526	3
B	Molecular clades	16	-3,881	-	1
C	Nominal species	39	-8,990	10,218	2

2.4.5 Divergence time analysis

Within the *Porites* mtGenomes analysed, the time calibrated phylogeny reconstruction recovered 16 main molecular clades (clades I to XVI). Following the inclusion of the oldest fossil record of *Porites*, the genera *Goniopora* and *Porites* diverged around 37.9 Mya, and the sister taxon Dendrophyllidae, basal to the phylogeny, at the beginning of the Eocene around 58.6 Mya (Fig. 2.3). As already evidenced by the rDNA, histone, and SNPs reconstructions, the 16 molecular clades split into two main groups. These two groups, A – comprising clades I, II, IV, V, VII, VIII, XV, and XVI, and B - comprising clades III, VI, IX, X,

XI, XII, XIII, and XIV, diverged at the end of the Miocene, around 7.7 Mya. Within group A, clade I and clade II are the basal groups, diverging around 6.8 Mya. The lineage leading to *P. somaliensis* (clade VII), diverged 4.4 Mya, while clade V and clade IV, VII, and XV diverged around 3.8 Mya. The lineage leading to clades IV, and to clade VII and clade XV diverged in the Pleistocene (around 1.99 Mya). Finally, *P.* cf *horizontalata* (clade XVI) split from all the lineages in clade V only in the Pleistocene, around 1.9 Mya. The nominal species nested within clade V have a recent divergence between 1.1 Mya and 0.1 Mya. Within group B, clade IX is the basal group, and diverged around 4.5 Mya. The lineage leading to *P. farasani* in clade III and *P. hadramauti* in clade VI, split from the lineage leading to clades X, XI, XII, XIII, and XIV, 3.8 Mya, while *P. farasani* in clade III and *P. hadramauti* in clade VI diverged around 2.6 Mya. *Porites* cf *hawaiiensis* (clade XI) and *P.* sp 12 (clade X) diverged around 3.2 Mya, and the lineage leading to *P. flavus* (clade XIV), 2.9 Mya. Clade XII (*P.* sp 7) and the species group in clade XIII, split 1.9 Mya. Clade XI and X only split 0.99 Mya, and the lineages within clade XIII, between 1.1 Mya and 0.1 Mya (Fig. 2.3).

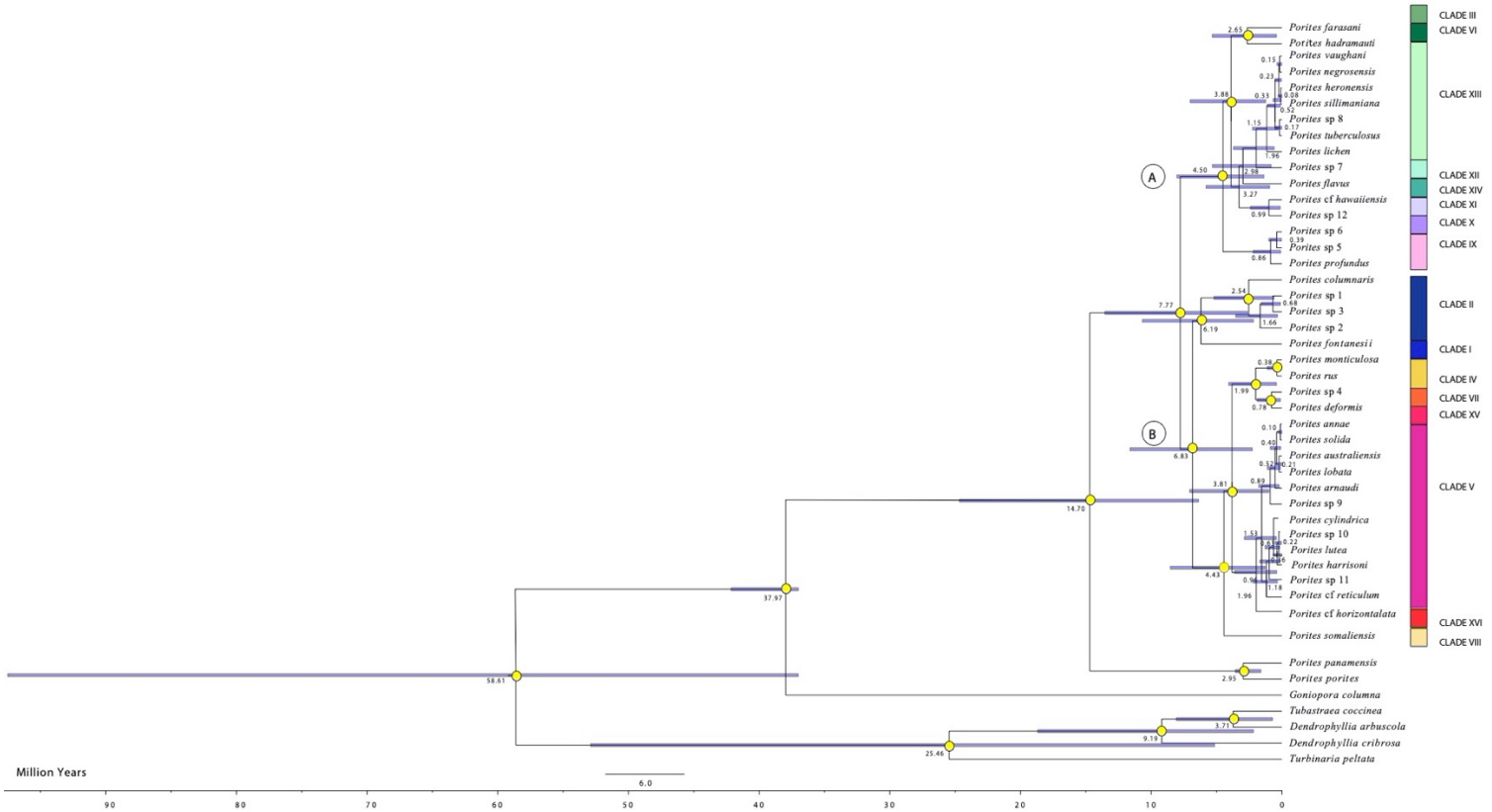


Figure 2.3 Species tree calibrated chronogram. Purple bars represent 95% highest posterior densities (HPD). Node symbols represent posterior probabilities as explained in the legend. Values at nodes represent estimate time of node divergence. The scale bar represents millions of years and is based on the ICS International Chronostratigraphic Chart.

2.4.6 Historical biogeographical analyses

When comparing among models, the DEC+J model was the most probable model of biogeographical range evolution for this dataset (LnL = -127.2, AIC weight = 0.268), followed by the DEC model (LnL = -127.2005, AIC weight 258.4011) (Table 2.3). The inclusion of the *jump dispersal* parameter J was not significant when comparing the DEC models using a likelihood ratio test (p = 0.97) (Table 2.3, Appendix 2.7). The parameters of the DEC+J model included: anagenetic dispersal rate d = 0.1051, extinction rate e = 0.0312, and cladogenetic dispersal rate j = 1e-0.5.

Under DEC+J model, the divergence between group A and group B had an unclear origin between the Arabian seas and the Indo-Pacific Oceans (the five biogeographical areas defined for the ancestral range analyses were: (A) Arabian seas, (I) Indian Ocean, (P) Pacific Ocean, (E) East Pacific Ocean, (C) and the Caribbean). The common ancestor of group A had an Arabian seas /Indo-Pacific distribution around 4.5 Mya that then diverged into an Arabian seas/Pacific Ocean lineage and another lineage with an Arabian seas/Indian Ocean distribution. Finally, the common ancestor of group B most probably originated in the Arabian seas around 7 Mya, with the second most likely hypothesis being an Indian Ocean origin, and finally, an Arabian seas/ Indian Ocean origin (Fig. 2.4, Appendix 2.8).

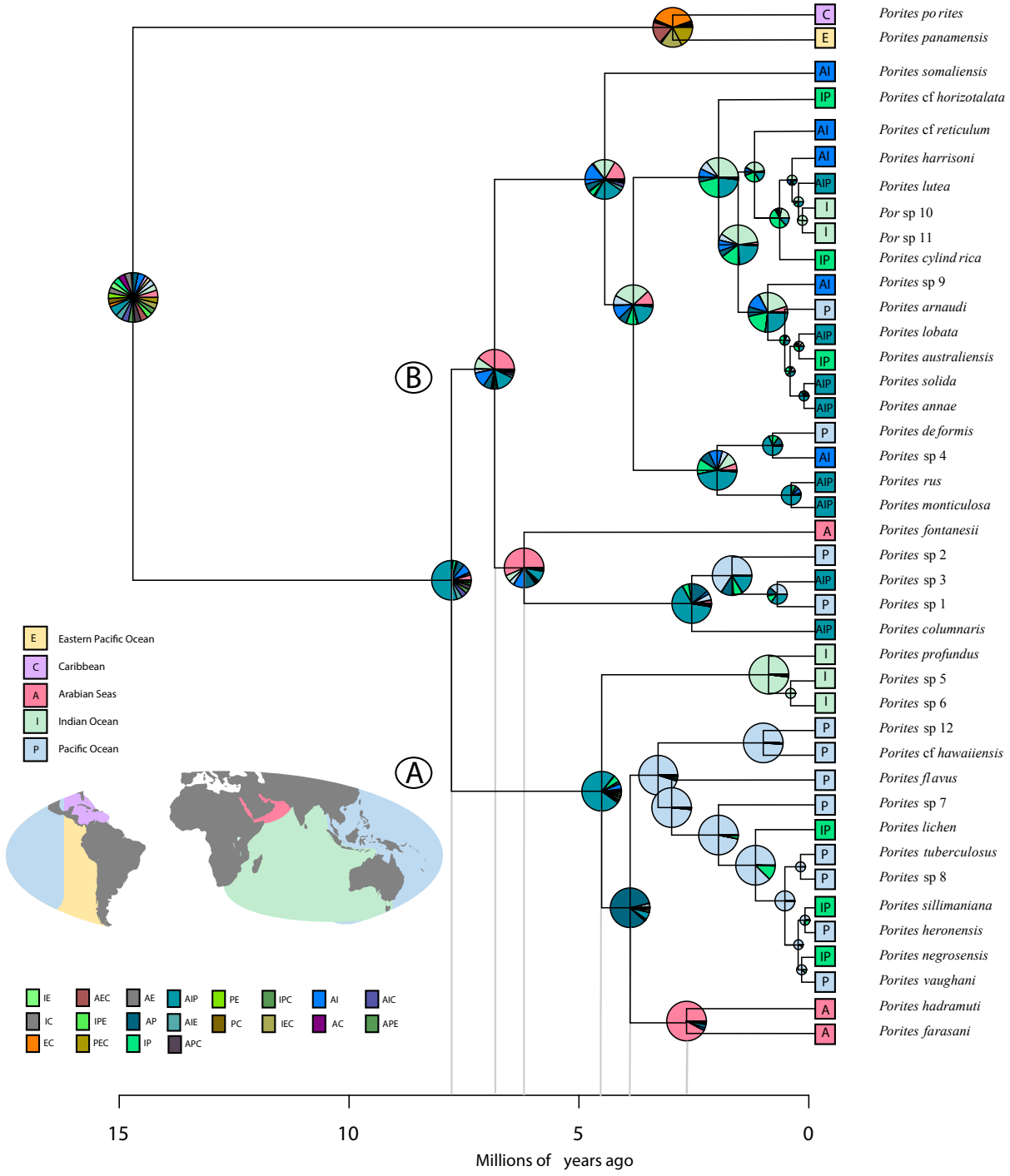


Figure 2.4 Ancestral area reconstruction of *Porites* using BioGeoBEARS on the same topology as the phylogenetic tree presented in Fig. 3.3. Pie charts depicting the probability of each inferred area are presented at major nodes. Coloured boxes at branch tips indicate range of extant species as illustrated on the map to the left. Caption refers to colours of areas in the map and pie charts.

Table 2.3 Results of BioGeoBEARS model testing. AIC and AICc comparisons of different models of biogeographical range evolution and estimates for: d (dispersal), e (extinction) and j (weight of jump dispersal/founder speciation). The best fitting model is highlighted in bold.

Model	No. of parameters	LnL	d	e	j	AIC	AIC weight	AICc	AICc weight
DEC	2	-127.2005	0.1053	0.03	0	258.4011	0.7306	258.6937	7.60E-01
DEC+J	3	-127.2	0.1051	0.0312	1.00E-05	260.4	0.2689	261	2.40E-01
DIVALIKE	2	-135.0489	0.1158	0.0305	0	274.0977	0.0001	274.3904	2.97E-04
DIVALIKE+J	3	-135.0496	0.1157	0.0307	1.00E-05	276.0992	0.0001	276.6992	9.35E-05

2.5 Discussion

2.5.1 Porites phylogenomic relationships, diversity, and taxonomy

The molecular lineages with respect to nominal species

Phylogenomic reconstructions and species delimitation approaches identified fewer taxa in *Porites* when compared to the traditional taxonomy of the genus. The analyses recovered 16 independently evolving lineages of *Porites* against 39 nominal species plus novel morphotypes initially identified. Eight of these lineages broadly correspond with eight nominal species, *i.e. P. fontanesii* (clade I), *P. farasani* (clade III), *P. hadramauti* (clade VI), *P. somaliensis* (clade VIII), *P.* cf *hawaiiensis* (clade XI), *P. flavus* (clade XIV), *P. deformis* (clade XV), and *P.* cf *horizontalata* (clade XVI), suggesting they are likely to be valid species. Nonetheless, confirmation of their taxonomic validity awaits collections of material from the type locations of these nominal species and other independent lines of evidence. The restricted geographic distribution of these taxa also suggests that they are valid species, as highlighted in Table 2.1

and Appendix 2.9, however, sampling more broadly would be required to confirm these restricted distributions.

Within the phylogenetic reconstructions, three clades are comprised entirely of specimens with morphologies that do not match any of the type specimens examined: *P.* sp 4 in clade VII (seven samples in the max tree phylogeny, Appendix 2.6); *P.* sp 7 in clade XII (five samples in the max tree phylogeny, Appendix 2.6); and *P.* sp 12 in clade X (three samples in the max tree phylogeny, Appendix 2.6). The distinctive morphologies of these groups of specimens together with their phylogenetic position and geographic distributions (Appendix 2.2), suggest that these morphotypes represent species new to taxonomy and await formal description (Table 2.1). Further lines of evidence such as quantitative morphological analyses are desirable/ necessary to establish whether or not these are good species.

A total of 28 nominal species and unidentified morphotypes in clade II, clade IV, clade V, clade IX, and clade XIII could not be distinguished based on a reduced-genomic approach, and clustered into five groups of unresolved species (Fig. 2.1, 2.2, Appendix 2.1, 2.4 – 2.6). The identification of convergence events among close related lineages can be complicated as a result/ or a combination of a) high morphological variability of one (unlikely) or few separate evolving entities that led to a high number of nominal species and thus confused taxonomy; b) incomplete lineage sorting (Mendes et al., 2016) and species of recent origin; and finally, c) hybridization and introgression. A possible, scenario, is that the species groups consist of genetically determined morphs within a single species. Indeed, morphological variability can often result in apparent genetic polyphyly through assignment of specimens to different species (Arrigoni et al., 2016b; Terraneo et al., 2016; Cunha et al., 2019). In cases, the presence of different morphs can be considered a precursor to speciation, where phenotypic morphs evolve into distinct species (West-Eberhard, 1986; Potkamp & Fransen, 2019), or where polymorphism expand the niches that a species can exploit (Galeotti & Rubolini, 2004). An alternative hypothesis is that incomplete lineage sorting and

weak genetic drift has resulted in a misleading phylogenetic reconstruction (de Queiroz, 1998, 2007). Under this scenario, the polyphyly of species found in these unresolved groups may be explained by rapid diversification or recent speciation of the clustered lineages (Funk & Omland, 2003), a scenario supported by the recent origin of these clades (see next paragraph). Furthermore, rapid species radiations produce co-occurring closely related species, that are not yet completely reproductively isolated, providing opportunity for introgression. In this case, phylogenetic signals may be hidden by gene transfer among divergent lineages undergoing hybridisation and introgression (van Oppen et al., 2000, 2002; Frade et al., 2010; Combosch & Vollmer, 2015; Forsman et al., 2017). In the Caribbean, hybridisation has been reported between the species *A. cervicornis* and *A. palmata*, and backcrossing of the hybrid *A. prolifera* with the parental species seems to occur at low frequencies too (Vollmer & Palumbi, 2002). Combosch et al., (2008) first reported hybridization among *Pocillopora damicornis*, *P. eydouxi*, and *P. elegans* in the Eastern Pacific, and one-way introgression among these species (Combosch & Vollmer, 2015). Nevertheless, these findings were not confirmed later by Johnston et al., 2019. The present work did not include analyses to test for the presence of hybridisation within the unresolved groups of species, yet future directions should incorporate such analyses.

Overall, it is important to underline that these pathways are not mutually exclusive, and indeed the current complex scenario might be best explained by a combination of the above-mentioned possibilities. Unresolved groups of species in corals are common, yet our understanding of these remains to date vague (Frade et al., 2010; Arrigoni et al., 2016b; Cunha et al., 2019). It is therefore compelling that alternative lines of evidence are integrated. Such could be derived from additional sources, such as the study of coral reproductive biology and algal symbiont association, and might allow a better evaluation of corals species boundaries and evolutionary history.

2.5.2 Current and Past Biogeography of Porites

Understanding current and historical distribution patterns of species can provide an external line of evidence to taxonomy, in particular when groups of nominal species remain unresolved based on genetic and morphological data. With regards to corals, several studies are revolutionising our understanding of distribution patterns. Indeed, for genera that were traditionally considered widespread, breaks between Indian and Pacific populations are now evident, with several species showing geographically restricted distributions (Flot et al., 2011; Stefani et al., 2011; Arrigoni et al., 2012, 2018; Pinzón et al., 2013; Kitano et al., 2014; Huang et al., 2014; Richards et al., 2016; Gélin et al., 2017, 2018). The integration of the genomic results of this chapter with the geographic distribution data of the recovered lineages, corroborates these general trends of corals biogeography. Indeed, in this chapter these patterns are highlighted also for the genus *Porites*. Data from this study, show that a) the majority of the molecular clades have a restricted distribution; b) only three out of 16 molecular clades recovered, are widespread in the Indo-Pacific; c) within these widespread Indo-Pacific clades, geographic subclustering of several morphotypes suggests a possible ongoing speciation for several unresolved lineages (Appendix 2.6, Appendix 2.9). Finally, d) the most widespread lineages are also the most diverse and the most recent, best exemplified by the groups of species in clade V and clade XIII (Appendix 2.9, Fig. 2.3). A similar scenario with a rapid diversification in the Indo-Pacific in a relatively short time-frame is evident in the genus *Pocillopora.* Indeed, Johnston et al., (2019), suggest the genus spread throughout the Indo-Pacific in less than 3 Mya, with some species as young as 1 Mya (such as in the case of *P. acuta* and *P. damicornis*), a process that could relate to high phenotypic plasticity favouring adaptation to different conditions. The presence of a high number of morphs within these young lineages might reflect theories according to which different morphological phenotypes correspond to precursors to speciation, where indeed different morphotypes evolve into different species. Nevertheless, many past lineages of *Porites* might have become extinct during and after the Neogene. In fact, even if past diversity in

Porites might appear poor based on molecular evidence, the fossil record shows a high extinction rate of Caribbean corals of the Neogene (Johnson et al., 1995) and also in Indo-Pacific Acropora of that era (Santodomingo et al., 2015).

Four of the species examined in this study are Arabian endemics, each with a distinct distribution. *Porites fontanesii* is widely distributed in the Red Sea and the Gulf of Aden, but not recorded in the Arabian Gulf. *Porites hadramauti* is restricted to the Gulf of Aden, *P.* sp 4 is found in the Gulf of Tadjoura, Gulf of Aden, Gulf of Oman, and *P. farasani* is a southern Red Sea endemic (Terraneo et al., 2019a). High rates of endemism are typical of several marine groups in the seas around the Arabian Peninsula. This region has been recognized as an endemism hotspot in the Indian Ocean (Obura, 2012; DiBattista et al., 2016a), and recent estimates suggest that 11% of corals around the Arabian Peninsula are endemic (Berumen el al., 2019), while endemism estimates are lower than 3% in other areas of the Indian Ocean (Veron et al., 2015; Obura, 2016). The evolutionary processes that lead to endemic hotspots in peripheral areas of the Indo-Pacific, such as the Red Sea and the Persian Arabian Gulf, remain elusive. However, the diversity of the habitats and environments, and the complex geological and paleoclimatic history of the seas around the Arabian Peninsula might have played a key role in shaping the current biodiversity patterns (Sheppard et al., 1992; Bosworth et al., 2005; DiBattista et al., 2016a). The Bab Al Mandeb strait is the only present connection between the Red Sea and the Gulf of Aden. Limited water exchange seasonally driven by the Indian Ocean monsoon system occurs trough this shallow and narrow channel, creating a potential barrier to genetic exchange between the Red Sea and the rest of the Indian Ocean (DiBattista et al., 2016a, 2016b). Moreover, a monsoon-driven upwelling system causes major fluctuations in the summer water temperature and nutrients in the Gulf of Aden, limiting reef development in this region, as opposed to the oligotrophic biodiverse waters of the Red Sea, and limiting the persistence of only some well adapted species in this region (Vénec-Peyré & Caulet, 2000; Benzoni et al., 2003).

Three lineages are were recorded only from New Caledonia in this study. Clade X, *P.* sp 12, clade XII, P. sp 7, and clade XV, *P. deformis*. Although *P.* sp 7 and *P.* sp 12 might endemics to New Caledonia, the type location of *P. deformis* (Nemenzo, 1955) is Cebu in the Philippines. Further molecular biodiversity assessments in other regions are required to confirm the distribution, indeed, the identity, of these taxa.

Clarifying how species distributions are historically shaped remains a central topic in evolutionary biology (Wiens & Donoghue, 2004; Bowen et al., 2013). Corals species distribution have proven to be better predicted by geological events rather than by present-day environmental conditions (Keith et al., 2013). For example, the Indo-Australian archipelago has long been considered a centre of origin for coral biodiversity, mainly based on the current high species richness in the area correlated with habitat availability and species dispersal limitation (Bellwood & Hughes, 2001; Connolly et al., 2003). Nevertheless, recent works on reef corals and fish, highlighted that rates of species origination are actually lower in the coral triangle compared to other areas (Huang et al., 2018, DiBattista et al., 2018), a result also supported by low endemism in this region (Huang et al., 2018, DiBattista et al., 2018).

With regards to *Porites* Indo-Pacific species, the BioGeoBEARS analyses showed that group B had over 60% probability of having an Arabian seas or Indian Ocean origin in the Neogene around 6.8 Mya (Fig. 2.4, Appendix 2.8). This ancestral distribution is consistent with the hypothesis of a centre of origin in the western and northern Indian Ocean during the Miocene (Bowen et al., 2013; Obura, 2016). According to this theory, multiple centres of origin were present in the Indian Ocean in the Cenozoic era, the first in the Tethys Sea during the Paleogene, and a more recent one in the Arabian seas and Mascarene Islands during the Neogene (Obura, 2016). Such theory is corroborated by geological events during the Neogene, when the peripheral areas of the north western Indian Ocean, such as the Arabian seas, were characterized by high tectonic activity (Bosworth et al., 2005). The fauna of these regions, is likely derived from a pool of species that originated in the

western and northern Indian Ocean, and spread east through the northern Indian Ocean gyre and the western Somali current. A good example is clade VIII, *P. somaliensis*. This lineage originated 4.5 Mya in the Pliocene and it is currently found in the Red Sea, the Gulf of Aden, and the western Indian-Ocean (Appendix 2.9). Subsequent diversification eastward towards the coral triangle and the Pacific Ocean might have occurred later during the Pliocene and Pleistocene, when climatic and oceanic fluctuations might have played an important role in processes of diversification, with the Mascarene Ridge acting through a stepping-stone for dispersal. Current distribution patterns and the dated phylogeny reconstruction of the basal clade of group B, showed a deep divergence of the lineage from which evolved clade I, *P. fontanesii*, an Arabian endemic species, and Clade II, *P. columnaris*, *P.* sp 1, *P.* sp 2, and *P.* sp 3, an Indo-Pacific clade, around 6.8 Mya in the Miocene, with further diversification of clade II lineages later in the Pleistocene around 2.5 Mya. Similarly, the lineage leading to clade VI, *P. rus* and *P. monticulosa*, and the sister clades VII, and VX, might have originated in the Indian Ocean around 4 Mya, and further diversified in the Pleistocene 1.9 Mya into a widespread Indo-Pacific lineage (clade VI), a restricted Indian and Arabian lineage (clade VII), and a Pacific only lineage (clade XV). Finally, the lineage leading to the diverse clade V and clade XVI, split 3.8 Mya, most likely in the Indian Ocean, and spread and diversified into the Indo-Pacific in the Pleistocene and Holocene (Fig. 2.4, Appendix 2.8).

Group A's common ancestor had an unclear Indo-Pacific ancestral distribution. The lineage diverged into an Indian Ocean restricted lineage (leading to clade IX, only found in Madagascar and Mayotte) 4.5 Mya, and two sister lineages with a disjunct distribution in the Arabian seas (the lineage leading to clade III and clade VI), and in the Pacific Ocean (Fig. 2.4, Appendix 2.8). Interestingly, the most ancient nodes seem to have an Indian or Arabian origin. Further diversification occurred later in the Pacific Ocean starting at the end of the Pliocene around 3.2 Mya.

2.6 Conclusions

Important gaps remain in the understanding of biodiversity, biogeography, and evolution of the genus *Porites,* and the present work demonstrates that there is an urgent need for a taxonomic revision of this genus. This work harnesses on the power of NGS coupled with phylogenomics and species delimitation methods, to help clarify the diversity and evolutionary relationships of the coral genus *Porites* at several localities in the Indian and Pacific Oceans. The results suggest the presence of 16 molecular lineages, 11 of which can be partly matched with a single nominal species and 5 of which include multiple nominal species and novel morphotypes. These results bring into question the validity of many of the nominal species in clades II, IV and V, IX, and XIII. However, the diverse range of morphologies and life histories within many of these clades, in particular clade V, suggest that NGS cannot on its own resolve species that most ecologists and biologist would accept as valid. Further studies encompassing qualitative morphological analyses, as well as ecological, symbiont association, and reproductive data will be necessary to determine the potential presence of functional differences and reproductive isolation mechanisms among the morphotypes nested within these groups of species. The results of this chapter highlighted interesting ancestral distribution of *Porites* species in the Indo-Pacific, showing evidence for an Indian or Arabian origin of at least eight out of the 16 molecular lineages recovered. Finally, the most ancient nodes of the reconstructed dated phylogeny also showed an Indian Ocean or Arabian seas ancestral distribution, corroborating the theory of an Indian Ocean centre of origin for coral diversity during the Cenozoic.

3. CHAPTER 3: A QUANTITATIVE APPROACH TO MORPHOLOGICAL SPECIES BOUNDARIES IN *PORITES*

3.1 Abstract

Species in the genus *Porites* are notoriously difficult to identify. In the previous chapter, molecular techniques suggest that the number of independently evolving lineages is much lower that the number of nominal species. In this chapter, I use multivariate statistics to quantitatively determine the number of groups in *Porites* on the basis of traditional skeletal characters used to discriminate species in the genus. Moreover, I tested for the effectiveness of the investigated morphological characters in discriminating 32 nominal species and unidentified morphotypes, and 14 of the 16 molecular clades described in chapter 2. A cluster analyses based on 22 morphological characters, suggested the presence of 28 morphological groups among the *Porites* specimens. PERMANOVA suggested that 95% of the variance in the skeletal characters was explained by the morphological groupings and 64% by the molecular clades. Canonical Analyses of Principal Coordinates (CAP) confirmed the presence of defined boundaries among the majority of the nominal species and morphotypes, while only partially confirming the molecular clades. Finally, the CAP correctly reassigned 79% of the samples to the original nominal species or morphology, and 59% to the molecular clades. Focusing on the groups of species in clade II, clade V, clade IX, and clade XII, the CAP analyses showed clear boundaries among the majority of the nominal species within the clades, with few exceptions, providing a further line of evidence with which to define species in *Porites*.

Keywords: multivariate statistics, biodiversity, species boundaries

3.2 Introduction

The traditional taxonomical classification of hard corals has been based on macro-skeletal characters, in particular vertically developed structures such as the septa, the columella, and the pali (see Budd et al., 2012 for glossary). These macro-morphological features remained the main source of evidence used for delimiting species and reconstructing evolutionary relationships among corals until the late 20th century, when the molecular revolution opened the era of molecular taxonomy. Fundamentally revolutionising our understanding of corals evolutionary history, the use of DNA taxonomy and phylogenetics indicated that Scleractinia classification systems based on a mostly qualitative assessment of morphological characters were severely flawed. Morphological based taxonomy is in fact subject to limitations, such as convergent evolution and homoplasy of skeletal characters (Fukami et al., 2004), high morphological variability and plasticity within and between colonies (Todd et al., 2008; Forsman et al., 2009b), and different rates of evolution of morphological features, that render inferences about the evolutionary history of corals particularly challenging (Van Oppen et al., 2001). Particularly, the reliance upon unquantified skeletal morphological characters in these classification schemes substantially contributed towards inaccurate reconstructions of evolutionary relationships at all taxonomic levels. At species level for instance, multiple nominal species have proven to be a single species (Stefani et al., 2011; Pinzón et al., 2013), or ecomorphs of a single species turned out to correspond to different species (Fukami et al., 2004; Knowlton et al., 1992). Finally, morphologically similar forms, can represent cryptic species with different reproductive modes or ecology (Baums et al., 2006; Boulay et al., 2014; Keshavmurthy et al., 2013; Schmidt-Roach et al., 2013). Nevertheless, the use of genetic differences to infer species delimitation in corals remains also challenging, due but not limited to, the number and type of analysed markers, slow rates of evolution of Anthozoan mitochondrial DNA (Hellberg, 2006), incomplete lineage sorting and regression. The identification of key morphological characters continues to be a fundamental framework for coral

taxonomy and systematics, and finally the use of multiple characters and the need to collect data from several independent techniques is compelling towards a better understanding of systematics, ecology and biodiversity in Scleractinia.

Porites (Link, 1807) is one of the most challenging coral genera in terms of taxonomic identification and the definition of species boundaries. The genus shows high variability at colony level; indeed, *Porites* can form encrusting, laminar, columnar, branching, or massive colonies. At the corallite level, *Porites* is characterized by highly perforated walls derived from complex patterns of growth and fusion of trabeculae and synapticulae (Bernard, 1905). Corallites are small, normally ranging from 0.7 to 2 mm, and their arrangement has been regarded as species–specific. In certain taxa, a well-developed coenosteum separates the corallites, but in others corallites have fused walls and no coenosteum is formed. The typically perforated septa are formed by a regular pattern of fusing trabeculae. The innermost trabecula can be distinct from the rest of the septal structure and is referred to as a palus (Chevalier & Beauvais, 1987; Vaughan & Wells, 1943), literally a vertical pole. *Porites* is distinct from the other scleractinian genera due to the presence of a peculiar pattern of septal fusion (Bernard, 1905), in which 12 septa are arranged into four couples of lateral pairs, a ventral triplet, and an opposite dorsal directive (Bernard, 1905: P. 13 Fig. 1, Veron & Pichon, 1982: P. 11 Fig. 2).

Most authors argue that *Porites* species show a continuum in all morphological characters and that these might not be discrete morphological units (Zlatraski et al., 1802; Vaughan, 1901; Bernard, 1905;). Yet, *Porites* species have been, and continue to be described based on corallite structures, particularly, the pattern of fusion of the ventral triplet, the presence of the columella (or lack thereof), and the number of pali. The small corallites, along with morphological plasticity (Muko et al., 2000; Smith et al., 2007; Padilla-Gamiño et al., 2012) and geographic variability, contribute to making the genus one of the most challenging in terms of species identification and

delimitation (Forsman et al., 2009b; Forsman et al., 2015, Thisthammer et al., 2018).

To date a few works have quantitatively assessed the value morphological characters in *Porites* taxonomy (Weil et al., 1992; Brakel, 1967; 1977; Budd et. 1994; Forsman et al., 2015; Forstel, 1976; Tisthammer et al., 2018). Forsman et al., (2015), identified a landmark of morphological characters able to distinguish *Porites lobata* Dana, 1846 and *Porites evermanni* Vaughan, 1907, two species often misidentified in the field. The quantitative use of taxonomic characters traditionally applied for species delimitation in *Porites* proved useful to distinguish these two species, and in particular, the arrangement of the ventral triplet (fused/ not fused), the number of pali, the calice width/ length, the fossa and calice area, had the largest influence on discriminating between these species.

In this chapter, multivariate statistics was applied in order to quantitatively determine the number of groups in *Porites* samples based on traditional skeletal characters used to discriminate species in the genus. Moreover, I tested if a total of 22 skeletal characters were able to discriminate *Porites* nominal species and morphotypes, and the molecular clades recovered in chapter 2. A blind reassignment of the samples to their original morphology and molecular lineage was used to validate the utility of the chosen morphological characters. Finally, I focused on the five unresolved groups of species recovered in chapter 2, demonstrating that the majority of nominal species and novel morphotypes nested within these groups of species are morphologically distinct. The results of this chapter were then integrated with the genomic data towards a preliminary revision of *Porites* taxonomy.

3.3 Materials and Methods

3.3.1 Collection and identification

A total of 124 *Porites* colonies were selected from the samples used in chapter 2 in order to include the highest number of morphotypes, molecular clades, and localities in the morphological examination (Table 3.1). Limitation in the number of samples analysed was constrained by the time available for the finalisation of this dissertation, since the dry skeletons are hosted by different institutions. Dry colonies were imaged with Canon G15 camera and a reference scale. Moreover, subsamples of 5 cm^2 were imaged using a Leica M80 microscope equipped with a Leica IC80HD camera at KAUST, at IRD, and at JCU, and a Leica M80 microscope at UNIMIB with a reference scale.

Table 3.1 List of coral specimens examined in the present study. For each sample, voucher number, species identification based on traditional taxonomy, molecular clade recovered in chapter 2, and quantitative morphological group, are listed.

SAMPLE ID	NOMINAL SPECIES	MOLECULAR CLADE	CLUSTER MORPHOLOGICAL GROUP
SA0038	*P. fontanesii*	I	Q
SA0181	*P. fontanesii*	I	Q
SA0310	*P. fontanesii*	I	Q
SA0725	*P. fontanesii*	I	Q
SA1641	*P. fontanesii*	I	Q
SA1028	*P. columnaris*	II	B
SA2080	*P. columnaris*	II	M

TAU134	*P. columnaris*	II	B
TAU168	*P. columnaris*	II	B
HS3750	*P.* sp2	II	E
HS3832	*P.* sp2	II	E
HS3840	*P.* sp3	II	G
TAU047	*P.* sp1	II	G
SA1516	*P. farasani*	III	S
SA172	*P. farasani*	III	S
TAU101	*P. monticulosa*	IV	P
TAU149	*P. monticulosa*	IV	P
TAU158	*P. monticulosa*	IV	P
TAU175	*P. monticulosa*	IV	P
TAU236	*P. monticulosa*	IV	P
TAU082	*P. rus*	IV	P
TAU083	*P. rus*	IV	P
TAU108	*P. rus*	IV	P
TAU247	*P. rus*	IV	P
MD120	*P. profundus*	IX	I
MD121	*P. profundus*	IX	I
MD4	*P. profundus*	IX	I
MD146	*P.* sp5	IX	X
MD25	*P.* sp5	IX	X
MD6	*P.* sp6	IX	V
MD66	*P.* sp6	IX	V

MD68	*P.* sp6	IX	V
SA0390	*P. annae*	V	L
SA0876	*P. annae*	V	M
SA1518	*P. annae*	V	M
SA2148	*P. annae*	V	M
HS3622	*P. australiensis*	V	E
HS3631	*P. australiensis*	V	E
TAU073	*P. australiensis*	V	E
TAU093	*P. australiensis*	V	E
TAU155	*P. australiensis*	V	E
TAU049	*P. cylindrica*	V	Y
TAU072	*P. cylindrica*	V	Y
TAU081	*P. cylindrica*	V	Y
TAU094	*P. cylindrica*	V	Y
TAU096	*P. cylindrica*	V	Y
HS3820	*P. lobata*	V	E
TAU071	*P. lobata*	V	E
TAU079	*P. lobata*	V	E
TAU106	*P. lobata*	V	E
TAU131	*P. lobata*	V	E
TAU179	*P. lobata*	V	E
TAU253	*P. lobata*	V	E
HS3707	*P. lutea*	V	K
HS3723	*P. lutea*	V	K
HS3725	*P. lutea*	V	K

TAU056	*P. lutea*	V	K
TAU060	*P. lutea*	V	K
TAU061	*P. lutea*	V	K
MD162	*P. reticulum*	V	Y
MD163	*P. reticulum*	V	Y
MD164	*P. reticulum*	V	Y
MD165	*P. reticulum*	V	Y
MD166	*P. reticulum*	V	Y
SA0149	*P. solida*	V	A
SA1490	*P. solida*	V	A
SA1705	*P. solida*	V	A
SA2136	*P. solida*	V	A
DJ75	*P.* sp4	VII	J
MD105	*P.* sp4	VII	J
P1	*P.* sp4	VII	J
P6	*P.* sp4	VII	J
MY172	*P. somaliensis*	VIII	I
P14	*P. somaliensis*	VIII	I
P5	*P. somaliensis*	VIII	I
HS3611	*P.* sp12	X	R
HS3630	*P.* sp12	X	R
HS3638	*P.* sp12	X	R
MQ168	*P. hawaiiensis*	XI	R
MQ178	*P. hawaiiensis*	XI	R

MQ183	*P. hawaiiensis*	XI	R
HS3640	*P.* sp7	XII	N
HS3641	*P.* sp7	XII	N
HS3872	*P.* sp7	XII	N
HS3873	*P.* sp7	XII	N
TAU235	*P. sillimaniana*	XIII	Z
TAU264	*P. sillimaniana*	XIII	Z
TAU004	*P. heronensis*	XIII	H
TAU005	*P. heronensis*	XIII	H
HS3639	*P. lichen*	XIII	D
HS3890	*P. lichen*	XIII	C
HS3892	*P. lichen*	XIII	D
TAU044	*P. lichen*	XIII	D
TAU046	*P. lichen*	XIII	C
TAU068	*P. lichen*	XIII	C
TAU110	*P. lichen*	XIII	C
TAU172	*P. lichen*	XIII	C
TAU231	*P. negrosensis*	XIII	AA
TAU237	*P. negrosensis*	XIII	AA
TAU251	*P. negrosensis*	XIII	AA
TAU034	*P.* sp8	XIII	F
TAU037	*P.* sp8	XIII	F
TAU038	*P.* sp8	XIII	F

TAU039	*P.* sp8	XIII	F
TAU043	*P.* sp8	XIII	F
HS3897	*P. tuberculosus*	XIII	BB
HS3903	*P. tuberculosus*	XIII	BB
TAU161	*P. tuberculosus*	XIII	BB
TAU248	*P. tuberculosus*	XIII	BB
TAU141	*P. vaughani*	XIII	U
TAU197	*P. vaughani*	XIII	V
TAU227	*P. vaughani*	XIII	V
TAU240	*P. vaughani*	XIII	V
TAU243	*P. vaughani*	XIII	U
TAU053	*P. flavus*	XIV	W
TAU058	*P. flavus*	XIV	W
TAU116	*P. flavus*	XIV	W
TAU117	*P. flavus*	XIV	W
TAU123	*P. flavus*	XIV	W
HS3860	*P. deformis*	XV	L
HS3863	*P. deformis*	XV	L
HS3864	*P. deformis*	XV	L
HS3866	*P. deformis*	XV	L
HS3867	*P. deformis*	XV	L

3.3.2 Morphological analyses

Multivariate statistics was used in order to quantitatively determine the number of groups present among *Porites* samples. The scope of the analyses was to

independently group samples sharing similar features regardless of the nominal species or molecular group identified from chapter 2. Later, I tested if these characters were better predictors of *Porites* nominal species and morphotypes or the molecular clades recovered in chapter 2. From the digital images produced, a total of 22 morphological variables were scored (Table 3.2), comprising numerical (N), ordinal (O) and categorical (C) variables. In particular, eight numerical characters were measured using *Image J* (Schneider et al., 2012). The average of three corallites per sample was used, for a total of 8184 scores. These characters were selected based on the original description of *Porites* nominal species, and previous studies of *Porites* taxonomy (Veron & Pichon 1982; Forsman et al., 2015; Tisthammer et al., 2018).

Statistical analyses were performed using PRIMER 6.1.15 (Primer-E, Plymouth, UK) with the add-on PERMANOVA+ package (Anderson et al., 2008) on Gower distance matrices (Gower et al., 1995). The Gower coefficient was selected in contrast to other coefficients, such as Bray-Curtis or Jaccard, because it can deal at the same time with numerical and categorical variables (Tuerhong & Kim 2014; Gonçalvez-Souza et al., 2019). A hierarchical cluster analyses was performed based on the investigated skeletal characters to determine the number of groups among the analysed samples sharing similar morphological characters. Permutational multivariate analyses of the variance (PERMANOVA) was performed to test for compositional differences among the morphological variables for the morphological groupings (32 levels) and the molecular clustering (14 levels). Two PERMANOVA tests, based on a Type III sums of squares and run using 9999 permutations, were performed considering the factors morphological groups and molecular clades, both fixed and orthogonal. Moreover, a Canonical Analysis of Principal coordinates (CAP) for each single factor was performed as a validation, effectively testing how well CAP can correctly re-allocate the samples to the morphological or molecular groups recovered in chapter 2 (Anderson & Willis, 2003). I finally performed a CAP for the factor morphological groups within the five

unresolved groups of species recovered in chapter 2. For designation of the molecular clades (I to XV), please refer to results of chapter 2.

Table 3.2 Corallite skeletal characters of *Porites* samples considered for morphological analyses. N= numerical variable, O= ordinal variable, C= categorical variable.

	Skeletal character	Character description	Character states	Character type
1	Corallum morphology	Colony level growth form	(0) massive; (1) columnar; (2) encrusting; (3) branching; (4) nodular; (5) folious	C
2	*Corallum surface*	Colony level surface growth form	(0) flat; (1) lobed; (2) knobby; (3) ridges	C
3	*Columns tips*	When columnar colony growth form, shape of the columns tips	(0) absent; (1) rounded; (2) tapered	C
4	*Branches tips*	When branching colony growth form, shape of the branchess tips	(0) absent; (1) rounded; (2) tapered; squared (3)	C
5	*Knob tips*	When nodular colony growth form, shape of the knobs tips	(0) absent; (1) rounded; (2) tapered;	C
6	*Branches thickness*	When branching colony growth form, thickness of branches	(0) absent; (1) regular (<3 cm); (2) thick (>3 cm)	C
7	*Corallite depth*	Depth from surface of the corallite to the fossa	(0) superficial (<0.2 mm); (1) shallow (0.2.-0.5 mm); (2) deep (>0.5 mm)	C
8	*Corallite shape*	Shape of the corallites	(0) polygonal; (1) rounded	C
9	*Number of septa*	Number of septa per corallites	0 to 12	O
10	*Septa reaching the columella*	Number of septa fully developed	(0) absent (<4); (1) irregular (4-6); (2) complete (6-8)	C
11	*Wall arrangement*	Corallite wall arrangement with respect to other corallites	(0) not shared; (1) irregular; (2) shared	C
12	*Coenosteum*	Development of coenosteum among corallites	(0) absent; (1) irregular; (2) developed	C
13	*Coenosteum surface*	Ornamentation of the coenosteum	(0) absent; (1) granules; (2) spines; (3) pores	C
14	*Synapticular ring*	Presence/ absence of the columella	(0) absent; (1) present	C

15	Centroids distance	Linear distance between the canters of two adjacent corralites	-	N
16	Corallite diameter	Linear longest diameter of a corallite	-	N
17	Wall width	Linear width of the wall of a corallite	-	N
18	Columella	Presence/ absence of the columella	(0) absent; (1) present:	C
19	Pali number	Numebr of pali per corallite	1 to 8	O
20	Triplet fusion pattern	Triplet not fused/ fused	(0) absent; (1) present:	C
21	Fossa diameter	Distance measured across corallite center from middle ventral palus to dorsal palus	-	N
22	Dorsal directive length	Linear distance from dorsal septum tip to inner theca margin	-	N

3.4 Results

A total of 28 discrete clusters were identified, from A) to BB) (Fig. 3.1a, b). Over-imposing the factor “nominal species”, a total of 17 of these groups (A, B, F, H, I, J, K, N, I, Q, S, V, W, X, Z, AA, BB), exclusively clustered samples belonging to a single nominal species or novel morphology (Fig. 3.1a). In particular group A - *Porites solida* (Forskål, 1775); group B - *Porites columnaris* (Klunzinger, 1879) (however, this nominal species was not monophyletic); group F - *Porites* sp 8; group H - *Porites heronensis* Veron, 1985; I - *Porites somaliensis* Gravier, 1910; group J - *Porites* sp 4; group K - *Porites lutea* Milne Edwards & Haime, 1851; group N - *P*orites sp 7; group I - *Porites profundus* Rehberg, 1892; group Q - *Porites fontanesii* Benzoni & Stefani, 2012; group S - *Porites farasani* Benzoni & Terraneo 2019; group V - *Porites* sp 6; group W - *Porites flavus* Veron, 2000; group Z - *Porites sillimaniana* Nemenzo, 1976; group AA - *Porites negrosensis* Veron, 1990; and group BB - *Porites tuberculosus* Veron, 2000. Group C and group D

included only *Porites lichen* (Dana, 1846) samples, while groups T and U, included only *Porites vaughani* Crossland, 1952 samples. The remaining seven groups (E, G, L, M, P, R, Y) included specimens of more than one nominal species or novel morphology: group E – *Porites australiensis* Vaughan, 1918*, P. lobata, Porites* sp 2; group G – *Porites* sp 1 and *Porites* sp 3; group L – *Porites deformis* Nemenzo, 1955 and *P. annae* Crossland, 1952; group M – *P. annae* and *P. columnaris*; group P – *Porites rus* (Forskål, 1775) and *Porites monticulosa* Dana, 1846*;* group R – *Porites hawaiiensis* Vaughan, 1907 and *Porites* sp 12; and group Y – *Porites cylindrica* Dana, 1846 and *Porites reticulum* Ortmann, 1892 (Fig. 3.1a).

Over-imposing the factor "molecular clade", a total of seven groups (I, K, N, P, Q, S, and W) were comprised of samples belonging to a single molecular clade: group I – clade VIII; group K – clade VII; group N – clade XII; group P – clade IV; group Q – clade I; group S – clade IIII; and group W – clade XIV. Groups A, K and Y, clustered samples belonging to clade V; groups B and G clustered samples recovered in clade II; groups O, V, and X, clustered samples belonging to clade IX; groups C, D, F, H, T, U, Z, AA, BB nested samples belonging to clade XIII. The remaining four groups (E, L, M, and R), were comprised of samples belonging to more than one molecular clade: group E – clade V and II; group L - clade XV and V; group M – clade V and II; and group R – clade X and XI (Fig. 3.1b).

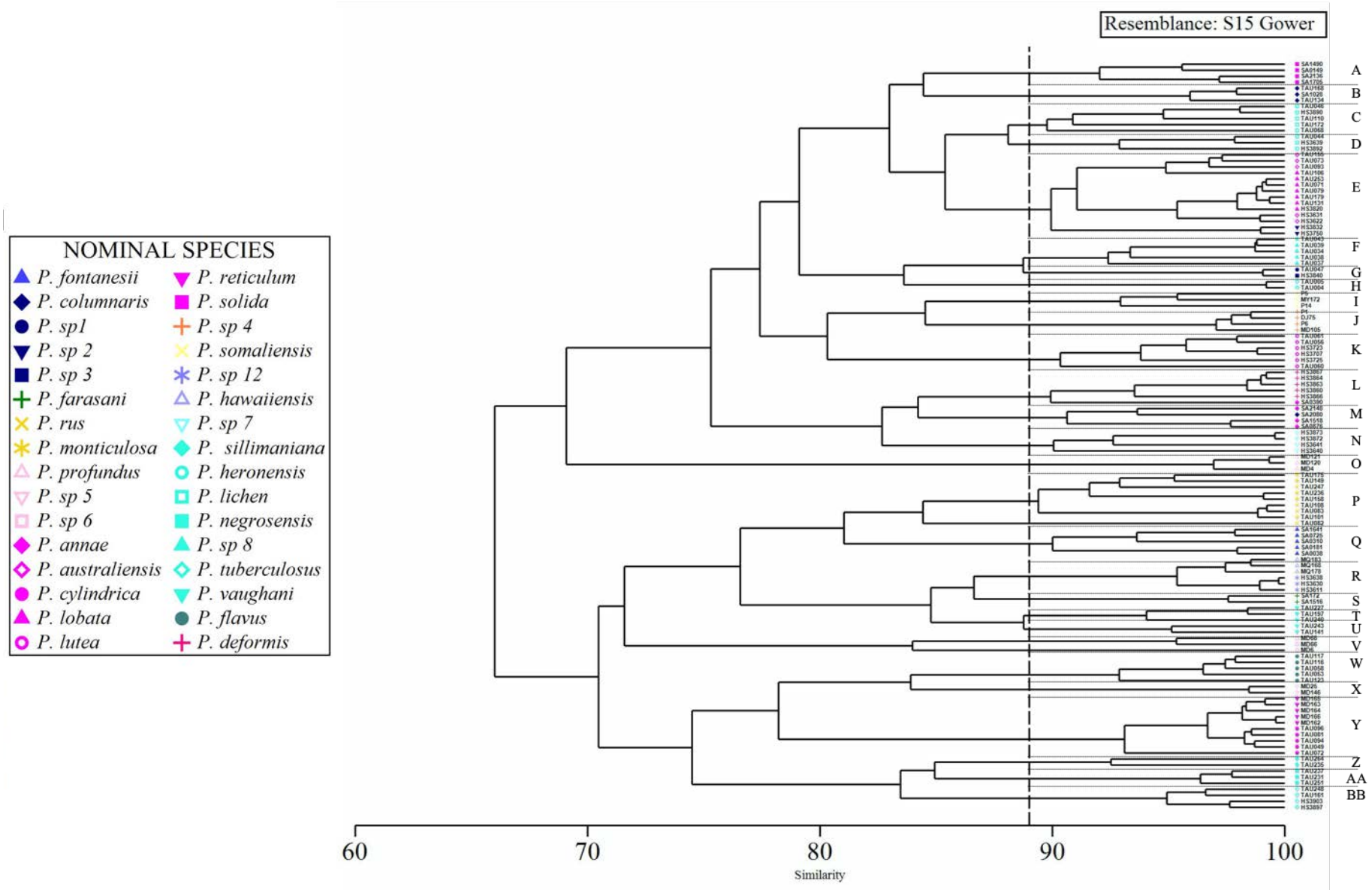
Following the PERMANOVA analyses, the characters examined significantly explained 95% of variance for the morphological groups ($P<0.001$), and 64% of the variance of the molecular clades ($P<0.001$) (Table 3.3).

For the examined specimens, CAP biplots of the averaged morphometric characters are reported in Fig. 3.2a, b. The CAP results show how many samples were blindly reassigned to the original nominal species or morphology, and the original molecular clade (Table 3.2a, b). Overall, 79% of the samples (98/ 124) were correctly reassigned to the original nominal species or morphology, and 59% (74/ 124) to the original molecular clade. In particular for the nominal species and morphotypes reassignment, 100% of the samples

were correctly blindly re-grouped as *P. fontanesii*, *P*. sp 2, *P. farasani*, *P. profundus*, *P. cylindrica*, *P*. sp 5, *P. reticulum, P. solida*, *P*. sp 4, *P.* sp 12; *P. hawaiiensis*; *P*. sp 7, *P. heronensis, P. negrosensis, P. tuberculosus,* and *P. flavus*. A lower percentage of correct reassignment occurred for the remaining samples: a total of 85% and 83% of the samples were correctly grouped as *P. lobata* and *P. lutea* respectively; misidentification occurred with *P*. sp 1 and *P.* sp 2 respectively. A total of 80% of the samples were correctly grouped as *P. monticulosa, P*. sp 8, *P. vaughani*, and *P. deformis*; in this case, misidentification occurred between *P. monticulosa* and *P. rus*, *P*. sp 8 and *P. lichen, P. vaughani* and *P*. sp 12, and *P. deformis* and *P*. sp 7. A total of 66% of the samples were correctly grouped as *P*. sp 6 and *P. somaliensis,* both misidentified with *P. lutea*, and 60% of the samples were correctly reassigned as *P. australiensis* while 40% of the samples were misidentified as *P. lobata;* 50% of the samples were correctly grouped as *P. rus* (misidentified with *P. monticulosa* and *P. fontanesii*) and *P. annae* (misidentified with *P. deformis* and *P*. sp 7); 37% and 25% of the samples were correctly grouped as *P. lichen* and *P. columnaris* respectively; *P. lichen* samples were placed by the blind reassignment with *P. columnaris*, *P*. sp 8, and *P*. sp 1, while *P. columnaris* samples were misidentified with *P. solida* and *P*. sp 7. Finally, no samples were correctly reassigned as *P*. sp 3 (misidentified as *P*. sp 1), *P*. sp 1 (misidentified as *P*. sp 3), and *P. sillimaninana* (misidentified with *P. tuberculosus* and *P. negrosensis*) (Fig. 3.2a, Table 3.4).

With regards to the reassignments to the original molecular clades, 100% of the samples were correctly placed into clade I, clade III, clade VII, clade VIII, clade X, clade XI, and clade XIV. A total of 88% and 80% of the samples were also correctly reassigned to clade IV and clade XV (with the remaining samples misidentified with clade I and clade VII respectively); a total of 62% to clade IX (misidentified with clade VIII and XIV), 48% to clade XIII (misidentified with clades II, X XI and XII), 38% to clade V (misidentified with clades II, VII, IX, and XII), 37% to clade II (misidentified with clades V and XII), 25% to molecular clade XII (misidentified with clades II and XV), and 20% into clade XIV (Fig. 3.3b, Table 3.5).

Following the overall results of chapter 2, a CAP was then run exclusively for the unresolved species groups in clades II, IV, V, XIII, and IX. With regards to clade II, samples of *P*. sp 2 were well separated from a group of samples belonging to *P. columnaris* (100% correct blind reassignment), while samples identified as *P*. sp 3 and *P*. sp 1 were intermixed (no sample correctly reassigned) (Table 3.6). Within clade IV, *P. rus* and *P. monticulosa* were intermixed and 55% of the samples re-classified correctly (Table 3.6). Within clade V, a total of six groups of species were recovered: *P. annae* (2 groups), *P. solida*, *P. lobata* and *P. australiensis*, *P. lutea*, and finally one group comprised of both *P. cylindrica* and *P. reticulum.* The blind reassignment correctly reclassified 100% of the samples to *P. australiensis*, *P. cylindrica*, *P. reticulum* and *P. solida*, while *P. lobata* and *P. lutea* were misidentified with *P. australiensis*, and finally *P. annae* was misidentified as *P. lobata* and *P. solida* (Table 3.6). Within molecular clade XIII, the CAP biplot shows six groups*: P. vaughani, P*. sp 8 and *P. heronensis, P. negrosensis, P. sillimaniana, P. negrosensis,* and finally *P. tuberculosus*. In this case, the CAP correctly reallocated the samples to the original nominal species (Table 3.6). Finally, for clade IX, the CAP correctly re-allocated all the samples to *P. profundus*, *P*. sp 5, and *P.* sp 6 (Table 3.6). CAP plots for clades II, V, and VIII are shown in Fig. 3.3 (a to c).


NOMINAL SPECIES
P. fontanesii
P. columnaris
P. sp1
P. sp 2
P. sp 3
P. farasani
P. rus
P. monticulosa
P. profundus
P. sp 5
P. sp 6
P. annae
P. australiensis
P. cylindrica
P. lobata
P. lutea
P. reticulum
P. solida
P. sp 4
P. somaliensis
P. sp 12
P. hawaiiensis
P. sp 7
P. sillimaniana
P. heronensis
P. lichen
P. negrosensis
P. sp 8
P. tuberculosus
P. vaughani
P. flavus
P. deformis
Resemblance: S15 Gower
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA
BB
60
70
80
90
100
Similarity

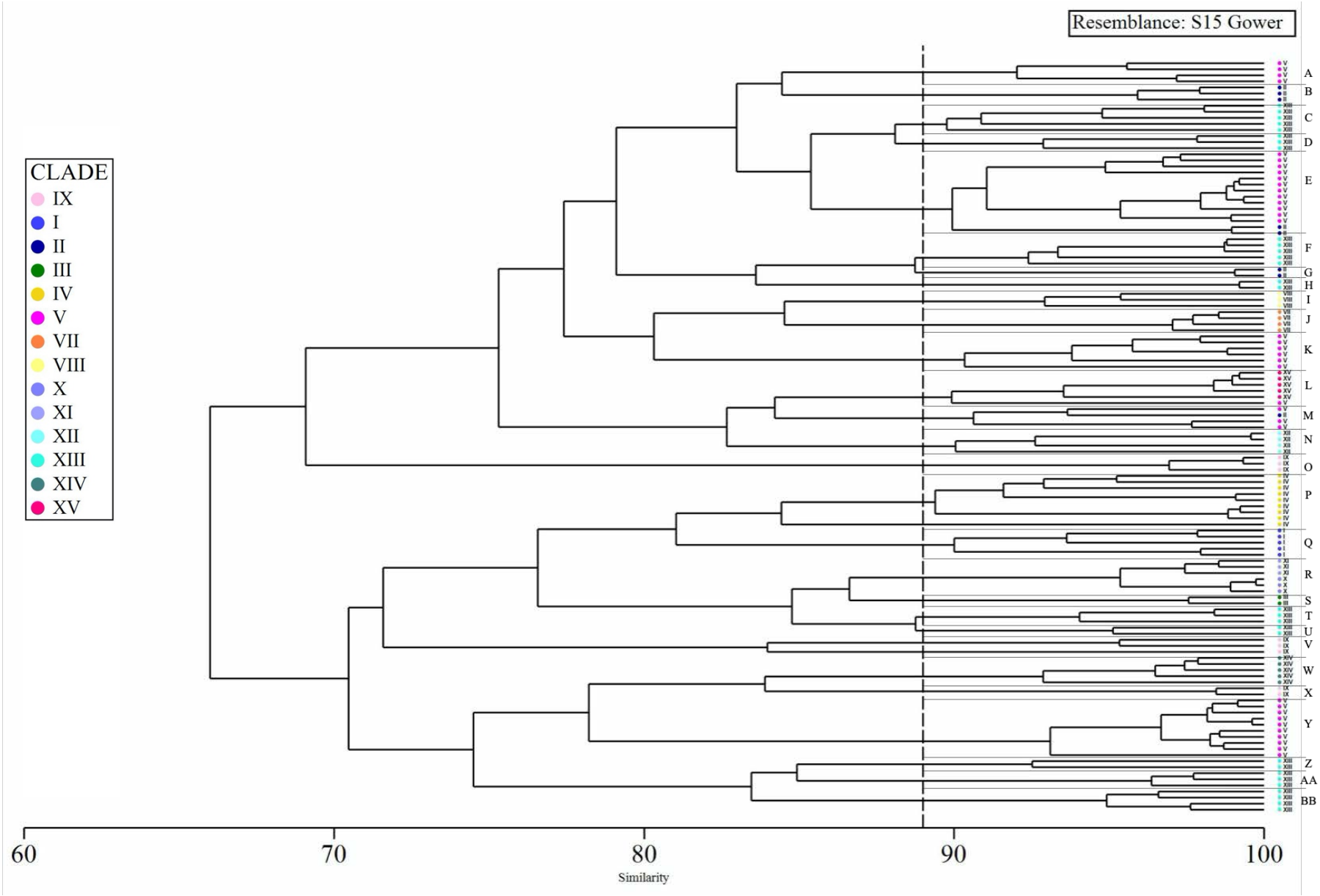
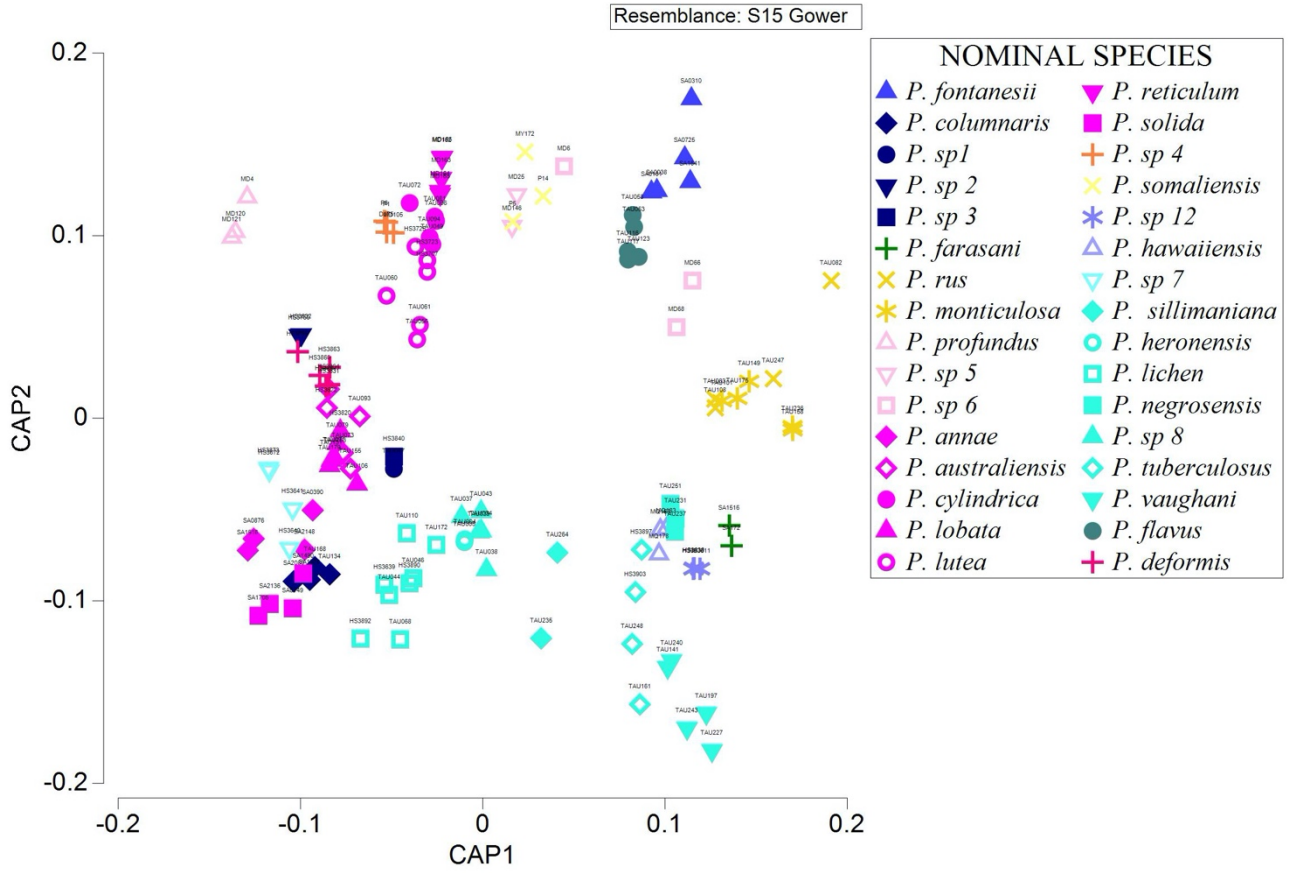


Figure 3.1 Cluster analyses of *Porites* morphology. Clusters are identified by capital letters from A-BB. Colours and symbol refer to (a) nominal species or novel morpholtypes of *Porites,* and (b) molecular clades of *Porites* from Chapter 2

Table 3.3 PERMANOVA results calculated for (a) the nominal species and (b) molecular clades. df = degrees of freedom.

	df	*SS*	*Pseudo-F*	*p*	*Unique perms*
(a) Nominal species	31	53504	65.08	0.0001	9797
Res	92	2439.9			
(b) Molecular clades	13	36042	15.342	0.0001	9866
Res	110	19902			


Resemblance: S15 Gower
CAP2
CAP1
0.2
0.1
0
-0.1
-0.2
-0.2
-0.1
0
0.1
0.2
NOMINAL SPECIES
P. fontanesii
P. columnaris
P. sp1
P. sp 2
P. sp 3
P. farasani
P. rus
P. monticulosa
P. profundus
P. sp 5
P. sp 6
P. annae
P. australiensis
P. cylindrica
P. lobata
P. lutea
P. reticulum
P. solida
P. sp 4
P. somaliensis
P. sp 12
P. hawaiiensis
P. sp 7
P. sillimaniana
P. heronensis
P. lichen
P. negrosensis
P. sp 8
P. tuberculosus
P. vaughani
P. flavus
P. deformis

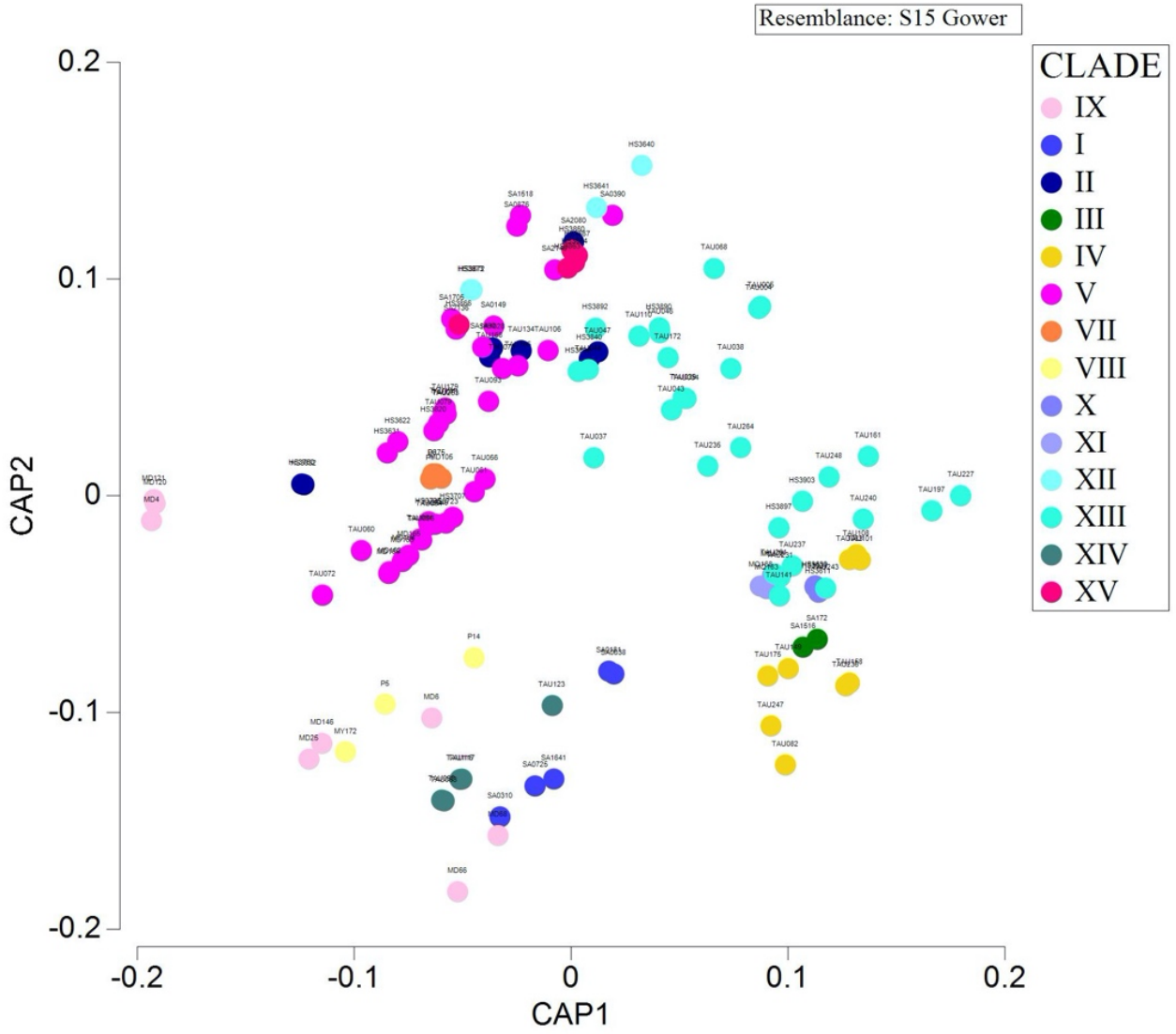


Figure 3.2 Canonical analyses of Principal Coordinates results based on 22 skeletal morphological characters in *Porites*. The symbols in the graph correspond to the analysed samples. Each colour and shape correspond to (a) *a priori* identified nominal species or morphology of *Porites,* and (b) *a priori* identified molecular clade of *Porites*

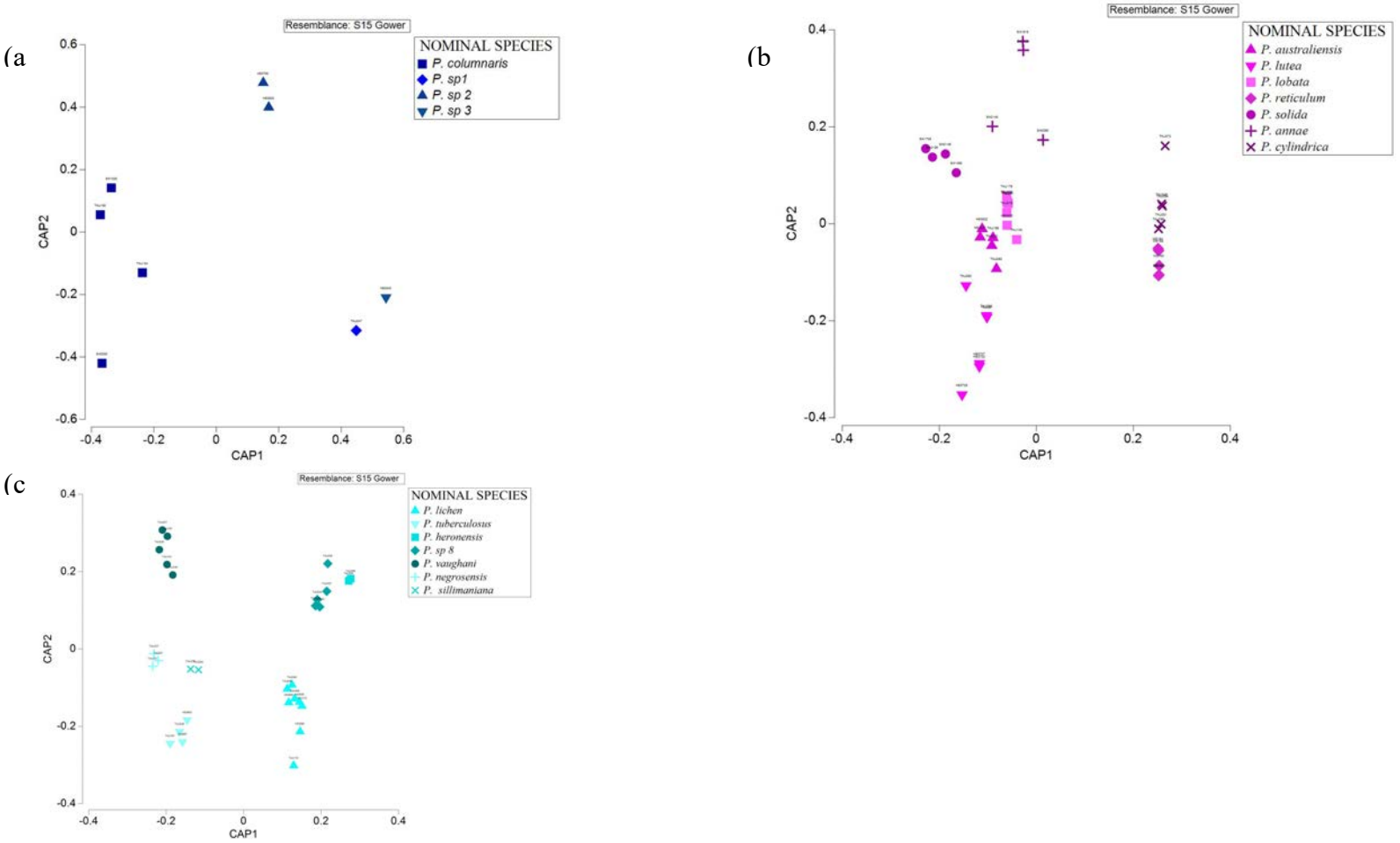


Figure 3.3 Canonical analyses of Principal Coordinates results based on 22 skeletal morphological characters in *Porites*. The symbols in the graph correspond to the analysed samples. Each colour and shape correspond to *a priori* identified nominal species or morphology of *Porites*. (a) clade II, (b) clade V, (c) clade VIII.

Table 3.4 Blind reassignment results of Canonical Analyses of Principal Coordinates (CAP). (a) Summary of reassignments of each sample to the original *Porites* nominal species or morphology. (b) Summary of reassignments of each sample to the original *Porites* molecular clade. Total number of samples and percentage of correct reassignment are reported in the last two columns.

(a)

Orig. group	P. fontanesii	P. columnaris	P. sp2	P. sp3	P. sp1	P. farasani	P. monticulosa	P. rus	P. profundus	P. sp5	P. sp6	P. annae	P. australiensis	P. cylindrica	P. lobata	P. lutea	P. reticulum	P. solida	P. sp4	P. somaliensis	P. sp12	*P. hawaiiensis*	*P. sp7*	*P. sillimaniana*	*P. heronensis*	*P. lichen*	*P. negrosensis*	*P. sp8*	*P. tuberculosus*	*P. vaughani*	*P. flavus*	*P. deformis*	Total	% correct
P. fontanesii	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	100
P. columnaris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	25
P. sp2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100
P. sp3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
P. sp1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

P. farasani	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100
P. monticulosa	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	80
P. rus	1	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	50
P. profundus	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	100
P. sp5	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	100
P. sp6	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	66.667
P. annae	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	50
P. austral	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	60

iensis																																				
P. cylindrica	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	100
P. lobata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	85.714
P. lutea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	83.333
P. reticulum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	100
P. solida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	100
P. sp4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	100
P. somaliensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	66.667

P. sp12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	100
P. hawaiiensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3	100
P. sp7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4	100
P. sillimaniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	2	0
P. heronensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	100
P. lichen	0	3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	8	37.5
P. negrosensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	100
P. sp8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	4	0	0	0	0	5	80

P. tuberculosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	4	100
P. vaughani	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	0	0	5	80
P. flavus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	100
P. deformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	4	5	80

(b)

Orig. group	I	II	III	IV	IX	V	VII	VIII	X	XI	XII	XIII	XIV	XV	total	%correct
I	5	0	0	0	0	0	0	0	0	0	0	0	0	0	5	100
II	0	3	0	0	0	2	0	0	0	0	3	0	0	0	8	37.5
III	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	100
IV	1	0	0	8	0	0	0	0	0	0	0	0	0	0	9	88.889
IX	0	0	0	0	5	0	0	1	0	0	0	0	2	0	8	62.5
V	0	14	0	0	1	14	3	0	0	0	4	0	0	0	36	38.889
VII	0	0	0	0	0	0	4	0	0	0	0	0	0	0	4	100
VIII	0	0	0	0	0	0	0	3	0	0	0	0	0	0	3	100
X	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	100
XI	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	100
XII	0	0	0	0	0	0	0	0	0	0	1	0	0	1	4	25
XIII	0	4	0	0	0	0	0	0	5	1	3	14	0	2	29	48.276
XIV	0	0	0	0	0	0	0	0	0	0	0	0	5	0	5	100
XV	0	0	0	0	0	0	0	0	0	0	1	0	0	4	5	80

Table 3.5 Blind reassignment results of Canonical Analyses of Principal Coordinates (CAP). Summary of reassignments of each sample to the original *Porites* nominal species or morphology Total number of samples and percentage of correct reassignment are reported in the last two columns. (a) clade II, (b) clade IV, (c) clade V, (d) clade IX, (e) clade XIII.

(a)

Orig. group	*P. columnaris*	*P.* sp2	*P.* sp3	*P.* sp1	Total	%correct
P. columnaris	4	0	0	0	4	100
P. sp2	0	2	0	0	2	100

P. sp3	0	0	0	1	1	0
P. sp1	0	0	1	0	1	0

(b)

Orig. group	*P. monticulosa*	*P. rus*	Total	%correct
P. monticulosa	4	1	5	80
P. rus	3	1	4	25

(c)

Orig. group	*P. annae*	*P. australiensis*	*P. cylindrica*	*P. lobata*	*P. lutea*	*P. reticulum*	*P. solida*	Total	%correct
P. annae	2	0	0	1	0	0	1	4	50
P. australiensis	0	5	0	0	0	0	0	5	100
P. cylindrica	0	0	5	0	0	0	0	5	100
P. lobata	0	1	0	6	0	0	0	7	85.714
P. lutea	0	1	0	0	5	0	0	6	83.333
P. reticulum	0	0	0	0	0	5	0	5	100
P. solida	0	0	0	0	0	0	4	4	100

(d)

Orig. group	*P. profundus*	*P.* sp5	*P.* sp6	Total	%correct

P. profundus	3	0	0	3	100
P. sp5	0	2	0	2	100
P. sp6	0	0	3	3	100

(e)

Orig. group	*P. silimaniana*	*P. heronensis*	*P. lichen*	*P. negrosensis*	*P. sp8*	*P. tuberculosus*	*P. vaughani*	Total	%correct
P. silimaniana	2	0	0	0	0	0	0	2	100
P. heronensis	0	2	0	0	0	0	0	2	100
P. lichen	0	0	8	0	0	0	0	8	100
P. negrosensis	0	0	0	3	0	0	0	3	100
P. sp8	0	0	0	0	5	0	0	5	100
P. tuberculosus	0	0	0	0	0	4	0	4	100
P. vaughani	0	0	0	0	0	0	5	5	100

3.5 Discussion

In the previous chapter, I highlight which clades in *Porites* phylogeny reconstruction are likely problematic due to a mismatch of morphological and molecular data. In this chapter I show that the use of morphological taxonomy in a quantitative framework can be applied to (a) confirm the validity of well supported morphological and molecular clades and (b) revisit species boundaries in unresolved groups of species when the molecules obscure diversity patterns. The comparison of dry type material with newly sampled specimens, form the baseline against which to choose key characters. These characters are then analysed in a quantitative framework. My quantitative morphological analyses show that the chosen characters were able to distinguish several species of *Porites*, supporting the validity of some nominal species whose status was uncertain in the molecular data. Nevertheless, a parsimonious explanation of my analyses better assigning colonies based on morphology then on genetic clades, could also be that different environments or microhabitat might result in divergent selection of morphological traits (Carlon et al., 2011).

A quantitative framework to describe new species was provided. In particular, I show that 22 morphological characters traditionally used in *Porites* taxonomy, quantitatively identified 28 groups from several localities in the Indo-Pacific Oceans. On the basis of these characters, the cluster analyses were able to quantitatively discriminate 17 of the 32 nominal species and novel morphotypes considered, and seven of the 14 molecular clades. The morphotypes that were quantitatively distinct were *P. fontanesii, P. columnaris, P. farasani, P. lutea, P. solida, P.* sp 4, *P. somaliensis, P.* sp 7, *P.* sp 8*, P. heronensis, P. sillimaniana, P. negrosensis, and P. tuberculosus, P. profundus, P.* sp 5, *P.* sp 6*,* and *P. flavus*. Similarly, for the molecular clusters, the morphological analyses distinguished clade I, III, IV, VII, VIII, XII, XIV. Lastly, concentrating on the molecular clades that cluster specimens from multiple nominal species and novel morphotypes, these characters proved useful in distinguishing also *P*. sp 2 in clade II, *P. annae* in clade V, and *P. lichen* and *P. vaughani* in clade XIII,

bringing the total number of well resolved species to 21. The species that remained unresolved within the species groups were *P.* sp 1 and *P.* sp 3 in clade II, *P. rus* and *P. monticulosa* in clade IV, *P. australiensis* and *P. lobata*, *P. cylindrica* and *P. reticulum* in clade V.

3.5.1 Integration of morphological and molecular data

The results of the present work, integrated with the results of the previous chapter, confirm the presence of six distinct morphological and molecular lineages comprised of a single nominal species or novel morphology: *P. fontanesii* in clade I, *P. farasani* in clade III, *P. somaliensis* in clade VIII, and *P. flavus* in clade XIV. The distinctiveness of *P.* sp 4 in clade VII and *P.* sp 7 in clade XII is also confirmed, suggesting these are species new to science.

Porites sp 4 forms massive colonies with a gibbous surface. At the corallite level, this morph has polygonal adjacent corallites. These are superficial, of 1 mm in diameter with 6 pali and a columella that are well developed and reach the corallite surface. Two characters in particular distinguish *Porites* sp 4. The first is the presence of a well-developed synapticular ring that joins the pali and can be seen with the naked eye; the second, is that *in situ* the polyps are always extended with two order of tentacles orders (Table 2.1). *Porites* sp 4 occurs in Djibouti, the Gulf of Aden, Mayotte and Madagascar. From this dataset, the distribution of *P.* sp 4 seems restricted to the north western Indian Ocean (Appendix 2.9). This pattern has already been recorded for several Scleractinia species, such as *Anomastrea irregularis* Merenzeller, 1901, *Lobophyllia eyithraea,* (Klunzinger, 1879)*, Micromussa indiana* Benzoni & Arrigoni, 2016 (Arrigoni et al., 2016)*, Oxypora convoluta* Veron, 2002*, Paraechinophyllia viariabilis* Benzoni, Arrigoni & Stolarski, 2019 (Arrigoni et al., 2019)*,* or *Sclerophyllia maxima* (Sheppard & Salm, 1988) (Arrigoni et al., 2015). The inclusion of *P.* sp 4 within this group of western Indian Ocean endemics, would strengthen the hypothesis of a hotspot for coral biodiversity in the western Indian Ocean (Obura, 2012).

Porites sp 7 forms small nodular colonies, that develop small knobby-like branches with rounded tips. At the corallite level this morphology has deep angular has corallites that can get up to 1.5 mm in diameter. The septal formula is not complete, and the number of septa varies from 4 to 6. A total of 4-5 pali is always present, and joined by a well-developed synapticular ring. Molecularly, *P*. sp 7 forms a well distinct clade (clade XII) based on the rDNA and SNPs reconstructions (Fig. 2.1a, 2.2a, b), yet is not distinguished from clade XIII based on the histone reconstruction (Fig. 2.1b). Nevertheless, the BFD* confirms the validity of this molecular lineage (Table 2.2). Taken together these results highlight a lack of resolution in the histone phylogenetic reconstruction, showing the limitations of reconstructions based on single regions or a limited number of loci.

According to the quantitative morphological examination, the position of *P*. sp 12 remains uncertain. Morphologically, *P*. sp 12 in close to *P.* cf *hawaiiensis* (holotype USNM 21624). Indeed, the morphological analyses did not distinguish between *P*. sp 12 in clade X (from New Caledonia) and *P.* cf *hawaiiensis*. Molecularly *P*. sp 12 forms a sister clade to *P.* cf *hawaiiensis*, indicating that the two are indeed closely related. *Porites* sp 12 forms encrusting colonies, characterized by a developed spinulated (bearing spines) coenosteum, small rounded corallites of less than 1 mm in diameter. The maximum number of pali in *P*. sp 12 is 5, while is 6 in *P.* cf *hawaiiensis,* but besides this character the species are comparable. Nevertheless, the molecular distinctness of *P*. sp 12, coupled with the geographic distributions of these two sister clades (*P. hawaiiensis* from the Marquesas Islands, and *P*. sp12 from New Caledonia – see chapter 2), suggest the presence of novel species of relatively recent origin (< 1Mya).

From a biogeographical point of view, both *P.* sp 7 and *P*. sp 12 have been so far reported only in New Caledonia (Appendix 2.9). No species of *Porites* have their type locality in New Caledonia, nor evidence of *Porites* endemic to New Caledonia has been reported so far. Further sampling is needed to corroborate the distribution of *P*. sp 7 and *P*. sp 12. Nevertheless,

endemicity of *P*. sp 7 and *P*. sp 12 to New Caledonia should not be excluded. For instance, *Polyciatuus fulvus* Wijsman-Best, 1970 and *Cantharellus numeae* Hoeksema & Best, 1984 are endemic corals from New Caledonia and their endemicity has been correlated with the terrigenous sediments that characterise several habitats around La Grande Terre (Gilbert et al., 2015).

Overall, the integration of morphological and molecular data from chapter 2 and chapter 3 are suggesting that the chosen characters could be generally useful in a revision of the genus that includes all the nominal species.

3.5.2 Unresolved groups of species

Several nominal species and novel morphotypes nested together within the clades II, V, IX, and XIII (see chapter 2). Quantitative morphological analyses, however, suggests that the majority of these nominal species and novel morphotypes are distinct.

Within clade II, *P. columnaris* and *P*. sp 2, are distinguished from each other, however, the remaining novel morphotypes, *P*. sp 3 and *P*. sp 1, were intermixed. This suggests that the qualitative morphological criteria used to define the novel morphology might be incorrect and let to an overestimation of diversity, and/or that the sample size for the quantitative morphological analyses was insufficient to discriminate *P*. sp 1 and *P*. sp 3. The holotype of *P. columnaris* has a columnar growth form as shown in the holotype picture available in Appendix 2.3, however the original description of the species also mentions the presence of massive growth forms (Klunzinger, 1879) (yet no designated type series is available to corroborate this). A specimen collected by Klunzinger and preserved in the NHMN in Paris (NHMN 4151), from the same locality and collected in the same year as the holotype, shows a columnar growth form, yet in this case the columns are short and rounded and not tapered. The main morphological distinction among *P. columnaris* and *P.* sp 1, *P*. sp 2 and *P*. sp 3 is the corallum morphology. *Porites* sp 1 and P. sp 3 are encrusting, while *P*. sp 2 is massive. From a biogeographical perspective, *P. columnaris*, described from the Red Sea, has since been recorded using a

morpho-molecular approach in the Red Sea, Djibouti, the Gulf of Aden, mainland Yemen, and Socotra (Terraneo et al., 2019b). This study extends the species range to Madagascar, Papua New Guinea and eastern Australia along the Great Barrier Reef (Fig. 2.1, 2.2, Appendix 2.1, 2.4 – 2.6). *Porites columnaris* is an Indo-Pacific species, as opposed to what previously thought. *Porites* sp. 1 was collected from Australia (on the Great Barrier Reef and Lord Howe Island), *P*. sp 2 from the Great Barrier Reef and New Caledonia, while *P*. sp 3 from Socotra and New Caledonia only. With regards to *P*. sp 3, this morph was sampled from Socotra Island and New Caledonia (Appendix 2.9). Further sampling is necessary to verify the distribution of this lineage at other localities. From the proposed morphological and molecular analyses, the likely scenario is that clade two is comprised of three species: *P. columnaris*, *P*. sp 2, and *P*. sp 1 and *P*. sp 3. Yet, the overlapping geographic distributions renders hard to discriminate where species boundaries lay within this clade and whether *P*. sp 1 and *P*. sp 3 are indeed morphotypes of a single species as the incomplete lineage sorting or hybridisation and introgression, are confusing the species boundaries. The study of the time and mode of reproduction of these morphotypes could provide an alternative confirmation when no clear understanding is provided by other evidence.

Both the cluster analyses and the CAP confirmed that the samples in clade IV from *P. rus* and *P. monticulosa* were not significantly different, corroborating the molecular findings. Taxonomic confusion persists around these two-nominal species, and detailed considerations should be taken. *Porites rus* was described as *Madrepora rus* Forskål, 1775 from the Red Sea. No holotype was deposited by Forskål. Crossland (1941) studying Forskål's collection held at Copenhagen museum, matched three specimens (N 51, 52, 14) with *P*. (*Synaraea) undulata* (Klunzinger 1879) originally described from the Red Sea, and named these specimens following the youngest name. The holotype of *P. undulata*, originally decribed as *Synaraea undulata*, shows a columnar growth form. The original name *P. rus* was resurrected by Veron & Pichon (1982), who attribute to this species several synonyms, comprising *P.*

undulata, as well as *P. monticulosa* Dana, 1846. *Porites monticulosa*, was described from Fiji. Although no distinction from *P. rus* is given in Dana's original description, besides the different type localities. The features distinguishing *P. monticulosa* from *P. rus* syntypes, are a columnar growth form, and smaller ridges in the former. At the corallite level, both species present corallites of less than 1 mm in diameter, enclosing 5-6 big pali, scattered among a developed granulated coenosteum, from where ridges develop (Table 2.1, Appendix 2.3). The synonymisation of *P. monticulosa* was somehow lost in Veron (2000), where the two nominal species were differentiated based on the "most common growth forms", and apparently not in relation with the type material. This distinction might derive by the inclusion in *P. rus* of growth forms typical of previously synonymised species, such as *P. convexa* (Verrill, 1864), which holotype presents short anastomosing knobs, but this is just a personal hypothesis. In the present work, I followed the information reported in WoRMS (Hoeksema & Cairns 2019) based on Veron (2000), and considered both *P. rus* and *P. monticulosa* as valid species. Besides the type material analysed, distinguished by a submassive growth form in *P. rus* and a columnar in *P. monticulosa*, I followed Veron (2000) indication and identified as *P. rus* colonies forming short branches. *P. monticulosa* forming flat plates or encrusting colonies. Molecular data and species delimitation analyses clustered these samples together in clade IV. Both morphotypes were intermixed in the Red Sea and Gulf of Aden, and in the Pacific Ocean. For example, SA2196 (Saudi Arabian Red Sea) present a columnar growth form comparable to the holotype of *P. monticulosa* from Fiji. Similarly, TAU247 from the Great Barrier Reef (Australia) has a submassive growth form, comparable to *P. rus* syntype N 51. The extended distribution of both growth forms in the Indo-Pacific (Appendix 2.9), together with the molecular indistinctness, and the corallite level similarities (Table 2.1), suggest the synonymisation of *P. monticulosa* with the former described nominal species *P. rus,* and an extension of *P. rus* range from the Red Sea to the Indo-Pacific. Nevertheless, until samples from the type locality of *P. monticulosa* are included, no taxonomic actions should be taken.

Within clade V, cluster analyses supported the distinctives of *P. lutea* and *P. solida*, while the CAP also separated *P. annae*. *Porites solida* originally from the Red Sea is a species described by Forskål. The author did not designate a holotype. Indeed, two syntypes were attributed to this species, which Forskål designates as form *a* and *b*, among a series of 14 specimens presenting variable morphology. After its description, the species name has been widely used in the literature, starting from Klunzinger. Indeed, he recovered similarities of some of his samples from the Red Sea with *M. solida* form *a* (the original combination for *P. solida* from Forskål) on the basis of the toughness and abundance of the coral but not based on morphological characters since he had no access to Forskål's collection. Klunzinger deposited a type for *P. solida* preserved at the British Museum, disregarding the syntypes from Forskål. At the same time, Klunzinger recognizes *M. solida* form *b*, to share morphological similarities with *P. lutea*. Later, Crossland in 1952, studying Klunzinger's collection, recognizes that both form *a* and *b* of Klunzinger corresponded to Forskål's form *b*. *Porites conglomerata* (*M. conglomerata*) has also been synonymized with *P. solida*, yet no holotype was designated by Esper. The drawing of this form, shows a massive colony with a bumpy surface, but the corallites details are hardly distinguished from the drawing, thus is hard to comment on this. Crossland provides a detailed description of the 14 specimens from Forskål, and designates sample n 17 as the species' most characteristic type. Crossland (1952) presents a photograph of specimen n 17, as well as a close-up of the corallites, which have been used in the present work. The corallite diameters range from 1.5 to 2 mm, and the depth of the corallites is around 0.5mm. The intracalicular structures vary in development, and the pali are variable in number, sometimes resembling the septal granules (Table 2.1, Appendix 2.3). It remains unclear to date what the original *P. solida* is and the morphological variability that this species encompasses. *Porites lutea* is a nominal species described by Milne Edwards and Haime, 1851 from Tonga. The holotype of *P. lutea* is at the Paris Museum, IK-2010-389, and it is the original specimen for *P. conglomerata* var *lutea* from

Quoy and Gaimard (1833), that Milne Edwards & Haime recognised as a different species from *P. conglomerata.* The holotype is a small submassive colony with a smooth surface, covered by shallow corallites. These are small in diameter, around 1 mm, adjacent and polygonal in shape. Within the corallites, 5 to 6 pali are developed. This is characteristic of this species, and such feature is visible at the naked eye in the holotype. Nevertheless, on the lower part of the colony, the characteristic pali are less developed. Walls are thin and the ventral triplet of septa is usually fused (Table 2.1, Appendix 2.3). It remains unclear if this sample is the actual holotype of *P. lutea*. According to Bernard (1905), the description of *P. lutea* was based on the specimen identified as *P. conglomerata* by Dana. *Porites lutea* was sampled from almost all the localities surveyed for this study (Appendix 2.9) confirming that it is a widely distributed species. *Porites annae* described by Crossland, 1952 from the Great Barrier Reef, Australia, was sampled only from the southern Red Sea, Djibouti, the Gulf Aden and the Gulf of Oman (Appendix 2.9). Considering the far distance from this sampling with respect to the type locality of the species, this identification might need to be reconsidered. *Porites annae* forms colonies with encrusting bases, from which short branches or knobs develop. The corallites are polygonal and adjacent, and range from 1.1 and 1.5 mm in their longest diameter. The calices on the columns differ from the those at the base of the colonies, in particular being deeper and with thin walls, while the basal ones are more superficial. The number of pali is variable, depending on the development of the ventral triplet fusion, yet they normally fuse forming a crown in the middle of the corallites. The walls are generally thin, forming a reticulated pattern (Table 2.1, Appendix 2.3). The most distinguishing feature of this species with respect to its congeners is the growth form and corallites size and depth. Phylogenetically, samples identified as *P. annae*, *P. solida* and *P. lutea* subcluster within clade V, and remain intermixed among samples belonging to other nominal species. Yet the consistent distinct forms suggest that these are valid species.

The morphological distinction between *P. lobata* and *P. australienesis*, and between *P. cylindrica* and *P. reticulum* were not supported by either cluster analysis or CAP. *Porites lobata* and *P. australiensis* are intermixed within the SNPs reconstructions (chapter 2) and have an overlapping geographical distribution (Appendix 2.9). *Porites australiensis* is a species described by Vaughan (1918) from Murray Island in Australia (Appendix 2.9). I sampled *P. australiensis* exclusively on the Great Barrier Reef and New Caledonia. The holotype of this species USNM 47233 has shallow corallites ranging from 1-1.5 mm, and has developed walls constituted by rows of denticles. In other parts of the colony the walls are thin and reticulate. Its 12 septa are irregular in development in different corallites, rarely bearing a palus per lateral pair, and a smaller palus rising from the dorsal directive. A total of 5-8 pali are visible at the naked eye (Table 2.1, Appendix 2.3). *Porites lobata* is another nominal species much mentioned in the literature. Originally was described from Dana, from Hawaii in 1846. Two syntypes of *P. lobata* are kept in the Smithsonian National Museum of Natural History, Washington D.C. These are USNM 464 and 652. Both are gibbous sub-massive colonies, but have different growth forms. The first specimen has an irregular surface with short knob-like protuberances, while the latter has a smoother surface. In USNM 653, the corallites are polygonal, with diameter ranging from 1.1 to 1.25 mm. The walls of the corallites are perforated. The intracalicular structers are also thin, and the septa fuse, forming reduced pali, variable in number. USNM 464 instead, has more developed walls in some part of the colony, while in other parts these are thin and resemble those of USNM 652. The corallites of this specimen have similar thin septa and pali, sometimes fused by a synapticular ring (Appendix 2.3). Overall, the integration of morphological, molecular and geographical results suggests that *P. australiensis* might be a junior synonym of *P. lobata.*

Porites cylindrica Dana, 1846 has its type locality in Fiji. The samples collected for this work range from Australia and the Coral Sea, to New Caledonia and Papua New Guinea. In the Indian Ocean, *P. cylindrica* was sampled from Singapore and Mayotte (Appendix 2.9). The syntype of *P.*

cylindrica USNM 708 is a caespitose colony with cylindrical branches that terminate with rounded or tapered tips. The corallites are superficial and polygonal, smaller than 1 mm in diameter. A granulated coenosteum is intercalated among some corallites, but is never abundant. A total of 6-7 pali are distinguished, and one of the septal trabeculae terminate with 1 granule (Table 2.1, Appendix 2.3). Interestingly, in the syntype only the apical part of the colony is composed of young coral tissue, while the rest is old skeleton. *Porites reticulum* is a species that has been lost in the taxonomic literature, and indeed its taxonomic status is currently not confirmed by WoRMS 2019 (Hoeksesema & Cairns, 2019). Originally described from Tanzania by Ortman (1892), this species is characterized by forming slightly attached or free-living branching colonies on soft substrata, which is a rare trait within the genus *Porites.* Another example is *Porites sverdrupi* inside and south of the Gulf of California (East Pacific), which has larger calices (López-Pérez 2013; Paz-García & Balart, 2016). Indeed, it forms slightly attached or free-living branching colonies above soft substrata. The branches terminate with rounded or tapered tips. Colonies are small. Corallites are <1 mm in diameter, and superficial (Table 2.1, Appendix 2.3). Although the holotype of this species is lost, based on the original description, this nominal species does not resemble any other species of *Porites* considered in this study. Moreover, the type locality of *P. reticulum* is close to Madagascar, where the samples identified as *P. reticulum* were collected (Appendix 2.9). Within clade V in the phylogeny, specimens identified as *P.*cf *reticulum* form a well distinct subclade, evidence that geneflow is reduced among this lineage and other species within the clade. Samples of *P.* cf r*eticulum* have only be recovered from Madagascar and from Socotra Island. This could be indicating a possible distribution of *P.* cf *reticulum* in the western Indian Ocean only, but this cannot be confirmed for now. *Porites cylindrica* and *P. reticulum* form subclusters within clade V in the phylogeny, and occur in separate geographic regions *i.e.* the Pacific and Indian oceans respectively. These results suggest they are likely to be valid species that neither species delimitation approaches nor quantitative

morphological analyses can distinguish. In this case, further lines of evidence will be required to confirm this hypothesis.

With regards to clade IX, *P. profundus*, *P.* sp 5 and *P.* sp 6 are morphologically distinct. *Porites profundus*, described by Rehberg (1892) with the type locality in Nosy Bé, Madagascar, is distinguishable from its congeners by having the largest calice diameter (2-2.5 mm), polygonal adjacent corallites, where the septa are hardly recognizable within the excavated fossa. The species forms branching colonies, with tapered or bifurcate branches tips (Table 2.1, Appendix 2.3). In this work, I extended the distribution of this species previously reported from Madagascar, also to Mayotte (Appendix 2.9). *Porites* sp 5 samples have a similar branching growth form to *P. profundus*, yet the branches in *P.* sp 5 are tapered or bear paddle-shaped tips. The corallites diameter in the latter does not exceed 1.2 mm (Table 2.1), and 4-5 pali are distinguishable. The last morph within this clade is *P.* sp. 6. *Porites* sp 6 is distinct from *P. profundus* and *P.* sp 5 at the colony level by forming foliouse colonies (Table 2.1). At the corallite level, it is distinct from *P. profundus* by having smaller corallites (1.5 mm), and from *P.* sp 5 by having less developed corallites structures, such as the lack of granulation on the scarcely developed septa. It differs from both *P. profundus* and *P.* sp 5 by having rounded corallites (Table 2.1). Moreover, this species has polyps extended during the day (Appendix 2.2a). *Porites* sp 6 was sampled in the same localities as *P. profundus* and *P.* sp 5, Madagascar and Mayotte. The morphological differences among three morphotypes, considered with their molecular position within one single species group, and their geographic overlapping distribution, suggests the presence of three sympatric lineages that started to diverge or where incomplete lineage sorting or hybridization might confuse boundaries within clade IX. The inclusion of further lines of evidence taxonomy such as reproductive trials, or the evaluation of the symbiont community for the three morphotypes, could in this case help understanding the presence of underling evolutionary processes.

Finally, within clade XIII, the nominal species *P. lichen*, *P. heronensis*, *P. sillimanina*, *P. negrosensis*, *P. tuberculosus*, *P. vaughani* and *P.* sp 8 were significantly separated by the CAP. However, the cluster analyses suggested the presence of two separate groups among samples of *P. lichen* and *P. vaughani*. Nevertheless, these separate groups are not confirmed by the CAP and I thus consider only one lineage for each. *Porites lichen* has a type location in Fiji. In this thesis, I included samples from Australia, New Caledonia, and Mayotte in the Indian Ocean (Appendix 2.9). The holotype USNM 666 is encrusting with flexed upward free margins. The corallites being rounded, with a maximum diameter of 1.2 mm, spaced within thin ridges that enclose 1 corallite at the time (Table 2.1, Appendix 2.3). Within this clade, are nested three nominal species with a branching growth form: *P. tuberculosus, P. sillimaniana*, and *P. negrosesnis*, characterized by the presence of developed ridges that surround single corallites or series of 3-4 corallites. *Porites tuberculosus* was described from Indonesia, and was named after its tuberculate coenosteum (Appendix 2.3). The holotype G55804 is a branching specimen with tapered and squared tips. The corallites have a diameter ranging 1.6-2 mm; they are irregularly spaced trough ridges in a coarse coenosteum, with the presence of 5-8 pali, and a columella (Table 2.1). The holotype UPZD SU D78 of *P. sillimaniana* is a specimen with anastomosing branches departing from a common base, tapering with canonical apices. The corallum shows circular corallites, smaller than 1 mm in diameter, containing 5 big pali and often no columella. The corallites are separated by coarse granulated walls. (Table 2.1, Appendix 2.3). Based on the type material, the main differences of *P. sillimaniana* with *P. tuberculosus* are the reduced corallite diameter, the presence of less developed and more regular ridges in *P. sillimaniana*, and finally the type localities (Table 2.1), although in this study they were both found on the Great Barrier Reef, Australia (Appendix 2.9). *Porites negrosensis* has its type locality in Negros Islands, in the Philippines. I sampled this species along the Great Barrier Reef, Australia and Papua New Guinea. The holotype G32478 is a colony with flat branches, shallow corallites

of 0.8-1.2 mm diameter, seated among coarse ridges. At the base of the corallum, the ridges are reduced and the colony surface becomes flat. Considering the genomic data, along with the above-mentioned discussion, it might be possible that these three nominal species represent different morphotypes of a continuous variable species, with variable corallite size. Also, in this case, fundamental would be the future inclusion of further life history traits to better understand where species boundaries lay among these morphotypes. With respect to *P. lichen, P. tuberculous, P. sillimaniana, and P. negrosensis,* differ in the corallum growth form, in the bigger corallite size for both *P. tuberculosus* and *P. sillimaniana*, and the presence of a developed granulated coenosteum forming tuberculated ridges among which the corallites lay (Table 2.1). From a geographical point of view, *P. lichen* has been sampled in the western Pacific, as well as in the western Indian Ocean, while the other three nominal species only in the Western Pacific Ocean and in the Coral Triangle. The widespread distribution of *P. lichen* with respect to the branching morphologies provides another line of evidence of the distinction of *P. lichen*.

Porites vaughani is morphologically distinct from the other species nested in clade XIII. Moreover, within the phylogeny reconstruction provided in Chapter 2, samples of *P. vaughani* form a subclade. The holotype of *P. vaughani*, NHM 1934.5.14.491A, is an encrusting colony with the Great Barrier Reef, Australia as the type locality. Underwater the colonies are distinguishable by having a crown of slightly extended tentacles (Terraneo personal observation). At the corallite level, small series of calices (1 mm in diameter) occur between a developed coenosteum, composed by spinulated processes, and that form ridges. For this reason, the species was initially placed within the subgenus *Synaraea*. A total of 5-7 pali are distinguished and a columella in most of the corallites (Table 2.1, Appendix 2.3). The species has been sampled only in the Great Barrier Reef – Australia (Appendix 2.9). The restrict geographic distribution coupled with the morphological and molecular data, suggest that *P. vaughani* is a valid species within clade XIII.

The morphological analyses suggest that *P. heronenesis* can be distinguished from the other representatives within clade XIII. The holotype of *P. heronensis* WAM162-84 is a colony with and encrusting base and a bumby surface. The corallites range between 1.1 and 1.5 mm in diameter, and present 5 pali. The type locality is Heron Island, Australia. I sampled this species along the Great Barrier Reef and Lord Howe Island in Australia (Appendix 2.9). Molecularly no clear subclade can be delineated within the SNPs reconstructions, where the two samples identified as *P. heronensis* were intermixed with *P. lichen*. Within the rDNA reconstruction, where more samples of *P. heronensis* are included, there is a partial subclustering of these samples, but these are always intermixed with *P. lichen* samples. From the current data, it remains to be confirmed where boundaries between *P. lichen* and *P. heronesis* are situated, and if they represent one single variable species, or two lineages started to diverge.

Porites sp 8 forms encrusting colonies that may form bumps. Underwater the colonies displayed tentacles extended during the day (Appendix 2.2a). Corals with this morphology were sampled from the Great Barrier Reef (1 sample), Lord Howe Island (4 samples), and the Solitary Islands (7 samples). At the corallum level, *P*. sp 8 can resemble *P. lichen* in having an encrusting bumpy growth form. Nevertheless, at the corallite level, *P*. sp 8 has smaller corallites, synapticular rings connecting the septa, which are thicker and smoother in *P*. sp 8 compared to *P. lichen* (Table 2.1, Appendix 2.3), while, there is a more prominent granulation in *P. lichen,* mostly on the pali. Finally, although the tentacle organization has hardly been regarded as an informative trait to species boundaries in Scleractinia, species-specific patterns are becoming interesting in the present study, such as the above-described tentacle arrangement in the present case, as well as previously mentioned for *P. columnaris* and *P.* sp 4. Based on the present data, *P. lichen* can be considered separate from *P*. sp 8. Moreover, within the phylogeny reconstruction, samples of *P*. sp 8 from Solitary Island form a distinct subclaster within clade XIII, separate from other species with similar a shape. Giving the remote location and the

phylogenetic position, it seems likely that these samples could represent a lineage within clade XIII distinct from *P.* sp 8 samples from Lord Howe Island.

A summary of the integrated morphological, molecular, and geographic considerations, is provided in Table 3.6.

Table 3.6 Summary of the molecular, morphological, and geographic results as presented in chapter 2 and the current chapter. An integration of these lines of evidence is provided, and future working directions suggested, towards a better understanding of species boundaries in *Porites*.

MOLECULAR CLADE	NOMINAL SPECIES	MOLECULAR LINEAGES	SUBCLUSTER	BIOGEOGRAPHY	MORPHOLOGICAL LINEAGES	INTEGRATED RESULTS	FUTURE DIRECTIONS
I	*P. fontanesii*	x	-	x	x	X	-more sampling
II	*P. columnaris*	x	-		x	unresolved	-more sampling -time/mode reproduction -breeding trials -micromorphology -symbiont association data -UCE/Exon capture
	P. sp 2				x		
	P. sp 1				x		
	P. sp 3						
III	*P. farasani*	x	-	x	x	X	-more sampling
IV	*P. monticulosa*	x	-	x	x	X	- sampling in type locality -micromorphology
	P. rus						
V	*P. annae*	x	-	x	x	X	- sampling in type locality -time/mode reproduction -breeding trials
	P. solida		-		x	X	
	P. lutea		-		x	X	
	P. australiensis		-	x	x	X	

	P. lobata		-				-symbiont association data -UCE/Exon capture - micromorphology
	P. cylindrica		x	x	x	X	
	P. reticulum		x	x		X	
VII	*P.* sp4	x	-	x	x	X	-more sampling
VIII	*P. somaliensis*	x	-	x	x	X	-more sampling
IX	*P. profundus*	x	x	x	x	X	-more sampling -breeding trials -symbiont association data -UCE/Exon capture - micromorphology
	P. sp 5	x	x		x	X	
	P. sp 6	x	x		x	X	
X	*P.* sp 12	x	-	x	x	X	-more sampling -breeding trials -symbiont association data - micromorphology -UCE/Exon capture
XI	*P. hawaiiensis*	x	-	x		X	
XII	*P.* sp 7	x	-	x	x	X	-more sampling
XIII	*P. sillimaniana*	x	x	x	x	x	- sampling in type locality -time/mode reproduction -breeding trials -symbiont association data - micromorphology -UCE/Exon capture
XIII	*P. negrosensis*		x	x	x	X	
XIII	*P. heronensis*		-	x	x	X	
XIII	*P. lichen*		-	-	x	unresolved	
XIII	*P. tuberculosus*		-	-	x		
XIII	*P.* sp 8		x	x	x	X	
XIII	*P. vaughani*		x	x	x	X	

XIV	*P. flavus*	x	-	x	x	X	-more sampling
XV	*P. deformis*	x	-	x	x	X	-more sampling

3.5.3 Future directions

Several questions remain to be answered for *Porites*, for example whether the species intermixed in these groups present different reproductive strategies or if hybridisation and introgression are common within these clades. Nevertheless, the presence of well-distinct morphotypes in five groups of species could suggest that reproductive barriers do exist. To finally clarify the status of these nominal species, further data and experiments are needed. A phylogeny reconstruction based on multiple characters derived from other methodologies such as reproductive trials and ecological surveys, might more effectively define species within the genus. Finally, the inclusion of modern genomic approaches such as UCE/exon capture could provide better molecular resolution within these problematic groups of species.

3.6 Conclusions

The delineation of species boundaries in *Porites* remains a challenging task. Despite the advances achieved through the use of genome wide molecular techniques, we still lack a comprehensive understanding of the evolutionary history and species boundaries in this genus. This works highlights that the main characters used for taxonomic identification and systematic reconstructions in *Porites* are able to discriminate many nominal species and novel morphotypes. The investigation of other morphological characters, such as micromorphological/ microstructural characters, could provide more useful tools. Finally, the integration of data derived from reproductive biology trials and ecological surveys might provide a further line of evidence when uncertainty among molecular and morphological reconstructions persist.

4. CHAPTER 4: REPRODUCTIVE TRAITS AS ALTERNATIVE LINES OF EVIDENCE FOR SPECIES BOUNDARIES IN PORITES

4.1 Abstract

Species boundaries in many if not most Scleractinia remain unclear. While molecular approaches have revealed that traditional coral taxonomy is fundamental flawed, they have yet to deliver a taxonomy that adequately reflects prominent differences in the ecology and biology of putative species. The genus *Porites* is a classic example. In this thesis, I used phylogenomics and quantitative morphological analyses to test different species hypotheses in the group. When these approaches produce conflcting answers, further lines of evidence need to be investigated. In this chapter, I focus on two sympatric nominal species *Porites lutea* and *P. cylindrica* that are morphologically distinct but were not separated using species delimitation methods based on the molecular data. In particular, I explore potential barriers to breeding between these species, including the timing of gamete release and gamete compatibility. At Orpheus Island, there was considerable overlap in the time of spawning, with *P. lutea* and *P. cylindrica* spawning on the same night with a maximum 2 hours of difference in the time of gamete release. At Sesoko Island there was no overlap, with colonies of the two species releasing gametes on different nights. Finally, the gametes of these species did not mix during *in vitro* breeding trials. These results suggest that *P. cylindrica* and *P. lutea* are good biological species that the phylogenomic approaches lack the resolution to recover. Similar breeding trials, along with other lines of evidence, are therefore likely to be a necessary feature of future work to define species boundaries in taxa for which current molecular approaches lack species level resolution.

4.2 Introduction

The results from chapter 2 and chapter 3 highlight the fact that molecular and morphological approaches often produce different answers when attempting

to resolve species in the *Porites*. This suggests that further lines of evidence are required to produce a taxonomy that accurately reflects differences in the life history of *Porites* species.

According to de Queiroz (1998), species can be considered as independent evolving metapopulation lineages, and the plethora of species concepts designed by evolutionary biologist should be regarded as "operational criteria" to provide different evidence aimed to distinguish evolutionary lineages. Since Mayr (1963), reproductive criteria have been widely used to define species. In fact, peculiar features of the breeding system, comprising gamete attraction, fertilisation, and time of reproduction, can provide boundaries to gene flow in potentially interbreeding lineages and result in genetic divergence (Coyne, 1992). In broadcast-spawning coral species, reproduction is highly synchronous within populations. In addition, in corals, lots of species spawn during the same night (Harrison et al. 1984; Baird et al., 2009). With the majority of spawners having a single oogenic seasonal cycle during the year, synchrony in gametes release is fundamental to guarantee success in fertilisation and reduce gamete dilution and predation (Levitan et al., 2004). Yet, the nature of these multi-species spawning events, where gametes belonging to many species get mixed in the water column, infers the existence of isolating mechanisms that maintain species boundaries in corals (Willis et al., 1997). In fact, despite simultaneous spawning, morphologically and genetic distinct corals co-exist in sympatry and coral species diversity is high, suggesting the existence of pre-zygotic or post-zygotic barriers. The incompatibility among gametes, together with different spawning times are considered primary mechanisms able to maintain pre-zygotic reproductive isolation (Palumbi, 1994). Exploring these mechanisms is fundamental to inform species boundaries and help clarify corals systematics. For example, breeding trials have been used to clarify the taxonomic status of *Acropora millepora* Ehrenberg, 1834 and *A. spathulata* Brook, 1981, two morphologically similar species that confounded taxonomist for over 10 years. Based on qualitiative morphological comparisons, Veron & Wallace (1984)

synonymised *A. spathulata* with *A. millepora*, however, breeding trials later demonstrated a lack of interbreeding between these two morphologies, leading to the resurrection of *A. spathulata* (Wallace & Wills, 1994).

Here, I use breeding trials to clarify species boundaries between *Porites cylindrica* and *P. lutea*. These two nominal species are nested in the same molecular clade, where they form distinct subclusters matching their distinct morphologies. According to species delimitation analyses they are one single species, while according to the quantitative morphological analyses, *P. cylindrica* and *P. lutea* are distinct. Both species are gonochoric, *i.e*. with each colony being male or female, broadcast spawners. On the Great Barrier Reef, they release gametes between October and November and in Okinawa between June and July (Baird et al., in review).

In this chapter, I conducted breeding trials between *P. lutea* and *P. cylindrica* over the course of two spawning seasons on the Great Barrier Reef in 2017 and 2018, as well as in the summer of 2018 in Okinawa (Japan), and provided evidence that these are good biological species.

Figure 4.1 Sympatric colonies of *Porites lutea* (massive) and *P. cylindrica* (branching).

4.3 Material and Methods

4.3.1 Samples collection and morphological identification

A total of 74 colonies were collected over three spawning seasons. In particular 23 *Porites* colonies belonging to *P. cylindrica* and *P. lutea* were collected in Pioneer Bay (-18º36'64''N; 146º29'28''E,) (Orpheus Island, QLD, Australia) between day one and day four after the full moon in November 2017. A total of 28 *Porites* colonies belonging to different nominal species were collected in front of Sesoko Island (26º38'.00''N; 127º51'56.24''E) (Okinawa, Japan) between day one and day five after the full moon in May 2018. Finally, 23 colonies of *Porites* belonging to different nominal species were collected in Pioneer Bay (Orpheus Island, QLD, Australia) between day one and day four after the full moon in November 2018. The sampling in Australia took place while scuba diving, between five and eight m depth. In particular, each coral colony was tagged and photographed in the field using a CanonG15 camera. A chunk of 20cm^2 was collected from each selected colony using hammer and chisel, and brought to the boat using a dish rack in order to avoid disturbing the colony. On the boat, the samples were placed in tanks full of freshly collected sea water in order to avoid exposing the corals to water temperatures different from their natural conditions. The sampling at Sesoko Island took place from the shore while snorkelling. The sampling methodology corresponded to the one explained above, but we did not use any means of transportation to reach the designated sampling spots, so the samples were brought to the research station immediately. At the research stations coral colonies were placed into tanks with controlled running sea water until spawning.

Specimens were individually identified by comparison with the type material and original descriptions.

4.3.2 Spawning observation, gamete collection, and ex situ breeding trials

Determining the sex of each colony of *Porites* before spawning is difficult. For this reason, in order to separate gametes of different sexes at spawning, from the day of collection until day eight after the full moon, each coral colony was isolated into a separate 20 L bucket half an hour prior to sunset time. At spawning, the sex of each colony and the time of eggs and sperm release was recorded. The gametes were collected using Pasteur pipettes and brought to a temperature-controlled room for breeding trials. Around 5000 eggs were mixed with sperm from different nominal species and let sit for 30 minutes to check for cleavage, which indicates fertilisation. Similarly eggs and sperm from the same nominal species were crossed and left undisturbed for 30 minutes to allow fertilisation and used as control to test for viability of the gametes. From each cross, a control of clean eggs was also set up in order to check for sperm contamination. Using a stereo-dissecting microscope, around 150 eggs per each cross were checked for fertilisation. Observations were repeated every 30 minutes for two hours in triplicates. At successful fertilisation, the crosses were checked until a fertilisation success of 80% was reached.

4.4 Results

4.4.1 Sample numbers and spawning observations

In November 2017, of the 21 colonies collected, eight colonies of *P. cylindrica* and three colonies of *P. lutea* spawned between November 7th and November 9th (Table 4.1). Fifty-seven % of the spawning *P. cylindrica* colonies were females as were 67% of the spawning *P. lutea* colonies. Sperm release in *P. cylindrica* started between 20:30 and 20:40; eggs release started between 21:00 and 22:00. Egg release in *P. lutea* colonies occurred between 21:50 and 22:30, and the one male colony released sperm at 23:00.

In Japan, of the 24 colonies collected, three *P. cylindrica* and four *P. lutea* spawned *ex situ*. All *the P. cylindrica* colonies that spawned were males,

compared to 50% of the spawning colonies of *P. lutea*. The time of gametes release differed between the two species by two days; all *P. cylidrica* colonies spawned on June 3rd and all *P. lutea* colonies spawned on June 6th (Table 4.1). Sperm release for *P. cylindrica* started at 21:30, while for *P. lutea* eggs were released between 21:45 and 22:30, and sperm release started at 22:30.

In November 2018, of the 21 colonies collected eight spawned *ex situ*: three P. *cylindrica* and five *P. lutea*. Two colonies of *P. lutea* spawned two nights in a row. Two colonies of *P. cylindrica* released sperm on November 25th and November 26th, one colony spawned eggs on November 26th. Two colonies of *P. lutea* spawned sperm on November 27th, while one colony released eggs. Finally, four colonies released sperm on November 28th. Both sperm and eggs release in *P. cylindrica* started at 20:30 pm, while *P. lutea* spawned sperm always at 22:00, and eggs at 22:30 (Table 4.1, Fig. 4.2).

Table 4.1 Summary of *ex situ* spawning data for the years 2017 and 2018 at Orpheus Island (Great Barrier Reef, Australia) and Sesoko Island (Okinawa, Japan). For each coral colony, identification code, genus and species, collection site, spawning day and time, sunset time, day of previous full moon (DOPFM), days after the previous full moon (DAPFM), and gamete sex are reported. Colony ID in bold represent colonies that spawned for more than one day. When colonies did not spawn, the data are summarized as n/a.

Colony ID	Genus	Species	Collection site	Spawning day	Spawning start time	Sunset time	DOPFM	DAPFM	Gamete release
TAUSP1	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	7.11.2017	20:59	18:20	4.11.2017	3	eggs
TAUSP2	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	7.11.2017	20:42	18:20	4.11.2017	3	sperm
TAUSP3	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	7.11.2017	20:58	18:20	4.11.2017	3	eggs
TAUSP4	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	7.11.2017	21:00	18:20	4.11.2017	3	eggs

TAUSP5	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	7.11.2017	20:43	18:20	4.11.2017	3	sperm
TAUSP6	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	8.11.2017	20:21	18:22	4.11.2017	4	sperm
TAUSP7	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP8	*Porites*	*lutea*	Pioneer bay-Orpheus Island	7.11.2017	23:00	18:20	4.11.2017	3	sperm
TAUSP9	*Porites*	*lutea*	Pioneer bay-Orpheus Island	9.11.2017	21:50		4.11.2017	5	eggs
TAUSP10	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP11	*Porites*	*lutea*	Pioneer bay-Orpheus Island	8.11.2017	22:36	18:22	4.11.2017	4	eggs
TAUSP12	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP19	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	8.11.2017	20:54	18:22	4.11.2017	4	eggs
TAUSP20	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP21	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	8.11.2017	21:00	18:22	4.11.2017	4	eggs
TAUSP22	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP23	*Porites*	*cylindrica*	Pioneer bay-	n/a	n/a	n/a	4.11.2017	n/a	n/a

			Orpheus Island						
TAUSP24	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP25	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP26	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP27	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP28	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TAUSP29	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	4.11.2017	n/a	n/a
TJPSP1	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP2	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP3	*Porites*	*cylindrica*	Research station-Sesoko Island	3.06.2018	21:30	19:43	29.05.2018	4	sperm
TJPSP4	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP5	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP6	*Porites*	*cylindrica*	Research station-	n/a	n/a	n/a	29.05.2018	n/a	n/a

			Sesoko Island						
TJPSP7	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP8	*Porites*	*lutea*	Research station-Sesoko Island	5.06.2018	22:30	19:44	29.05.2018	6	sperm
TJPSP9	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP10	*Porites*	*lutea*	Research station-Sesoko Island	5.06.2018	22:30	19:44	29.05.2018	6	eggs
TJPSP11	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP12	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP13	*Porites*	*cylindrica*	Research station-Sesoko Island	3.06.2018	21:30	19:43	29.05.2018	4	sperm
TJPSP14	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP15	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP16	*Porites*	*cylindrica*	Research station-Sesoko Island	3.06.2018	21:30	19:43	29.05.2018	4	sperm
TJPSP17	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP18	*Porites*	*lutea*	Research station-	n/a	n/a	n/a	29.05.2018	n/a	n/a

			Sesoko Island						
TJPSP19	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP20	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP21	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP22	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP23	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP24	*Porites*	*cylindrica*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP25	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP26	*Porites*	*lutea*	Research station-Sesoko Island	n/a	n/a	n/a	29.05.2018	n/a	n/a
TJPSP27	*Porites*	*lutea*	Research station-Sesoko Island	5.06.2018	21:45	19:44	29.05.2018	6	eggs
TJPSP28	*Porites*	*lutea*	Research station-Sesoko Island	5.06.2018	22:30	19:44	29.05.2018	6	sperm
T11	*Porites*	*lutea*	Pioneer bay-Orpheus Island	27.11.2018	22:30	18:59	23.11.2018	4	eggs
T12	*Porites*	*lutea*	Pioneer bay-	n/a	n/a	n/a	23.11.2018	n/a	n/a

			Orpheus Island						
T13	*Porites*	*lutea*	Pioneer bay-Orpheus Island	27.11.2018	22:00	18:59	23.11.2018	4	sperm
T13	*Porites*	*lutea*	Pioneer bay-Orpheus Island	28.11.2018	22:00	18:59	23.11.2018	5	sperm
T14	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T15	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T16	*Porites*	*lutea*	Pioneer bay-Orpheus Island	28.11.2018	22:00	18:59	23.11.2018	5	sperm
T17	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T18	*Porites*	*lutea*	Pioneer bay-Orpheus Island	28.11.2018	22:00	18:59	23.11.2018	5	sperm
T19	*Porites*	*lutea*	Pioneer bay-Orpheus Island	27.11.2018	22:00	18:59	23.11.2018	4	sperm
T19	*Porites*	*lutea*	Pioneer bay-Orpheus Island	28.11.2018	22:00	18:59	23.11.2018	5	sperm
T20	*Porites*	*lutea*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T21	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T22	*Porites*	*cylindrica*	Pioneer bay-	n/a	n/a	n/a	23.11.2018	n/a	n/a

			Orpheus Island						
T23	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T24	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T25	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	26.11.2018	20:30	18:58	23.11.2018	3	eggs
T26	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T27	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	25.11.2018	20:30	18:57	23.11.2018	2	sperm
T28	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T29	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T30	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	n/a	n/a	n/a	23.11.2018	n/a	n/a
T34	*Porites*	*cylindrica*	Pioneer bay-Orpheus Island	26.11.2018	20:30	n/a	23.11.2018	3	sperm

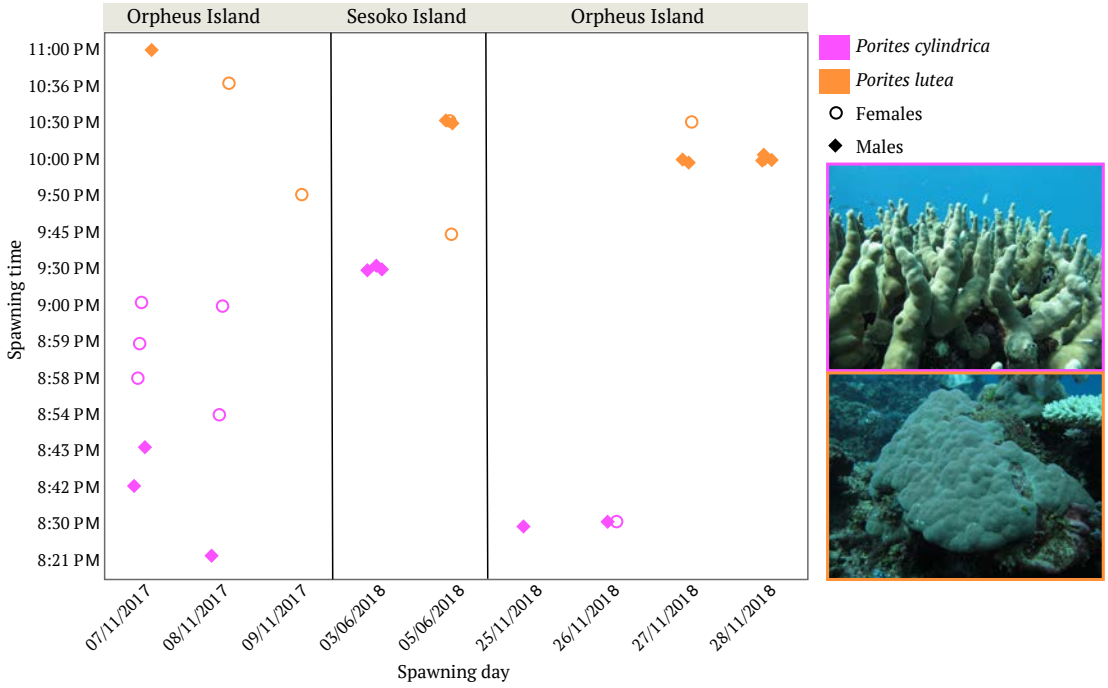


Figure 4.2 *Ex situ* spawning day and time at Orpheus and Sesoko Island for the years 2017 and 2018. For each colony, the nominal species is highlighted with different colours, and the sex with the different symbols

4.4.2 *Ex situ* breeding trials

At Orpheus Island in 2017, fertilisation occurred within *P. cylindrica* in 50% of the trials. The egg controls did not fertilise, indicating that there was no contamination from other sperm. On November 7th, eggs and sperm successfully crossed at 23:20 and 23:39, 1:30 hours after mixing – 84.14% fertilisation (138/164 eggs), and 73.75% fertilisation (103/140 eggs). Some eggs were fertilised at 23:30 pm, yet only with a 4.6% fertilisation (152 eggs). No other fertilisation occurred between *P. cylindrica* gametes. On November 8th eggs and sperm crossed at 22:56 – 87.2% fertilisation (75/86 eggs), 1:40 h after mixing. Only one egg was fertilised at 22:56 – 0.64% (1/154 eggs). No crosses were ever observed between *P. cylindrica* and *P. lutea* (Table 4.2).

In 2018 trials, fertilisation was observed in 100% of *P. lutea* crosses on November 26th. The egg controls showed no contamination from foreign sperm for all the mixes. Fertilisation occurred at 00:15 and 00:30, – 64.61 % (84/130 eggs) and 73.85 % fertilisation (113/153 eggs), 1:40 hours after mixing. No colonies of P*. cylindrica* spawned on the same night of *P. lutea* in 2019, thus no species crosses were conducted (Table 4.1, Table 4.2).

In Sesoko Island, Okinawa, during June 2018 mass spawning, fertilisation was observed within *P. lutea*. Fertilisation occurred in 50% of the control crosses on June 5th. Fertilisation occurred at 00:30, 1:30 hour after gametes mixing – 80% fertilisation (120/150 eggs), and 74.55% (112/150 eggs). No colonies of *P. cylindrica* spawned during the same night of *P. lutea*, thus no breeding trial was conduct between the two (Table 4.1, Table 4.2).

Table 4.2 Summary of results from the *ex situ* fertilisation trials within and between *Porites lutea* and *Porites cylindrica* at Orpheus Island (2017). Proportions of fertilisation are shown.

				Eggs					
Year	Site	DAPFM	Sperm	*P. cylindrica* TAUSP3	*P. cylindrica* TAUSP4	*P. cylindrica* TAUSP1	*P. cylindrica* TAUSP19	*P. cylindrica* TAUSP21	*P. lutea* TAUSP11

2017	Orpheus Island	3	*P. cylindrica* TAUSP2	4.6% (7/152)	0 (0/150)	0 (0/150)	-	-	-
			P. cylindrica TAUSP5	84.14% (138/164)	0 (0/150)	73.57% (103/140)	-	-	-
			P. lutea TAUSP8	0.66% (1/150)	0 (0/150)	-	-	-	-
		4	*P. cylindrica* TAUSP6	-	-	-	0.64% (1/154)	87.2% (75/86)	0 (0/150)
			Egg control	0 (0/156)	0 (0/150)	0 (0/150)	0 (0/150)	0 (0/82)	0 (0/150)

Eggs

Year	Site	DAPFM	Sperm	*P. lutea* TJP8	*P. lutea* TJP28
2018	Sesoko Island	6	*P. lutea* TJP10	80% (120/150)	0 (0/150)
			P. lutea TJP27	74.66% (112/150)	0 (0/150)
			Egg control	0 (0/156)	0 (0/150)

Eggs

Year	Site	DAPFM	Sperm	*P. lutea*

				T11	
2018	Orpheus Island	3	*P. lutea* T13	73.85% (113/153)	
			P. lutea T19	64.61% (84/130)	
			Egg control	0 (0/150)	

4.5 Discussion

Results of this chapter suggest that *P. lutea* and *P. cylindrica* do not interbreed, and that both the time of reproduction and gamete incompatibility are barriers to maintain boundaries between these species.

On Orpheus Island during 2017 the time of eggs and sperm release between *P. cylindrica* and *P. lutea* colonies differed from 2 to 2:30 hours, with *P. cylindrica* always spawning earlier in the evening (Table 4.1, Fig. 4.2). Differences in spawning times and gamete incompatibility are the main barriers to gene flow among sympatric populations (Knowlton 1993, 1997; Palumbi 1994; Dai et al., 2000) and species with as little as 1:30 hour difference in spawning times have proven to be genetically divergent. Indeed, differences on the scale of hours are sufficient to maintain species boundaries in *Acropora* and *Montastrea* in relation to diffusion and dilution of sperm in the ocean (van Oppen et al., 2002; Fukami et al., 2003; Wei et al., 2011). In *Acropora*, field-based observations showed a sudden drop in sperm concentration 30 minutes after spawning, decreasing the chances for gametes encounter and thus hybridization (Fukami et al., 2003). Estimates of

fertilisation potential in the *Montastrea annularis* species complex, showed that sperm has maximum fertilisation potential for about 1 hour, after which dilution and aging decrease the chances of breeding (Levitan et al., 2004). From the data collected in this dissertation, and previous spawning observation on *Porites* at the same location (Willis et al., 1984), 1:30 hour seems to be the time threshold after which fertilisation potential decreases in *Porites* (Table 4.1, Fig. 4.2)

No interspecific crosses occurred during the non-choice breeding trials experiments at Orpheus Island in 2017, suggesting that these are good biological species maintained by gamete incompatibility (Table 4.2). Similar results are common in closely related *Acropora* species that spawn in synchrony in Taiwan (Wei et al., 2011). Nevertheless, the observations of this study have a small sample size, and would need to be repeated over more years to be confident that hybridisation is not a regular feature of breeding between these two species.

In contrast to 2017, in 2018 on Orpheus, *P. lutea* and *P. cylindrica* did not spawn at the same time (Table 4.1, Fig. 4.2). Similarly, at Sesoko Island, where gamete release differed by several days between these species (Table 4.1, Fig. 4.2).

The most plausible explanation for *P. lutea* and *P. cylindrica* being molecularly indistinct is recent speciation between these two lineages, rather hybridisation or introgression. In fact, the evidence from this chapter suggests that these species do not interbreed and the evidence from chapter 2 suggests that the clade that contains P*. lutea* and *P. cylindrica* (clade V) is between 1.5 and 0.1 Mya (as shown in Fig. 2.4 and Appendix 2.8 of chapter 2), which would appear to be insufficient time for genetic polymorphisms to become fixed. Nevertheless, ongoing divergence or incipient speciation could explain the lack of genetic divergence in the dataset, as one effective migrant per generation could homogenize gene frequencies in a panmictic population.

4.6 Conclusions

In this study, I explored potential boundaries to breeding, including the timing of reproduction and gamete compatibility between two nominal species of *Porites,* to clarify species boundaries. The results from observations of spawning date and time, as well as non-choice interspecific breeding trials, showed that hybridization between *P. lutea* and *P. cylindrica* is unlikely, and reproductive isolation seems maintained between these two lineages at Orpheus Island and Sesoko Island. Corroborating these results and the findings of the previous chapters, I can hypothesise that *P. lutea* and *P. cylindrica* are two valid biological species of recent origin or undergoing speciation. Finally, similar breeding trials, along with other lines of evidence, are therefore likely to be a necessary feature to define species boundaries in taxa for which current molecular and morphological data are in conflict.

5. CHAPTER 5: CONCLUSIONS

This dissertation represents a substantial contribution towards the formulation of an hypothesis on the evolutionary history of the coral genus *Porites.* The use of traditional molecular taxonomy with the integration of micromorphological data, revolutionized the understanding of Scleractinia taxonomy, systematics, and evolution during the past 15 years (Fukami et al., 2004, 2008; Wallace et al., 2007; Benzoni et al., 2007, 2010; Richards et al., 2008, 2013; Forsman et al., 2009, 2017; Budd & Stolarski, 2009, 2011; Kitahara et al., 2016; Stolarski et al., 2011; Huang et al., 2011, 2014; Budd et al., 2012; Pinzon et al., 2013; Schmidt-Roach et al., 2013a, 2013b, 2014; Terraneo et al., 2014, 2016, 2017; Kitano et al., 2014; Arrigoni et al., 2014, 2016a, b, 2017, 2018). Nevertheless, this approach is still far from providing a clear and definitive hypothesis of Scleractinia evolutionary history, especially when some of the most important and specious genera such as A*cropora, Montipora,* and *Porites* still await revision. Several limitations inherited with traditional morphological and molecular data, together with the incongruence among morphological and molecular reconstructions, as well as nuclear and mitochondrial phylogenies, urge towards the use of alternative line of evidence to clarify species boundaries and evolution for these recalcitrant groups (Todd, 2008; Van Oppen et al., 2001; Fukami et al. 2004). Clarifying evolutionary relationships in Scleractinia can provide background information that could be applied to a variety of fields, from ecological, biological, and paleontological studies, to biodiversity assessments, and finally conservation.

To better understand evolutionary relationships in *Porites,* in this work, different lines of evidence derived from genome-wide molecular data, morphology, and reproductive biology data, were used in synergy following the unified concept of species proposed by de Quiroz (1998). According to de Queiroz (1998), species can be considered as independent evolving metapopulation lineages, and the plethora of species concepts designed by evolutionary biologists should be integrated to provide different lines of evidence aimed to distinguish evolutionary lineages. The results from this thesis

show that this approach can be helpful in clarifying the taxonomy and evolutionary relationships of one of the most challenging scleractinian taxa in terms of species identification. The approach employed here could be applied to explore relationships within other problematic coral genera, and provide the basis for a new framework to future coral taxonomy when integrated with further analyses or lines of evidence.

This thesis comprises the largest number of samples of *Porites* morpho-molecularly assessed to date from the Indian and Pacific Oceans, comprising the seas around the Arabian Peninsula. Before this dissertation, *Porites* molecular data were produced from the Pacific and eastern Pacific, comprising Hawaii and Japan, and from the Atlantic Caribbean (Forsman et al., 2009, 2011, 2015, 2017; Kitano et al., 2014; Hellberg et al., 2016; Tisthammer et al., 2018). Only six sequences of *Porites* from the Arabian region were analysed using a combined morpho-molecular approach and deposit to GenBank (https://www.ncbi.nlm.nih.gov/nucleotide/) (Benzoni & Stefani, 2012). With over 600 ezRAD libraries, almost complete mitochondrial genomes, rDNA and histone regions, and 163,637 SNPs for 312 samples, this work represent the most comprehensive geographical molecular database of *Porites* produced so far, as well as the biggest coral molecular database produced with next generation sequencing to date.

Overall, in this thesis I prove that *Porites* diversity from the Indian and Pacific Oceans as previously assessed is not representative of real biodiversity and biogeography patterns, and needs to be re–evaluated in light of a rapidly changing taxonomic framework. Descriptions of new species, expansion of ranges for other species, and phylogenetic works at several taxonomic levels, are in fact providing a new understanding of regional biogeography and evolution for several taxa (Bouwmeester et al., 2015; Arrigoni et al., 2016a, 2016b; Terraneo et al., 2014, 2016, 2017; Berumen et al., 2019). For example, high endemism in the western and northern Indian Ocean, comprising the Arabian region, coupled with phylogenetics, and paleooceanography support an “Indian Ocean Centre of Origin” hypothesis for shallow marine

organisms (Obura, 2016), according to which the Indian Ocean is a second hotspot for shallow marine biodiversity after the Coral Triangle. Endemism, by definition, encompasses species with restricted geographical distribution, that are characterised by either ancient origin (derived from an ancestral widespread species) (Willis, 1922) or are young and newly established (Stebbins & Major, 1965). Neutral models of speciation, comprising allopatric speciation, parapatric and peripatric speciation, can thus contribute towards the establishment of these endemism patterns. Moreover, the presence of specific ecological conditions, can also constrain the distribution of endemic species (ecological speciation trough local adaptation) (Stebbins, 1980). According to the" Indian Ocean Centre of Origin" theory, current high endemism areas in the Indian Ocean, such as the Red Sea, the Arabinan Sea, and the Mascarene Islands, were centre of marine biodiversity origin during the Oligocene. For corals, this pattern is supported by endemism and deep divergence within several coral genera, comprising *Acropora, Coscinaerea, Stylophora, and Siderastrea* (Obura, 2016), and the high tectonic activities of the above-mentioned areas during the Neogene (Bosworth et al., 2005). The results of this thesis, show unexpected origin of at least eight molecular lineages in the Arabian region or in the Indian Ocean around 7 Mya, and the presence of *Porites* endemics in the western Indian Ocean and Arabian Peninsula. Providing a better understanding of current biodiversity patterns and endemism, can finally provide new insights into the origin of marine biodiversity in the India n Ocean.

From the analyses of this dissertation, at least 16 lineages (chapter 2) showed unclear origin in the Arabian-Indian-Pacific Oceans. Within the Indo-West Pacific biogeographic region (Ekman, 1934), the Indo-Malayan region is considered the centre of diversity for hard corals, and corresponds to the overlap of several species' (80-90 genera - Veron 2000) distribution ranges. This has been related with the current and past environmental conditions of the region, as well as past geological events, which might be reflected by the dispersal and settlement capability of coral larvae. For the state of this

dissertation, inclusion of samples from the Coral Triangle was not possible, but this is encouraged for future studies in order to include several nominal species described from the region, and validate the Coral Triangle as an hotspot of *Porites* diversity.

Following a unified concept of species, I integrated the newly produced molecular findings with a quantitative analysis of skeletal morphological characters, with the aim of identifying morphometric keys to species identification in *Porites*. The characters chosen showed corroboration of several nominal species analysed within the genus and provided a quantitative framework to discriminate nominal species within unresolved groups of species.

Species boundaries were finally tested integrating reproductive biology data for two nominal species of *Porites* that present differences at the macro and micromorphological level, yet are nested within the same clade. Following the breeding trials, no hybrid embryos were produced, challenging the possibility for hybridization as source of novelty between these two species, and suggesting that the genomic similarities between *P. lutea* and P*. cylindrica* might indeed be a result of incomplete lineage sorting between two recent lineages undergoing speciation.

Overall, this dissertation contributes important basic knowledge that could be applied to future conservation strategies for reef corals diversity. Elucidating where species boundaries lay, and providing evolutionary information on how species are related is essential knowledge for an efficient protection and preservation of biological diversity. Indeed, it has been suggested that in the future, the loss of phylogenetic diversity might be higher than the loss of species, because threatened species seem to have a non-random distribution in the phylogeny (Huang, 2012; Curnick et al. 2015; Forest et al., 2015). Nevertheless, assessments of biodiversity are still mainly based on species counts, yet the intrinsic problems associated with the high variability of coral morphologies render these assessments inaccurate, a situation that could be improved by incorporating genetic and phylogenetic data.

The results from this work provide extensive background data for future works and a significant contribution to the knowledge of the evolutionary history of *Porites* and taxonomy of *Porites*. Integrating morphological and genomic evidence, I discuss the position of 15% of *Porites* nominal species. Although for this dissertation no formal taxonomic action has been taken, 1) I suggest the validation of 15 species which status has been confirmed using an integrated approach: *P. fontanesii, P. farasani, P. annae, P. soldia, P. lutea, P. cylindirca, P. reticulum, P. somaliensis, P. profundus, P. sillimaniana, P. negrosensis, P. heronesis, P. vaughani, P. flavus, P. deformis*; 2) I formally described two new species of *Porites, P farasani* and *P. hadramauti* (Terraneo et al. 2019b); 3) I suggest the presence of three additional undescribed species which await formal description (now included as *P*. sp 4, *P*. sp 7, and *P*. sp 12). 4) I propose future work to consider the synonymysation of *P. monticulosa* with *P. rus*, and *P. australienis* with *P. lobata*. 5) I finally propose the designation of a neotype for *P. reticulum*. The status of the remaining species and morphologies will need further analyses to be corroborated.

Overall, results from reproductive trials between *P. lutea* and *P. cylindrica* provide evidence that lineages indistinguishable using genome wide data, already acquired different reproductive strategies that reduce geneflow among sympatric species, a scenario corroborated by the subclustering within the unresolved groups of species and the recent origin of these species. Finally, integrating lines of evidence from different life history traits can provide a clarification when genomic, biogeographical, and morphological data disagree.

LIST OF PUBLICATIONS

Published papers

Terraneo, T. I., Benzoni, F., Baird, A. H., Arrigoni, R., Berumen, M. L. Morphology and molecules reveal two new species of *Porites* (Scleractinia, Poritidae) from the Red Sea and the Gulf of Aden. (2019). *Systematics and Biodiversity*.
Contribution: I designed the study, collected part of the samples, performed genetic labwork and analyses, performed species delimitation analyses, performed imaging with Scanning Electron Microscopy, contributed with the formal species description and wrote the paper.

Terraneo, T. I., Fusi, M., Hume, C. C., Arriogni, R., Voolstra, C. R., Benzoni, F., Forsman Z. H., Berumen, M. L. Environmental latitudinal gradients and host specificity shape Symbiodiniaceae distribution in Red Sea *Porites* corals. (2019). *Journal of Biogeography*.
Contribution: I designed the study, collected part of the samples, performed genetic analyses, prepared MiSeq libraries, performed data analyses with contribution of M. F and wrote the paper

Terraneo, T. I., Arrigoni, R., Benzoni, F., Forsman, Z. H., & Berumen, M. L. (2018). Using ezRAD to reconstruct the complete mitochondrial genome of *Porites fontanesii* (Cnidaria: Scleractinia). *Mitochondrial DNA Part B*, *3*(1), 173-174.
Contribution: I designed the study, performed genomic labwork, performed reads assembly, phylogenomic analyses, genome annotation and wrote the paper.

Terraneo, T. I., Arrigoni, R., Benzoni, F., Forsman, Z. H., & Berumen, M. L. (2018). The complete mitochondrial genome of *Porites harrisoni* (Cnidaria: Scleractinia) obtained using next-generation sequencing. *Mitochondrial DNA Part B*, *3*(1), 286-287.
Contribution: I designed the study, performed genomic labwork, performed reads assembly, phylogenomic analyses, genome annotation and wrote the paper.

Berumen, M. L., Arrigoni, R., Bouwmeester, J., Terraneo, T. I., & Benzoni, F. (2019). Biodiversity of Red Sea corals. Chapter 7 in *Coral Reefs of the Red Sea* (Voolstra, C.R., and Berumen, M.L. (eds)). Springer.
Contribution: I was in charge of the "Climate change and Red Sea corals" paragraph writing and proofreading of the remaining paragraphs of the book chapter.

Arrigoni, R., Maggioni, D., Montano, S., Hoeksema, B. W., Seveso, D., Shlesinger, T., Terraneo, T. I., Tiethbol, M. D., Berumen, M. L. (2018). An integrated morpho-molecular approach to delineate species boundaries of *Millepora* from the Red Sea. *Coral Reefs*, *37*(4), 967-984.
Contribution: I helped collecting samples along the Saudi Arabian Red Sea and contributed for the molecular lab work and molecular analyses. I finally contributed with the ms writing.

Arrigoni, R., Berumen, M. L., Stolarski, J., Terraneo, T. I., & Benzoni, F. (2018). Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics*.

Contribution: I contributed with the molecular lab work and molecular analyses. I finally contributed with the ms writing.

Terraneo, T. I., Arrigoni, R., Benzoni, F., Tietbohl, M. D., & Berumen, M. L. (2017). Exploring the genetic diversity of shallow-water Agariciidae (Cnidaria: Anthozoa) from the Saudi Arabian Red Sea. *Marine Biodiversity*, *47*(4), 1065-1078.
Contribution: I designed the study, collected part of the samples, performed genetic labwork and analyses, and wrote the paper.

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. *Invertebrate Systematics*, *31*(2), 141-156.
Contribution: I helped collecting samples and took part in the molecular lab work and molecular analyses. I helped imaging the samples with Scanning Electron Microscopy and contributed with the ms writing.

Arrigoni, R., Berumen, M. L., Chen, C. A., Terraneo, T. I., Baird, A. H., Payri, C., & Benzoni, F. (2016). Species delimitation in the reef coral genera *Echinophyllia* and *Oxypora* (Scleractinia, Lobophylliidae) with a description of two new species. *Molecular Phylogenetics and Evolution*, *105*, 146-159.
Contribution: I took part in the molecular lab work and molecular analyses and contributed with the ms writing.

Arrigoni, R., Benzoni, F., Terraneo, T. I., Caragnano, A., & Berumen, M. L. (2016). Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea. *Scientific Reports*, *6*, 34612.
Contribution: I helped collecting samples and took part in the molecular lab work and molecular analyses. I helped imaging the samples with Scanning Electron Microscopy and contributed with the ms writing.

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. *Molecular Phylogenetics and Evolution*, *102*, 278-294.
Contribution: I designed the study, collected the samples, performed genetic labwork and analyses, performed species delimitation analyses, performed imaging with Scanning Electron Microscopy, performed imaging with Optical microscopy, performed morphometric analyses and wrote the paper.

Arrigoni, R., Benzoni, F., Huang, D., Fukami, H., Chen, C. A., Berumen, M. L., ...Terraneo, T.I.,... & Zayasu, Y. (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. *Contributions to Zoology*, *85*(4).
Contribution: I helped collecting samples and took part in the molecular lab work and molecular analyses. I finally contributed with the ms writing.

Papers under revision

Terraneo, T. I., Arriogni, R., Benzoni, F., Mariappan, K. G., Baird, A. H., Forsman, Z. H., Wooster, M. K., Bouwmeester, J., Marshell, J., Berumen, M. L. Phylogenomics and phylogeography of *Porites* from the Arabian Peninsula. *Under revision in Systematic Biology*.

Contribution: I designed the study, collected part of the samples, performed genetic labwork and analyses, performed genomic library preparation, performed phylogenomic analyses and wrote the paper

Coker D. J., DiBattista J. D., Stat, M., Arrigoni, R., Reimer J., Terraneo, T. I., Villalobos Vazquez de la Parra, R., Nowicki J. P., Bunce, M., Berumen, M. L. Metabarcoding approaches increase dietary resolution for benthic feeding butterflyfishes. Under revision in *Scientific Reports*.

Contribution: I contributed with the study design, performed analyses on coral samples and helped with the ms writing. I contributed with presence/ absence data for a variety of coral genera.

References

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. *The Quarterly Review of Biology*, *79*(2), 161-179.

Alexander, D. H., Novembre, J., & Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Research*, *19*(9), 1655-1664.

Alloiteau, J. (1957). *Contribution à la systématique des Madréporaires fossiles* (Vol. 1). Centre National de la Recherche Scientifique.

Ament-Velásquez, S. L., Breedy, O., Cortés, J., Guzman, H. M., Wörheide, G., & Vargas, S. (2016). Homoplasious colony morphology and mito-nuclear phylogenetic discordance among Eastern Pacific octocorals. *Molecular Phylogenetics and Evolution*, *98*, 373-381.

Anderson, M., Gorley, R. N., & Clarke, R. K. (2008). *Permanova+ for primer: Guide to Software and Statistical Methods*. Primer-E Limited.

Andrews, K. R., Good, J. M., Miller, M. R., Luikart, G., & Hohenlohe, P. A. (2016). Harnessing the power of RADseq for ecological and evolutionary genomics. *Nature Reviews Genetics*, *17*(2), 81.

Appeltans, W., Ahyong, S. T., Anderson, G., Angel, M. V., Artois, T., Bailly, N., ... & Costello M, J. (2012). The magnitude of global marine species diversity. *Current Biology*, *22*(23), 2189-2202.

Arnheim, N., Krystal, M., Schmickel, R., Wilson, G., Ryder, O., & Zimmer, E. (1980). Molecular evidence for genetic exchanges among ribosomal genes on nonhomologous chromosomes in man and apes. *Proceedings of the National Academy of Sciences*, *77*(12), 7323-7327.

Arrigoni, R., Stefani, F., Pichon, M., Galli, P., & Benzoni, F. (2012). Molecular phylogeny of the robust clade (Faviidae, Mussidae, Merulinidae, and Pectiniidae): an Indian Ocean perspective. *Molecular Phylogenetics and Evolution*, *65*(1), 183-193.

Arrigoni, R., Terraneo, T. I., Galli, P., & Benzoni, F. (2014). Lobophylliidae (Cnidaria, Scleractinia) reshuffled: pervasive non-monophyly at genus level. *Molecular Phylogenetics and Evolution*, *73*, 60-64.

Arrigoni, R., Berumen, M. L., Terraneo, T. I., Caragnano, A., Bouwmeester, J., & Benzoni, F. (2015). Forgotten in the taxonomic literature: resurrection of the scleractinian coral genus *Sclerophyllia* (Scleractinia, Lobophylliidae) from the Arabian Peninsula and its phylogenetic relationships. *Systematics and Biodiversity*, *13*(2), 140-163.

Arrigoni, R., Benzoni, F., Terraneo, T. I., Caragnano, A., & Berumen, M. L. (2016a). Recent origin and semi-permeable species boundaries in the scleractinian coral genus *Stylophora* from the Red Sea. *Scientific Reports*, *6*, 34612.

Arrigoni R., Berumen M.L., Chen C.A., Terraneo T.I., Baird A.H., Payri C., Benzoni F. (2016b). Species delimitation in the reef coral genera Echinophyllia and Oxypora (Scleractinia, Lobophylliidae) with a description of two new species. *Molecular Phylogenetics and Evolution*,105:146–-159.

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. *Invertebrate Systematics*, *31*(2), 141-156.

Arrigoni, R., Berumen, M. L., Stolarski, J., Terraneo, T. I., & Benzoni, F. (2018). Uncovering hidden coral diversity: a new cryptic lobophylliid scleractinian from the Indian Ocean. *Cladistics.*

Babcock, R. C., Bull, G. D., Harrison, P. L., Heyward, A. J., Oliver, J. K., Wallace, C. C., & Willis, B. L. (1986). Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Marine Biology*, *90*(3), 379-394.

Babcock, R. C., Wills, B. L., & Simpson, C. J. (1994). Mass spawning of corals on a high latitude coral reef. *Coral Reefs*, *13*(3), 161-169.

Babcock, R. (1995). Synchronous multispecific spawning on coral reefs: potential for hybridization and roles of gamete recognition. *Reproduction, Fertility and Development*, *7*(4), 943-950.

Baird, A. H., Guest, J. R., & Willis, B. L. (2009). Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 551-571.

Baird, N. A., Etter, P. D., Atwood, T. S., Currey, M. C., Shiver, A. L., Lewis, Z. A., ... & Johnson, E. A. (2008). Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PloS One*, *3*(10), e3376.

Baker, A. C. (2001). Ecosystems: reef corals bleach to survive change. *Nature*, *411*(6839), 765.

Barbeitos, M. S., Romano, S. L., & Lasker, H. R. (2010). Repeated loss of coloniality and symbiosis in scleractinian corals. *Proceedings of the National Academy of Sciences*, *107*(26), 11877-11882.

Baxter, S. W., Davey, J. W., Johnston, J. S., Shelton, A. M., Heckel, D. G., Jiggins, C. D., & Blaxter, M. L. (2011). Linkage mapping and comparative genomics using next-generation RAD sequencing of a non-model organism. *PloS One*, *6*(4), e19315.

Bellwood, D. R., & Hughes, T. P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, *292*(5521), 1532-1535.

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827.

Benzoni, F., Bianchi, C. N., & Morri, C. (2003). Coral communities of the northwestern Gulf of Aden (Yemen): variation in framework building related to environmental factors and biotic conditions. *Coral Reefs*, *22*(4), 475-484.

Benzoni, F., Stefani, F., Stolarski, J., Pichon, M., Mitta, G., & Galli, P. (2007). Debating phylogenetic relationships of the scleractinian *Psammocor*a: molecular and morphological evidences. *Contributions to Zoology*, *76*(1), 35-54.

Benzoni, F., Stefani, F., Pichon, M., & Galli, P. (2010). The name game: morpho-molecular species boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). *Zoological Journal of the Linnean Society*, *160*(3), 421-456.

Benzoni, F., & Stefani, F. (2012). *Porites fontanesii*, a new species of hard coral (Scleractinia, Poritidae) from the southern Red Sea, the Gulf of Tadjoura, and the Gulf of Aden. *Zootaxa*, *3447*, 56–68.

Berkelmans, R., & Van Oppen, M. J. (2006). The role of zooxanthellae in the thermal tolerance of corals: a 'nugget of hope'for coral reefs in an era of climate change. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1599), 2305-2312.

Bernard, H. (1905) The family Poritidae. II. - The genus Porites. Part I. - Porites of the Indo-Pacific Region. Catalogue of the Madreporarian Corals in the British Museum (Natural History) 5: 1-303, pls. 1-35.

Berumen, M.L., Arrigoni, R., Bouwmeester, J., Terraneo, T., I., & Benzoni, F. (2019). Biodiversity of Red Sea corals. Chapter 7 in *Coral Reefs of the Red Sea* (Voolstra, C.R., and Berumen, M.L. (eds)). Springer.

Birky, C. W., Maruyama, T., & Fuerst, P. (1983). An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. *Genetics*, *103*(3), 513-527.

Boekschoten, G. J., & Best, M. B. (1988). Fossil and recent shallow water corals from the Atlantic islands off western Africa. *Zool Meded*, *62*(99), 112.

Bongaerts, P., Riginos, C., Ridgway, T., Sampayo, E. M., van Oppen, M. J., Englebert, N., ... & Hoegh-Guldberg, O. (2010). Genetic divergence across habitats in the widespread coral *Seriatopora hystrix* and its associated *Symbiodinium. PLoS One, 5*(5).

Bolger A.M., Lohse M., Usadel B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics*. 30:2114–2120.

Bosworth, W., Huchon, P., & McClay, K. (2005). The Red Sea and Gulf of Aden basins. *Journal of African Earth Sciences*, *43*(1-3), 334-378.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., ... & Drummond, A. J. (2014). BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *10*(4), e1003537.

Bourne, D. G., Morrow, K. M., & Webster, N. S. (2016). Insights into the coral microbiome: underpinning the health and resilience of reef ecosystems. *Annual Review of Microbiology*, *70*, 317-340.

Bowen, B. W., Rocha, L. A., Toonen, R. J., & Karl, S. A. (2013). The origins of tropical marine biodiversity. *Trends in Ecology & Evolution*, *28*(6), 359-366.

Bouwmeester, J., Benzoni, F., Baird, A. H., & Berumen, M. L. (2015). *Cyphastrea kausti* sp. n.(Cnidaria, Anthozoa, Scleractinia), a new species of reef coral from the Red Sea. *ZooKeys*, (496), 1.

Bridge, T. C., Luiz, O. J., Kuo, C. Y., Precoda, K., Madin, E. M., Madin, J. S., & Baird, A. H. (2020). Incongruence between life-history traits and conservation status in reef corals. *Coral Reefs*, 1-9.

Brown, W. M., George, M., & Wilson, A. C. (1979). Rapid evolution of animal mitochondrial DNA. *Proceedings of the National Academy of Sciences*, *76*(4), 1967-1971.

Brown, W. M., Prager, E. M., Wang, A., & Wilson, A. C. (1982). Mitochondrial DNA sequences of primates: tempo and mode of evolution. *Journal of Molecular Evolution*, *18*(4), 225-239.

Bruno, J. F., & Edmunds, P. J. (1997). Clonal variation for phenotypic plasticity in the coral *Madracis mirabilis*. *Ecology*, *78*(7), 2177-2190.

Bryant, D., Bouckaert, R., Felsenstein, J., Rosenberg, N. A., & RoyChoudhury, A. (2012). Inferring species trees directly from biallelic genetic markers: bypassing gene trees in a full coalescent analysis. *Molecular Biology and Evolution*, *29*(8), 1917-1932.

Budd, A. F. (1993). Variation within and among morphospecies of *Montastraea*. *Courier Forschungsinstitut Senckenberg*, *164*, 241-254.

Budd, A. F., & Stolarski, J. (2009). Searching for new morphological characters in the systematics of scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific Mussidae. *Acta Zoologica*, *90*(2), 142-165

Budd, A. F., & Stolarski, J. (2011). Corallite wall and septal microstructure in scleractinian reef corals: comparison of molecular clades within the family Faviidae. *Journal of Morphology*, *272*(1), 66-88.

Budd, A. F., Romano, S. L., Smith, N. D., & Barbeitos, M. S. (2010). Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data.

Budd, A.F., Fukami, H., Smith, N.D., Knowlton, N. (2012). Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*. 166:465–529.

Cairns, S. D. (1982). Antarctic and subantarctic Scleractinia.

Cairns, S. D. (1984). An application of phylogenetic analysis to the Scleractinia: Family Fungiidae. In Fourth International Symposium Fossil Cnidaria. Palaeontographica Americana

Cairns, S. D. (1991). Catalog of the type specimens of stony corals (Milleporidae, Stylasteridae, Scleractinia) in the National Museum, Smithsonian Institution. *Smithsonian Contributions to Zoology.*

Cairns, S. D. (1997). A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*.

Cairns, S. D. (1999). Species richness of recent Scleractinia. *Atoll Research Bulletin*, *459*(459), 1-46.

Cairns, S. D. (2001). A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*.

Cariou, M., Duret, L., & Charlat, S. (2013). Is RAD-seq suitable for phylogenetic inference? An in-silico assessment and optimization. *Ecology and Evolution*, *3*(4), 846-852.

Carlon, D. B., Budd, A. F., Lippé, C., & Andrew, R. L. (2011). The quantitative genetics of incipient speciation: heritability and genetic correlations of skeletal traits in populations of diverging *Favia fragum* ecomorphs. *Evolution: International Journal of Organic Evolution, 65*(12), 3428-3447.

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., ... & Wood, E. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, *321*(5888), 560-563.

Chan, W. Y., Peplow, L. M., & van Oppen, M. J. (2019). Interspecific gamete compatibility and hybrid larval fitness in reef-building corals: Implications for coral reef restoration. *Scientific Reports*, *9*(1), 4757.

Chen, C. A., Chang, C., Wei, N. V., Chen, C., Lin, H., Dai, C., & Wallace, C. C. (2004). Secondary structure and phylogenetic utility of the ribosomal Internal Transcribed Spacer 2 (ITS2) in scleractinian corals, *43*(4), 759–771. *Zoological Studies* 43, no. 4 (2004): 759-771.

Chen, C. A., Wallace, C. C., & Wolstenholme, J. (2002). Analysis of the mitochondrial 12S rRNA gene supports a two-clade hypothesis of the evolutionary history of scleractinian corals. *Molecular Phylogenetics and Evolution*, *23*(2), 137-149.

Chevalier, J. P. (1966). Contribution á l'etude des Madréporaires des côtes occidentales de l'Afrique tropicale. *Bulletin de l'IFAN, 28*(4), 1356-1405.

Chevalier, J. P., & Beauvais, L. (1987). Ordre des scléractiniaires. *Traité de Zoologie*, *3*(3), 403-764.

Claereboudt, M. R. (2006). Reef Corals and Coral Reefs of the Gulf of Oman. The Historical Association of Oman.

Combosch, D. J., & Vollmer, S. V. (2015). Trans-Pacific RAD-Seq population genomics confirms introgressive hybridization in Eastern Pacific *Pocillopora* corals. *Molecular Phylogenetics and Evolution*, *88*, 154-162.

Conception, G.T., Crepeau, M.W., Wagner, D., Kahng S.E., Toonen, R.J. (2008). An alternative to ITS, a hypervariable, single-copy nuclear intron in corals, and its use in detecting cryptic species within the octocoral genus *Carijoa*. *Coral Reefs*. *27*:323–336.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302-1310.

Connolly, S. R., Bellwood, D. R., & Hughes, T. P. (2003). Indo-Pacific biodiversity of coral reefs: deviations from a mid-domain model. *Ecology*, *84*(8), 2178-2190.

Coyne, J. A. (1992). Genetics and speciation. *Nature*, *355*(6360), 511.

Cruaud, A., Gautier, M., Galan, M., Foucaud, J., Sauné, L., Genson, G., ... & Rasplus, J. Y. (2014). Empirical assessment of RAD sequencing for interspecific phylogeny. *Molecular Biology and Evolution*, *31*(5), 1272-1274.

Cunha, R. L., Forsman, Z. H., Belderok, R., Knapp, I. S., Castilho, R., & Toonen, R. J. (2019). Rare coral under the genomic microscope: timing and relationships among Hawaiian Montipora. *BMC Evolutionary Biology*, *19*(1), 153.

Curnick, D. J., Head, C. E. I., Huang, D., Crabbe, M. J. C., Gollock, M., Hoeksema, B. W., ... & Rosen, B. R. (2015). Setting evolutionary-based conservation priorities for a phylogenetically data-poor taxonomic group (S cleractinia). *Animal Conservation, 18(*4), 303-312.

Dai, C. F., Fan, T. Y., & Yu, J. K. (2000). Reproductive isolation and genetic differentiation of a scleractinian coral *Mycedium elephantotus*. *Marine Ecology Progress Series*, *201*, 179-187.

Daly, M., Fautin, D. G., & Cappola, V. A. (2003). Systematics of the hexacorallia (Cnidaria: Anthozoa). *Zoological Journal of the Linnean Society*, *139*(3), 419-437.

Dana, J.D. (1846-1849). Zoophytes. United States Exploring Expedition during the years 1838-1842. *Lea and Blanchard, Philadelphia.* 7: 1-740, 61 pls. (1846: 1-120, 709-720; 1848: 121-708, 721-740; 1849: atlas pls. 1-61).

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., ... & McVean, G. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*(15), 2156-2158.

DiBattista, J. D., Roberts, M. B., Bouwmeester, J., Bowen, B. W., Coker, D. J., Lozano-Cortés, D. F., ... Kochzius, M. (2016a). A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. *Journal of Biogeography*, *43*(3), 423–439

DiBattista, J. D., Howard Choat, J., Gaither, M. R., Hobbs, J. P. A., Lozano-Cortés, D. F., Myers, R. F., ... & Berumen, M. L. (2016b). On the origin of endemic species in the Red Sea. *Journal of Biogeography*, *43*(1), 13-30.

DiBattista, J. D., Alfaro, M. E., Sorenson, L., Choat, J. H., Hobbs, J. P. A., Sinclair-Taylor, T. H., ... & Friedman, M. (2018). Ice ages and butterflyfishes: Phylogenomics elucidates the ecological and evolutionary history of reef fishes in an endemism hotspot. *Ecology and Evolution*, *8*(22), 10989-11008.

Diekmann, O., Bak, R., Stam, W., & Olsen, J. (2001). Molecular genetic evidence for probable reticulate speciation in the coral genus *Madracis* from a Caribbean fringing reef slope. *Marine Biology*, *139*(2), 221-233.

Dimond, J. L., Gamblewood, S. K., & Roberts, S. B. (2017). Genetic and epigenetic insight into morphospecies in a reef coral. *Molecular Ecology*, *26*(19), 5031-5042.

Dover, G. (1982). Molecular drive: a cohesive mode of species evolution. *Nature*, *299*(5879), 111.

Duncan, P. M. (1885). On the structure of the ambulacra of some fossil genera and species of regular Echinoidea. *Quarterly Journal of the Geological Society*, *41*(1-4), 419-453.

Eaton, D.A., Ree, R.H. (2013). Inferring phylogeny and introgression using RADseq data: an example from flowering plants (*Pedicularis*: Orobanchaceae). *Systematic Biology*. 62:689–706.

Emerson, K. J., Merz, C. R., Catchen, J. M., Hohenlohe, P. A., Cresko, W. A., Bradshaw, W. E., & Holzapfel, C. M. (2010). Resolving postglacial phylogeography using high-throughput sequencing. *Proceedings of the National Academy of Sciences*, *107*(37), 16196-16200.

Esper, E. J. C. (1797). *Fortsetzungen der Pflanzenthiere in Abbildugen nach der Natur mit Farben erleuchtet nebst Beschreibungen* (Vol. 1). In der Raspeschen Buchhandlung.

Faircloth, B. C., McCormack, J. E., Crawford, N. G., Harvey, M. G., Brumfield, R. T., & Glenn, T. C. (2012). Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology*, *61*(5), 717-726.

Falkowski, P. G., Dubinsky, Z., Muscatine, L., & Porter, J. W. (1984). Light and the bioenergetics of a symbiotic coral. *Bioscience*, *34*(11), 705-709.

Faure, G. (1977). Annotated checklist of the corals in the Mascarene Archipelago, Indian Ocean. *Atoll Research Bulletin.* 203: 1-2

Fenner, D. (2005). Corals in Hawai'i: Field Guide to Hard, Black, and Soft Corals of Hawai'i and the Northwest Hawaiian Islands, Including Midway. Mutual Publishing Company.

Fisher, R., Knowlton, N., Brainard, R. E., & Caley, M. J. (2011). Differences among major taxa in the extent of ecological knowledge across four major. *PLoS One*, *6*(11). doi:10.1371/journal.pone.0026556

Flot, J. F., Blanchot, J., Charpy, L., Cruaud, C., Licuanan, W. Y., Nakano, Y., ... & 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 Ecology*, *11*(1), 22.

Flot, J. F., Licuanan, W. Y., Nakano, Y., Payri, C., Cruaud, C., & Tillier, S. (2008). Mitochondrial sequences of *Seriatopora* corals show little agreement with morphology and reveal the duplication of a tRNA gene near the control region. *Coral Reefs*, *27*(4), 789-794.

Flot, J. F., & Tillier, S. (2007). The mitochondrial genome of *Pocillopora* (Cnidaria: Scleractinia) contains two variable regions: the putative D-loop and a novel ORF of unknown function. *Gene*, *401*(1-2), 80-87.

Fogarty, N. D. (2012). Caribbean acroporid coral hybrids are viable across life history stages. *Marine Ecology Progress Series*, *446*, 145-159.

Forest, F., Crandall, K. A., Chase, M. W., & Faith, D. P. (2015). Phylogeny, extinction and conservation: embracing uncertainties in a time of urgency. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences*, *370*(1662), 20140002-20140002.

Forsman, Z. H., & Birkeland, C. (2009a). *Porites randalli*: a new coral species (Scleractinia, Poritidae) from American Samoa. *Zootaxa*, *2244*(1), 51-59.

Forsman, Z. H., Barshis, D. J., Hunter, C. L., & Toonen, R. J. (2009b). Shape-shifting corals: molecular markers show morphology is evolutionarily plastic in *Porites*. *BMC Evolutionary Biology*, *9*(1), 45.

Forsman, Z., Wellington, G. M., Fox, G. E., & Toonen, R. J. (2015). Clues to unraveling the coral species problem: distinguishing species from geographic variation in *Porites* across the Pacific with molecular markers and microskeletal traits. *PeerJ*, *3*, e751.

Forsman, Z. H., Knapp, I. S. S., Tisthammer, K., Eaton, D. A. R., Belcaid, M., & Toonen, R. J. (2017). Coral hybridization or phenotypic variation? Genomic data reveal gene flow between *Porites lobata* and *P. compressa*. *Molecular Phylogenetics and Evolution*, *111*, 132-148.

Forskål, P. (1775). *Flora Aegyptiaco-Arabica: Sive Descriptiones Plantarum, Quas Per Aegyptum Inferiorem Et Arabiam Felicem; Accedit Tabula Arabiae Felicis Geographico-Botanica*. Ex Officina Mölleri, Aulae Typographi. Prostat Apud Heineck Et Faber.

Frade, P.R., Reyes-Nivia, M.C., Faria, J., Kaandorp, J.A., Luttikhuizen, P.C., Bak, R.P.M. (2010). Semi-permeable species boundaries in the coral genus *Madracis*: introgression in a brooding coral system. *Molecular Phylogenetics and Evolution*, *57*:1072–1090.

France, S. C. (2001). Analysis of variation in mitochondrial DNA sequences (ND3, ND4L, MSH) among Octocorallia (= Alcyonaria) (Cnidaria: Anthozoa). *Bulletin of the Biological Society of Washington*, *10*, 110-118.

France, S. C., & Hoover, L. L. (2002). DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). *Hydrobiologia*, *471*(1-3), 149-155.

Frost, S. H. (1977). Miocene to Holocene evolution of Caribbean province reef-building corals. In *Proceedings of the 3rd International Coral Reef Symposium* (Vol. 2, pp. 353-359).

Fukami, H., Omori, M., Shimoike, K., Hayashibara, T., & Hatta, M. (2003). Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Marine Biology*, *142*(4), 679-684.

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*(6977), 832.

Fukami, H., Chen, C. A., Budd, A. F., Collins, A., Wallace, C., Chuang, Y. Y., ... & Knowlton, N. (2008). Mitochondrial and nuclear genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PloS One*, *3*(9), e3222.

Funk, D. J., & Omland, K. E. (2003). Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 397-423.

Galeotti, P., & Rubolini, D. (2003). The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society, 82*(2), 237-248.

Garrison, E., Marth, G. (2012). Haplotype-based variant detection from short-read sequencing. *arXiv Prepr arXiv12073907:1–9.*

Gattuso, J. P., Magnan, A., Billé, R., Cheung, W. W., Howes, E. L., Joos, F., ... & Hoegh-Guldberg, O. (2015). Contrasting futures for ocean and society from different anthropogenic CO2 emissions scenarios. *Science*, *349*(6243), aac4722.

Gélin, P., Postaire, B., Fauvelot, C., & Magalon, H. (2017). Reevaluating species number, distribution and endemism of the coral genus *Pocillopora* Lamarck, 1816 using species delimitation methods and microsatellites. M*olecular Phylogenetics and Evolution, 109*, 430-446.

Gélin, P., Fauvelot, C., Bigot, L., Baly, J., & Magalon, H. (2018). From population connectivity to the art of striping Russian dolls: the lessons from *Pocillopora* corals. *Ecology and Evolution, 8*(2), 1411-1426

Gilbert, A., Heintz, T., Hoeksema, B. W., Benzoni, F., Fernandez, J. M., Fauvelot, C., & Andréfouët, S. (2015). Endangered New Caledonian endemic mushroom coral *Cantharellus noumeae* in turbid, metal-rich, natural and artificial environments. M*arine Pollution Bulletin, 100*(1), 359-369.

Glynn, P. W., Maté, J. L., Baker, A. C., & Calderón, M. O. (2001). Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño–Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science*, *69*(1), 79-109.

Goff-Vitry, L. M. C., Rogers, A. D., & Baglow, D. (2004). A deep-sea slant on the molecular phylogeny of the Scleractinia. *Molecular Phylogenetics and Evolution*, *30*(1), 167-177.

Gonçalves-Souza, T., Garey, M. V., da Silva, F. R., Albuquerque, U. P., & Provete, D. B. (2019). Multidimensional Analyses for Testing Ecological, Ethnobiological, and

Conservation Hypotheses. In *Methods and Techniques in Ethnobiology and Ethnoecology* (pp. 87-110). Humana Press, New York, NY.

Gordon, J., Knowlton, N., Relman, D. A., Rohwer, F., & Youle, M. (2013). Superorganisms and holobionts. *Microbe*, *8*(4), 152-153.

Gottscho, A. D., Wood, D. A., Vandergast, A. G., Lemos-Espinal, J., Gatesy, J., & Reeder, T. W. (2017). Lineage diversification of fringe-toed lizards (Phrynosomatidae: Uma notata complex) in the Colorado Desert: Delimiting species in the presence of gene flow. *Molecular Phylogenetics and Evolution*, *106*, 103-117.

Gower, J. C. (1985). Properties of Euclidean and non-Euclidean distance matrices. *Linear Algebra and its Applications*, *67*, 81-97.

Harriott, V. J. (1983). Reproductive ecology of four scleratinian species at Lizard Island, Great Barrier Reef. *Coral Reefs*, *2*(1), 9-18.

Harrison, P. L. (1990). Reproduction, dispersal and recruitment of scleractian corals. *Coral reefs*.

Harrison, P. L., Babcock, R. C., Bull, G. D., Oliver, J. K., Wallace, C. C., & Willis, B. L. (1984). Mass spawning in tropical reef corals. *Science*, *223*(4641), 1186-1189.

Harvey, M. G., Smith, B. T., Glenn, T. C., Faircloth, B. C., & Brumfield, R. T. (2016). Sequence capture versus restriction site associated DNA sequencing for shallow systematics. *Systematic Biology*, *65*(5), 910-924.

Hatta, M., Fukami, H., Wang, W., Omori, M., Shimoike, K., Hayashibara, T., ... & Sugiyama, T. (1999). Reproductive and genetic evidence for a reticulate evolutionary history of mass-spawning corals. *Molecular Biology and Evolution*, *16*(11), 1607-1613.

Hayashibara, T., Shimoike, K., Kimura, T., Hosaka, S., Heyward, A., Harrison, P., ... & Omori, M. (1993). Patterns of coral spawning at Akajima Island, Okinawa, Japan. *Marine Ecology Progress Series*, 253-262.

Hebert, P. D., Cywinska, A., Ball, S. L., & Dewaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1512), 313-321.

Hellberg, M. E. (2006). No variation and low synonymous substitution rates in coral mtDNA despite high nuclear variation. *BMC Evolutionary Biology*, *6*(1), 24.

Hellberg, M. E., Prada, C., Tan, M. H., Forsman, Z. H., & Baums, I. B. (2016). Getting a grip at the edge: recolonization and introgression in eastern Pacific *Porites* corals. *Journal of Biogeography*, *43*(11), 2147-2159.

Hennig, W. (1999). Phylogenetic systematics. University of Illinois Press.

Herrera, S., & Shank, T. M. (2016). RAD sequencing enables unprecedented phylogenetic resolution and objective species delimitation in recalcitrant divergent taxa. *Molecular Phylogenetics and Evolution*, *100*, 70-79.

Herrera, S., Watanabe, H., & Shank, T. M. (2015). Evolutionary and biogeographical patterns of barnacles from deep-sea hydrothermal vents. *Molecular Ecology*, *24*(3), 673-689.

Hillis, D. M., & Dixon, M. T. (1991). Ribosomal DNA: molecular evolution and phylogenetic inference. *The Quarterly Review of Biology*, *66*(4), 411-453.

Hipp, A. L., Eaton, D. A., Cavender-Bares, J., Fitzek, E., Nipper, R., & Manos, P. S. (2014). A framework phylogeny of the American oak clade based on sequenced RAD data. *PloS One*, *9*(4), e93975.

Hirose, M., & Hidaka, M. (2006). Early development of zooxanthella-containing eggs of the corals Porites cylindrica and Montipora digitata: The endodermal localization of zooxanthellae. *Zoological Science*, *23*(10), 873-882.

Hoegh-Guldberg, O. (2015). Reviving the Ocean Economy: the case for action-2015. WWF International. *Gland, Switzerland, Geneva*.

Hoeksema, B. W. (1989). Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen, 254*(1), 1-295.

Hoeksema, B. W., & Dai, C. F. (1991). Scleractinia of Taiwan: II. Family Fungiidae (including a new species). *Bulletin of the Institute of Zoology, Academia Sinica, 30*(3), 203-228.

Hoeksema, B. W., & Cairns, S. (2019). World list of Scleractinia. *Scleractinia. Accessed through: World Register of Marine Species at: http://www. marinespecies. org/aphia. php*.

Huang, D. (2012). Threatened reef corals of the world. *PLoS One, 7*(3), e34459.

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. *Journal of Molecular Evolution*, *66*(2), 167-174.

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 Evolutionary Biology*, *11*(1), 37.

Huang, D., Benzoni, F., Fukami, H., Knowlton, N., Smith, N. D., & Budd, A. F. (2014). Taxonomic classification of the reef coral families Merulinidae, Montastraeidae, and Diploastraeidae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, *171*(2), 277-355.

Huang, D., Goldberg, E. E., Chou, L. M., & Roy, K. (2018). The origin and evolution of coral species richness in a marine biodiversity hotspot. *Evolution*, *72*(2), 288-302.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., ... & Lough, J. M. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, *301*(5635), 929-933.

Hughes, T. P., Ayre, D., & Connell, J. H. (1992). The evolutionary ecology of corals. *Trends in Ecology and Evolution*, *7*(9), 292–295. doi:10.1016/0169-5347(92)90225-Z

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., ... & Bridge, T. C. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373.

Hume, B. C., D'Angelo, C., Smith, E. G., Stevens, J. R., Burt, J., & Wiedenmann, J. (2015). *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. *Scientific Reports*, *5*, 8562.

Hume, B. C., Voolstra, C. R., Arif, C., D'Angelo, C., Burt, J. A., Eyal, G., ... & Wiedenmann, J. (2016). Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to Holocene climate change. *Proceedings of the National Academy of Sciences*, *113*(16), 4416-4421.

Hunter, C. L. (1997). The utility of ITS sequences in assessing relationships among zooxanthellae and corals. In *Procinding of the 8th International Coral Reef Symposium, 1997* (Vol. 2, pp. 1599-1602).

Johnson, K. G., Budd, A. F., & Stemann, T. A. (1995). Extinction selectivity and ecology of Neogene Caribbean reef corals. *Paleobiology*, 52-73.

Johnston, E. C., Forsman, Z. H., Flot, J. F., Schmidt-Roach, S., Pinzón, J. H., Knapp, I. S., & Toonen, R. J. (2017). A genomic glance through the fog of plasticity and diversification in *Pocillopora*. *Scientific Reports*, *7*(1), 5991.

Karl, S. A., & Bowen, B. W. (1999). Evolutionary significant units versus geopolitical taxonomy: molecular systematics of an endangered sea turtle (genus Chelonia). *Conservation Biology*, *13*(5), 990-999.

Kass, R. E., & Raftery, A. E. (1995). Bayes factors. *Journal of the American Statistical Association*, *90*(430), 773-795.

Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, *30*(4), 772–780.

Keith, S. A., Baird, A. H., Hughes, T. P., Madin, J. S., & Connolly, S. R. (2013). Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1763), 20130818.

Kerr, A. M. (2005). Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony. *Biological Reviews*, *80*(4), 543-558.

Kerr, A. M., Baird, A. H., & Hughes, T. P. (2010). Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proceedings of the Royal Society B: Biological Sciences*, *278*(1702), 75-81.

Keshavmurthy, S., Meng, P. J., Wang, J. T., Kuo, C. Y., Yang, S. Y., Hsu, C. M., ... & Chen, C. A. (2014). Can resistant coral-*Symbiodinium* associations enable coral communities

to survive climate change? A study of a site exposed to long-term hot water input. *PeerJ*, *2*, e327.

Khan, T. M. A., & Shaukat, A. R. S. S. (2014) Two new records of Scleractinian Corals from Saint Martin's Island, Bangladesh.

Kitahara, M. V., Cairns, S. D., Stolarski, J., & Miller, D. J. (2013). Deltocyathiidae, an early-diverging family of Robust corals (Anthozoa, Scleractinia). *Zoologica Scripta*, *42*(2), 201-212.

Kitahara, M. V., Fukami, H., Benzoni, F., & Huang, D. (2016). The new systematics of Scleractinia: integrating molecular and morphological evidence. In *The Cnidaria, Past, Present and Future* (pp. 41-59). Springer, Cham.

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*(5), e98406.

Klunzinger, C.B., (1879). Die Korallenthiere des Rothen Meeres, 2. Theil: Die Steinkorallen. Erster Abschnitt: Die Madreporaceen und Oculinaceen: 1-88, pls. 1-10. Gutmann, Berlin

Knapp, I., Puritz, J., Bird, C., Whitney, J., Sudek, M., Forsman, Z., & Toonen, R. (2016). ezRAD—an accessible next-generation RAD sequencing protocol suitable for non-model organisms_v3. 1. *Protocols. io Life Sciences Protocol Repository*.

Knowlton, N. (1993). Sibling species in the sea. *Annual Review of Ecology and Systematics*, *24*(1), 189-216.

Knowlton, N., Mate, J. L., Guzman, H. M., Rowan, R., & Jara, J. (1997). Direct evidence for reproductive isolation among the three species of the *Montastraea annularis* complex in Central America (Panama and Honduras). *Marine Biology*, *127*(4), 705-711.

Knowlton, N. (2001). Who are the players on coral reefs and does it matter? The importance of coral taxonomy for coral reef management. *Bulletin of Marine Science*, 69(2), 305-308.

Laborel, J. (1974). West African reef corals: an hypothesis on their origin. In *Proceedings of the Second International Coral Reef Symposium* (Vol. 1, No. 1, pp. 425-443). Great Barrier Reef Committee Brisbane.

Ladner, J. T., & Palumbi, S. R. (2012). Extensive sympatry, cryptic diversity and introgression throughout the geographic distribution of two coral species complexes. *Molecular Ecology*, *21*(9), 2224-2238

LaJeunesse, T. C., Pettay, D. T., Sampayo, E. M., Phongsuwan, N., Brown, B., Obura, D. O., ... & Fitt, W. K. (2010). Long-standing environmental conditions, geographic isolation and host–symbiont specificity influence the relative ecological dominance

and genetic diversification of coral endosymbionts in the genus *Symbiodinium*. *Journal of Biogeography*, *37*(5), 785-800.

Lamarck, J. B. D. M. (1801). *Système des animaux sans vertèbres ou tableau général des classes, des ordres et des genres de ces animaux...* L'auteur.

Land, V., J. (ed). (2008). UNESCO-IOC Register of Marine Organisms (URMO)

Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*(6), 1695-1701.

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, *9*(4), 357.

Leaché, A. D., Fujita, M. K., Minin, V. N., & Bouckaert, R. R. (2014). Species delimitation using genome-wide SNP data. *Systematic Biology*, *63*(4), 534-5.

Levitan, D. R., Fukami, H., Jara, J., Kline, D., McGovern, T. M., McGhee, K. E., ... & Knowlton, N. (2004). Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution*, *58*(2), 308-323.

Li, H., & Durbin, R. (2009). Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics*, *25*(14), 1754-1760.

Linnaeus, C. V. (1758). Systema naturae, vol. 1. *Systema Naturae.*

Lischer, H. E., & Excoffier, L. (2011). PGDSpider: an automated data conversion tool for connecting population genetics and genomics programs. *Bioinformatics*, *28*(2), 298-299.

Lopez, J. V., & Knowlton, N. (1997). Description of *Montastrea* coral sibling species with multiple genetic loci. In *Proceding of the 8th International Coral Reef Symposium* (Vol. 2, pp. 1613-1618).

López-Pérez, R. A. (2013). Species composition and morphologic variation of *Porites* in the Gulf of California. Coral Reefs, 32(3), 867-878.

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.

Mann, C. C., & Plummer, M. L. (1992). The butterfly problem. *Atlantic Monthly*, *1*, 47-59.

Márquez, L. M., Miller, D. J., MacKenzie, J. B., & van Oppen, M. J. (2003). Pseudogenes contribute to the extreme diversity of nuclear ribosomal DNA in the hard coral *Acropora*. *Molecular Biology and Evolution*, *20*(7), 1077-1086.

Matzke, N. J. (2013). Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, *5*(4).

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology*, *63*(6), 951-970.

Mayr, E. (1963). Animal species and evolution. *Animal Species and Evolution.*

Mayr, E. (1970). *Populations, species, and evolution: an abridgment of animal species and evolution* (Vol. 19). Harvard University Press.

Mcfadden, C. S., & Hutchinson, M. B. (2004). Molecular evidence for the hybrid origin of species in the soft coral genus *Alcyonium* (Cnidaria: Anthozoa: Octocorallia). *Molecular Ecology*, *13*(6), 1495-1505.

McFadden, C. S., France, S. C., Sánchez, J. A., & Alderslade, P. (2006). A molecular phylogenetic analysis of the Octocorallia (Cnidaria: Anthozoa) based on mitochondrial protein-coding sequences. *Molecular Phylogenetics and Evolution*, *41*(3), 513-527.

McFadden, C. S., Haverkort-Yeh, R., Reynolds, A. M., Halàsz, A., Quattrini, A. M., Forsman, Z. H., ... & Toonen, R. J. (2017). Species boundaries in the absence of morphological, ecological or geographical differentiation in the Red Sea octocoral genus *Ovabunda* (Alcyonacea: Xeniidae). *Molecular Phylogenetics and Evolution*, *112*, 174-184.

Medina, M., Weil, E., & Szmant, A. M. (1999). Examination of the *Montastraea annularis* species complex (Cnidaria: Scleractinia) using ITS and COI sequences. *Marine Biotechnology*, *1*(1), 89-97.

Miller, K. J. (1994). Morphological Mendes, F. K., & Hahn, M. W. (2016). Gene tree discordance causes apparent substitution rate variation. *Systematic Biology*, 65(4), 711-721.

Miller, K. J. (1994). Morphological variation in the coral genus *Platygyra*: environmental influences and taxonomic implications. *Marine Ecology-Progress Series, 110,* 19-19.

Miller, K., & Babcock, R. (1997). Conflicting morphological and reproductive species boundaries in the coral genus *Platygyra. The Biological Bulletin*, *192*(1), 98-110.

Miller, K. J., & Benzie, J. A. H. (1997). No clear genetic distinction between morphological species within the coral genus *Platygyra*. *Bulletin of Marine Science*, *61*(3), 907-917.

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *2010 Gateway Computing Environments Workshop (GCE)* (pp. 1-8).

Milne Edwards H., & Haime, J. (1851) Recherches sur les polypiers. Mémoire 7. Monographie des Poritides. Annales des Sciences Naturelles, Zoologie, Series 3, 16: 21-70.

Milne Edwards, H., & Haime, J. (1857). Histoire naturelle des Coralliaires ou Polypes proprement dits (Coraux, Gorgones, Eponges, etc.) (Vol. 2). Librairie encyclopédique de Roret.

Milne Edwards, H. (1860). Histoire naturelle des coralliaires ou polypes proprement dits (Vol. 3). Librairie encyclopédique de Roret.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215-233.

Muko, S., Kawasaki, K., Sakai, K., Takasu, F., & Shigesada, N. (2000). Morphological plasticity in the coral *Porites sillimaniani* and its adaptive significance. *Bulletin of Marine Science*, *66*(1), 225-239.

Munday, P. L., Leis, J. M., Lough, J. M., Paris, C. B., Kingsford, M. J., Berumen, M. L., & Lambrechts, J. (2009). Climate change and coral reef connectivity. *Coral reefs*, *28*(2), 379-395.

Murakami T, Kawano H, Yamamoto Y, Mizutani A, Shimokawa S (2015) Numerical simulation for initial dynamic state of bundle based on field observations of Acroporidae spawning in Amitori Bay, Iriomote Island, Japan. *J JSCE 71*: I 1225-I 1230

Obura, D. (2012). The diversity and biogeography of Western Indian Ocean reef-building corals. *PloS One*, *7*(9), e45013.

Obura, D. (2016). An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences defining a biogeographic realm. *Journal of Biogeography*, *43*(2), 229-242.

Odorico, D. M., & Miller, D. J. (1997). Variation in the ribosomal internal transcribed spacers and 5.8 S rDNA among five species of Acropora (Cnidaria; Scleractinia): patterns of variation consistent with reticulate evolution. *Molecular Biology and Evolution*, *14*(5), 465-473.

Odum, H. T., & Odum, E. P. (1955). Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs*, *25*(3), 291-320.

Ogilvie, M. M. (1896). III. Microscopic and systematic study of madreporarian types of corals. *Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character*, (187), 83-345.

Oliver, T. A., & Palumbi, S. R. (2009). Distributions of stress-resistant coral symbionts match environmental patterns at local but not regional scales. *Marine Ecology Progress Series*, *378*, 93-103.

Oppen, M. V., Willis, B. L., Vugt, H. V., & Miller, D. J. (2000). Examination of species boundaries in the *Acropora cervicornis* group (Scleractinia, Cnidaria) using nuclear DNA sequence analyses. *Molecular Ecology*, *9*(9), 1363-1373.

Oppen, M. V., 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? *Molecular Biology and Evolution*, *18*(7), 1315-1329.

Oppen, M. V., Willis, B. L., Van Rheede, T., & Miller, D. J. (2002a). Spawning times, reproductive compatibilities and genetic structuring in the *Acropora aspera* group: evidence for natural hybridization and semi-permeable species boundaries in corals. *Molecular Ecology*, *11*(8), 1363-1376.

Oppen, M. V., Catmull, J., McDonald, B. J., Hislop, N. R., Hagerman, P. J., & Miller, D. J. (2002b). The mitochondrial genome of *Acropora tenuis* (Cnidaria; Scleractinia) contains a large group I intron and a candidate control region. *Journal of Molecular Evolution*, *55*(1), 1-13.

Oppen, M. V., Koolmees, E. M., & Veron, J. E. N. (2004). Patterns of evolution in the scleractinian coral genus *Montipora* (Acroporidae). *Marine Biology*, *144*(1), 9-18.

Oppen, M. V., & Lough, J. M. (2018). Synthesis: Coral Bleaching: patterns, processes, causes and consequences. In *Coral Bleaching* (pp. 343-348). Springer, Cham.

Pallas, P. S. (1766). *Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum... descriptiones etc*. Varrentrapp.

Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics*, *25*(1), 547-572.

Pante, E., Abdelkrim, J., Viricel, A., Gey, D., France, S. C., Boisselier, M. C., & Samadi, S. (2015). Use of RAD sequencing for delimiting species. *Heredity*, *114*(5), 450.

Paz-García, D. A., Hellberg, M. E., García-de-León, F. J., & Balart, E. F. (2015). Switch between morphospecies of *Pocillopora* corals. *The American Naturalist*, *186*(3), 434-440.

Paz-García, D. A., & Balart, E. F. (2016). New record of the endemic coral *Porites sverdrupi* (Gulf of California): do fluctuations in seawater temperature regulate its southernmost range limit?. *Marine Biodiversity, 46*(2), 499-502

Pinzón, J. H., Sampayo, E., Cox, E., Chauka, L. J., Chen, C. A., Voolstra, C. R., & LaJeunesse, T. C. (2013). Blind to morphology: genetics identifies several widespread ecologically common species and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal of Biogeography*, *40*(8), 1595-1608.

Pochon, X., Forsman, Z. H., Spalding, H. L., Padilla-Gamiño, J. L., Smith, C. M., & Gates, R. D. (2015). Depth specialization in mesophotic corals (*Leptoseris* spp.) and associated algal symbionts in Hawai'i. *Royal Society Open Science*, *2*(2), 140351.

Potkamp, G., & Fransen, C. H. (2019). Speciation with gene flow in marine systems. *Contributions to Zoology, 88(*2), 133-172

Prada, C., DeBiasse, M. B., Neigel, J. E., Yednock, B., Stake, J. L., Forsman, Z. H., ... & Hellberg, M. E. (2014). Genetic species delineation among branching Caribbean Porites corals. *Coral Reefs*, *33*(4), 1019-1030.

Pratlong, M., Rancurel, C., Pontarotti, P., & Aurelle, D. (2017). Monophyly of Anthozoa (Cnidaria): why do nuclear and mitochondrial phylogenies disagree? *Zoologica Scripta*, *46*(3), 363-371.

Puritz, J. B., Hollenbeck, C. M., & Gold, J. R. (2014). dDocent: a RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ*, *2*, e431.

Quattrini A.M., Faircloth B.C., Duenas L.F., Bridge T.C., Brugler M.R., Calixto-Botía I.F., DeLeo D.M., Forět S., Herrera S., Lee S.M.Y., Miller D.J., Prada C., Radis-Baptista G., Ramíz-Portilla C., Sánchez J.A., Rodríguez E., McFadden C.S. (2018) Universal target-enrichment baits for anthozoan (Cnidaria) phylogenomics: new approaches to long-standing problems. *Molecular Ecology Resources, 18*:281–295.

Queiroz De, K. (1998). The general lineage concept of species, species criteria, and the process of speciation. *Endless forms: species and speciation*.

Queiroz De, K. (2007). Species concepts and species delimitation. *Systematic biology*, *56*(6), 879-886.

Quinlan, A. R., & Hall, I. M. (2010). BEDTools: a flexible suite of utilities for comparing genomic features. *Bioinformatics*, *26*(6), 841-842.

Quoy, J.R.C., & J.P. Gaimard. (1833). Zoologie IV: Zoophytes. In:Zoologie. Voyage de la corvette l'Astrolabe: exécuté par ordre du roi, pendant les années 1826-1827-1828-1829 / sous le commandement de J. Dumont d'Urville. pp. 1-390. Paris, J. Tastu.

Rambaut, A., & Drummond, A. J. (2007). Tracer v1. 6 http://beast. bio. ed. ac. uk.

Randall, R. H. (1976). Some problems in reef coral taxonomy. *Micronesica*, *15*(1), 151-156.

Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*(1), 4-14.

Rehberg, H. (1892). Neue und wenig bekannte Korallen. *Abhandlungen aus dem Gebiete der Naturwissenschaften Hamburg.* 12: 1-50

Reitzel, A. M., Herrera, S., Layden, M. J., Martindale, M. Q., & Shank, T. M. (2013). Going where traditional markers have not gone before: utility of and promise for RAD sequencing in marine invertebrate phylogeography and population genomics. *Molecular Ecology*, *22*(11), 2953-2970.

Reyes-Bonilla, H., & Carricart-Ganivet, J.P. (2000) Porites arnaudi a new species of stony coral (Anthozoa: Scleractinia: Poritidae) from oceanic islands of the eastern Pacific Ocean. Proceedings of the Biological Society of Washington. 113: 561-571.

Richards, Z. T., van Oppen, M. J., Wallace, C. C., Willis, B. L., & Miller, D. J. (2008). Some rare Indo-Pacific coral species are probable hybrids. *PLoS One*, *3*(9), e3240.

Richards, Z. T., Miller, D. J., & Wallace, C. C. (2013). Molecular phylogenetics of geographically restricted *Acropora* species: implications for threatened species conservation. *Molecular Phylogenetics and Evolution*, *69*(3), 837-851.

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. *Conservation Genetics, 17*(3), 577-591.

Roberts, J. M., Wheeler, A., Freiwald, A., & Cairns, S. (2009). *Cold-water corals: the biology and geology of deep-sea coral habitats*. Cambridge University Press.

Rohwer, F., Seguritan, V., Azam, F., & Knowlton, N. (2002). Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series*, *243*, 1-10.
Rosser, N. L. (2015). Asynchronous spawning in sympatric populations of a hard coral reveals cryptic species and ancient genetic lineages. *Molecular Ecology*, *24*(19), 5006-5019.

Romano, S. L., & Palumbi, S. R. (1996). Evolution of scleractinian corals inferred from molecular systematics. *Science*, *271*(5249), 640-642.

Romano, S. L., & Palumbi, S. R. (1997). Molecular evolution of a portion of the mitochondrial 16S ribosomal gene region in scleractinian corals. *Journal of Molecular Evolution*, *45*(4), 397-411.

Romano, S. L., & Cairns, S. D. (2000). Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science*, *67*(3), 1043-1068.

Ronquist, F. (1997). Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, *46*(1), 195-203.

Rosenberg, E., Koren, O., Reshef, L., Efrony, R., & Zilber-Rosenberg, I. (2007). The role of microorganisms in coral health, disease and evolution. *Nature Reviews Microbiology*, *5*(5), 355.

Rosic, N., Ling, E. Y. S., Chan, C. K. K., Lee, H. C., Kaniewska, P., Edwards, D., ... & Hoegh-Guldberg, O. (2015). Unfolding the secrets of coral–algal symbiosis. *The ISME journal*, *9*(4), 844.

Rosser, N. L., Thomas, L., Stankowski, S., Richards, Z. T., Kennington, W. J., & Johnson, M. S. (2017). Phylogenomics provides new insight into evolutionary relationships and genealogical discordance in the reef-building coral genus *Acropora*. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1846), 20162182.

Rosser, N. L. (2016). Demographic history and asynchronous spawning shape genetic differentiation among populations of the hard coral Acropora tenuis in Western Australia. *Molecular Phylogenetics and Evolution*, *98*, 89-96.

Rowan, R., & Knowlton, N. (1995). Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceedings of the National Academy of Sciences*, *92*(7), 2850-2853.

Rubin, B. E., Ree, R. H., & Moreau, C. S. (2012). Inferring phylogenies from RAD sequence data. *PloS one*, *7*(4), e33394.

Sampayo, E. M., Ridgway, T., Franceschinis, L., Roff, G., Hoegh-Guldberg, O., & Dove, S. (2016). Coral symbioses under prolonged environmental change: living near tolerance range limits. *Scientific Reports*, *6*, 36271.

Sánchez, J. A., & Dorado, D. (2008). Intragenomic ITS2 variation in Caribbean seafans. In *Procedings of the 11th International Coral Reef Symposium* (pp. 1383-1387).

Santodomingo, N., Wallace, C. C., & Johnson, K. G. (2015). Fossils reveal a high diversity of the staghorn coral genera *Acropora* and *Isopora* (Scleractinia: Acroporidae) in the Neogene of Indonesia. *Zoological Journal of the Linnean Society*, *175*(4), 677-763.

Schmidt-Roach, S., Lundgren, P., Miller, K. J., Gerlach, G., Noreen, A. M., & Andreakis, N. (2013a). Assessing hidden species diversity in the coral *Pocillopora damicornis* from Eastern Australia. *Coral Reefs*, *32*(1), 161-172.

Schmidt-Roach, S., Miller, K. J., & Andreakis, N. (2013b). *Pocillopora aliciae*: a new species of scleractinian coral (Scleractinia, Pocilloporidae) from subtropical Eastern Australia. *Zootaxa*, *3626*(4), 576-582.

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. *Zoological Journal of the Linnean Society*, *170*(1), 1-33

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671.

Shearer, T. L., & Coffroth, M. A. (2008). DNA BARCODING: Barcoding corals: limited by interspecific divergence, not intraspecific variation. *Molecular Ecology Resources*, *8*(2), 247-255.

Shearer, T. L., Van Oppen, M. J. H., Romano, S. L., & Wörheide, G. (2002). Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology*, *11*(12), 2475-2487.

Sheppard, C. R. C. (1981). The reef and soft-substrate coral fauna of Chagos, Indian Ocean. *Journal of Natural History*, *15*(4), 607-621.

Sheppard, C. R. (1987). Coral species of the Indian Ocean and adjacent seas: a synonymized compilation and some regional distributional patterns. *Atoll Research Bulletin*.

Sheppard, C. R. (1998). Biodiversity patterns in Indian Ocean corals, and effects of taxonomic error in data. *Biodiversity and Conservation*, *7*(7), 847-868.

Sheppard, C., Price, A., & Roberts, C. (1992). Marine ecology of the Arabian region: patterns and processes in extreme tropical environment.

Shimoike, K. (1999). Observation of coral spawning in Akajima Island with newly found spawning patterns. *Midoriishi (19)*, 29-31.

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: International Journal of Organic Evolution*, *65*(11), 3274-3284.

Smith L.W., Barshis D., Birkeland C. 2007. Phenotypic plasticity for skeletal growth, density and calcification of *Porites lobata* in response to habitat type. *Coral Reefs, 26*:559–567.

Stamatakis, A. (2014). RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, *30*(9), 1312-1313.

Smith, H., Epstein, H., & Torda, G. (2017). The molecular basis of differential morphology and bleaching thresholds in two morphs of the coral *Pocillopora acuta*. *Scientific Reports*, *7*(1), 10066.

Souter, P. (2010). Hidden genetic diversity in a key model species of coral. *Marine Biology, 157*(4), 875-885.

Spalding, M. D., & Grenfell, A. M. (1997). New estimates of global and regional coral reef areas. *Coral Reefs*, *16*(4), 225-230.

Stampar, S. N., Maronna, M. M., Kitahara, M. V., Reimer, J. D., & Morandini, A. C. (2014). Fast-evolving mitochondrial DNA in Ceriantharia: a reflection of Hexacorallia paraphyly? *PLoS One*, *9*(1), e86612.

Stebbins, G., L. (1980). Rarity of plant species: A synthetic viewpoint. *Rho- dora*, 82(829), 77–86.

Stebbins, G., L., & Major, J. (1965). Endemism and speciation in the Cali- fornia flora. Ecological *Monographs*, 35(1), 1–35. https://doi.org/10. 2307/1942216

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*(4), 1033

Stobie, C. S., Cunningham, M. J., Oosthuizen, C. J., & Bloomer, P. (2019). Finding stories in noise: mitochondrial portraits from RAD data. *Molecular Ecology Resources, 19*:191–205.

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 Evolutionary Biology*, *11*(1), 316.

Sultan, S. E. (2000). Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, *5*(12), 537-542.

Szmant, A. M., Weil, E., Miller, M. W., & Colon, D. E. (1997). Hybridization within the species complex of the scleractinan coral *Montastraea annularis*. *Marine Biology*, *129*(4), 561-572.

Tautz, D., Arctander, P., Minelli, A., Thomas, R. H., & Vogler, A. P. (2003). A plea for DNA taxonomy. *Trends in Ecology & Evolution*, *18*(2), 70-74.

Terraneo, T. I., Berumen, M. L., Arrigoni, R., Waheed, Z., Bouwmeester, J., Caragnano, A., ... & Benzoni, F. (2014). P*achyseris inattesa* sp. n. (Cnidaria, Anthozoa, Scleractinia): a new reef coral species from the Red Sea and its phylogenetic relationships. *ZooKeys*, (433), 1.

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. *Molecular Phylogenetics and Evolution*, *102*, 278-294.

Terraneo, T. I., Arrigoni, R., Benzoni, F., Tietbohl, M. D., & Berumen, M. L. (2017). Exploring the genetic diversity of shallow-water Agariciidae (Cnidaria: Anthozoa) from the Saudi Arabian Red Sea. *Marine Biodiversity*, *47*(4), 1065-1078.

Terraneo, T. I., Arrigoni, R., Benzoni, F., Forsman, Z. H., & Berumen, M. L. (2018a). Using ezRAD to reconstruct the complete mitochondrial genome of *Porites fontanesii* (Cnidaria: Scleractinia). *Mitochondrial DNA Part B*, *3*(1), 173-174.

Terraneo, T. I., Arrigoni, R., Benzoni, F., Forsman, Z. H., & Berumen, M. L. (2018b). The complete mitochondrial genome of *Porites harrisoni* (Cnidaria: Scleractinia) obtained using next-generation sequencing. *Mitochondrial DNA Part B*, *3*(1), 286-287.

Terraneo, T. I., Benzoni, F., Baird, A. H., Arrigoni, R., & Berumen, M. L. (2019a). Morphology and molecules reveal two new species of Porites (Scleractinia, Poritidae) from the Red Sea and the Gulf of Aden. *Systematics and Biodiversity*, *17*(5), 491-508.

Terraneo, T. I., Fusi, M., Hume, B. C., Arrigoni, R., Voolstra, C. R., Benzoni, F., ... & Berumen, M. L. (2019b). Environmental latitudinal gradients and host-specificity shape Symbiodiniaceae distribution in Red Sea Porites corals. *Journal of Biogeography*, *46*(10), 2323-2335.

Tisthammer, K. H., & Richmond, R. H. (2018). Corallite skeletal morphological variation in Hawaiian Porites lobata. *Coral Reefs*, *37*(2), 445-456.

Todd, P. A. (2008). Morphological plasticity in scleractinian corals. *Biological Reviews*, *83*(3), 315-337.

Toonen, R. J., Puritz, J. B., Forsman, Z. H., Whitney, J. L., Fernandez-Silva, I., Andrews, K. R., & Bird, C. E. (2013). ezRAD: a simplified method for genomic genotyping in non-model organisms. *PeerJ*, *1*, e203.

Tonk, L., Sampayo, E. M., Chai, A., Schrameyer, V., & Hoegh-Guldberg, O. (2017). *Symbiodinium* (Dinophyceae) community patterns in invertebrate hosts from inshore marginal reefs of the southern Great Barrier Reef, Australia. *Journal of Phycology*, *53*(3), 589-600.

Tuerhong, G., & Kim, S. B. (2014). Gower distance-based multivariate control charts for a mixture of continuous and categorical variables. *Expert Systems with Applications*, *41*(4), 1701-1707.

Vaughan, T.W. (1918). Some shallow-water corals from Murray Island (Australia), Cocos-Keeling Island, and Fanning Island. *Papers from the Department of Marine Biology of the Carnegie Institution of Washington.* 9 (213): 49-234, pls. 20-93.

Vaughan, T. W., & Wells, J. W. (1943). Revision of the suborders, families and genera of Scleractinia. *Geological Society of America special Papers, 44,* 1-363.

Vénec-Peyré, M. T., & Caulet, J. P. (2000). Paleoproductivity changes in the upwelling system of Socotra (Somali Basin, NW Indian Ocean) during the last 72,000 years: evidence from biological signatures. *Marine Micropaleontology*, *40*(3), 321-344.

Veron, J.E.N. & Pichon, M. (1982). Scleractinia of Eastern Australia – Part IV. Family Poritidae. *Australian Institute of Marine Science Monograph Series,* 5: 1-159.

Veron, J.E.N (1985). New Scleractinia from Australian coral reefs. *Records of the Western Australian Museum,* 12: 147-183.

Veron, J. E. N. (1995). *Corals in space and time: the biogeography and evolution of the Scleractinia*. Cornell University Press.

Veron, J. E. N. (2000). *Corals of the World* (No. C/593.6 V4).

Veron, J., Stafford-Smith, M., DeVantier, L., & Turak, E. (2015). Overview of distribution patterns of zooxanthellate Scleractinia. *Frontiers in Marine Science*, *1*, 81.

Vine, P. (1986). *Red Sea Invertebrates.* Immel Publishing, London. 224 pp.

Vollmer, S. V., & Palumbi, S. R. (2002). Hybridization and the evolution of reef coral diversity. *Science*, *296*(5575), 2023-2025.

Vollmer, S. V., & Palumbi, S. R. (2004). Testing the utility of internally transcribed spacer sequences in coral phylogenetics. *Molecular Ecology*, *13*(9), 2763-2772.

Wagner, C. E., Keller, I., Wittwer, S., Selz, O. M., Mwaiko, S., Greuter, L., ... & Seehausen, O. (2013). Genome-wide RAD sequence data provide unprecedented resolution of species boundaries and relationships in the L ake V ictoria cichlid adaptive radiation. *Molecular Ecology*, *22*(3), 787-798.

Wallace, C. C., Chen, C. A., Fukami, H., & Muir, P. R. (2007). Recognition of separate genera within Acropora based on new morphological, reproductive and genetic evidence from *Acropora togianensis*, and elevation of the subgenus *Isopora* Studer, 1878 to genus (Scleractinia: Astrocoeniidae; Acroporidae). *Coral Reefs*, *26*(2), 231-239.

Wallace, C. C., & Willis, B. L. (1994). Systematics of the coral genus *Acropora*: implications of new biological findings for species concepts. *Annual Review of Ecology and Systematics*, *25*(1), 237-262.

Warner, P. A., van Oppen, M. J., & Willis, B. L. (2015). Unexpected cryptic species diversity in the widespread coral *Seriatopora hystrix* masks spatial-genetic patterns of connectivity. *Molecular Ecology, 24*(12), 2993-3008.

Wei, N. V., Wallace, C. C., Dai, C., Ruby, K., Pillay, M., & Chen, C. A. (2006). "Analyses of the ribosomal internal transcribed spacers (ITS) and the 5.8 S gene indicate that extremely high rDNA heterogeneity is a unique feature in the scleractinian coral genus *Acropora* (Scleractinia; Acroporidae)." *Zoological Studies, 45*, 3: 404-418.

Wei, N. V., Hsieh, H. J., Dai, C. F., Wallace, C. C., Baird, A. H., & Chen, C. A. (2012). Reproductive isolation among Acropora species (Scleractinia: Acroporidae) in a marginal coral assemblage. *Zoological Studies*, *51*, 85-92.

Wells, J. W. (1933). *Corals of the Cretaceous of the Atlantic and Gulf coastal plains and western interior of the United States* (Vol. 18, No. 67). Harris co.

Wells, J. W. (1956). Scleractinia, p. F328–F444. *Treatise on Invertebrate Paleontology, Pt. F, Coelenterata. Geological Society of America and University of Kansas Press, Lawrence*.

West-Eberhard, M. J. (1986). Alternative adaptations, speciation, and phylogeny (a review). *Proceedings of the National Academy of Sciences, 83*(5), 1388-1392.

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, *19*(12), 639-644.

Wijsman-Best, M. (1972). Systematics and ecology of New Caledonian Faviinae (Coelenterata-Scleractinia). *Bijdragen tot de Dierkunde, 42(*1), 3-90.

Willis, B. L., Babcock, R. C., Harrison, P. L., Oliver, J. K., & Wallace, C. C. (1985). Patterns in the mass spawning of corals on the Great Barrier Reef from 1981 to 1984.

Willis, B. L., Babcock, R. C., Harrison, P. L., & Wallace, C. C. (1997). Experimental hybridization and breeding incompatibilities within the mating systems of mass spawning reef corals. *Coral Reefs*, *16*(1), S53-S65.

Willis, B. L., van Oppen, M. J., Miller, D. J., Vollmer, S. V., & Ayre, D. J. (2006). The role of hybridization in the evolution of reef corals. *Annual Review of Ecology and Systematics*, *37*, 489-517.

Willis, J. C. (1922). Age and Area, a Study in Geographical Distribution and Origin of Species, by JC Willis,... with Chapters by Hugo De Vries, HB Guppy, Mrs. EM Reid, James Small... The University Press.

Willis, S. C., Hollenbeck, C. M., Puritz, J. B., Gold, J. R., & Portnoy, D. S. (2017). Haplotyping RAD loci: an efficient method to filter paralogs and account for physical linkage. *Molecular Ecology Resources*, *17*(5), 955-965.

Wolstenholme, J. K. (2004). Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). *Marine Biology*, *144*(3), 567-582.

Zhang J., Kobert K., Flouri T., Stamatakis A. (2013). PEAR: a fast and accurate Illumina Paired-End reAd mergeR. *Bioinformatics*, *30*:614–620

Ziegler, M., Roder, C. M., Büchel, C., & Voolstra, C. R. (2015). Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. *Frontiers in Marine Science*, *2*, 4.

Zlatarski, V. N., Martinez Estalella, N., & Jablensky, B. (1982). Les Scléractiniaires de Cuba avec des données sur les organismes associés. *Editions l'Académie bulgare des Sciences, Sofia*. 472 pp.

Appendices

Appendix 1.1 A nomenclature for the genus *Porites*, including the authority, the type location for the species, the status of the type materials, the museum where the type is held, the accession number of the type, the current taxonomic status at WoRMS and the authority for any synonym. Names followed by (*) indicate species for which the original description was not available. bor = basis of record, was used when Synonymy authority was not identified. The list of museum abbreviations is provided at the end of the table. Numbers in brackets refer to type localities as represented in Appendix 2.2. Species in bold are the one included in the morphological and molecular analyses of this study.

Appendix 2.1 List of coral specimens examined in the present study. For each sample, voucher number, species identification based on morphology, sampling locality and body of water (Locality), collector, and latitude and longitude (GPS) are provided. FB is Francesca Benzoni, TIT is Tullia Isotta Terraneo, RA is Roberto Arrigoni, JB is Jessica Bouwmeester, DC is Darren Coker, MC is Michelle Claerebout, MT is Matthew Tietbhol, MLB is Michael L Beruemen, AM is Alison Monroe

Appendix 2.2 Map showing type localities (numbered dots) of the examined nominal species and sampling localities (yellow circles) of the specimens collected for this study (Appendix 1.1). Code for sampling localities: SA = Saudi Arabia; DJ = Djibouti; AD = Aden; Y = Yemen; BA = Bir ali-Yemen; BU = Burum-Yemen; SO = Socotra Island-Yemen; P = Balhaf-Yemen; TOM = Gulf of Oman; QA = Qatar MY = Mayotte Island; MD = Madagascar; PFB = Papua New Guinea; TAU = Eastern-Australia (Great Barrier Reef, Coral Sea, Lord Howe Island); AU = Solitary Islands; HS = New Caledonia; MQ = Marquesas Islands. Numbers in the stars refer to type localities in Appendix 1.1.

Appendix 2.3 Images of each nominal species recovered in this study. For each species we reported: (a) an *in situ* image of a typical morphology with a close up; (b) a zoom in of the dry skeletal stuctures of the same specimen; when available (c) the species holotype with a close up.

Appendix 2.4 Phylogenetic reconstruction based on rDNA region. Node values represent BI posterior probabilities and ML bootstrap supports. Roman numbers from I to XVI refer to the assigned clade numbers. Colour codes are explained in the legend.

Appendix 2.5 RAxML tree based on "coral-min" dataset, that allowed for 50% missing data, and consted of 1,637 SNPs. Values at nodes represent ML bootstrap supports. Roman numbers from I to XVI refer to the assigned molecular clade numbers. Colour codes are explained in the legend

Appendix 2.6 RAxML tree based on "coral-max" dataset, that allowed for 50% missing data and consisted of 163,637 SNPs. Values at nodes represent ML bootstrap supports. Roman numbers from I to XVI refer to the assigned molecular clade numbers. Colour codes are explained in the legend

Appendix 2.7 Results of BioGeoBEARS Likelihood Ratio Tests (LRT) for the two pairs of nested models (DEC vs. DEC+J, DIVALIKE vs. DIVALIKE+J).

Appendix 2.8 Ancestral area reconstruction of *Porites* using BioGeoBEARS on the same topology as the phylogenetic tree presented in Fig. 3.3. Coloured boxes at each node and corner are colour coded for the area with the highlest ML probability. Areas are illustrated on the map to the left. Caption refers to colours of areas in the map and boxes.

Appendix 2.9 Distribution maps for each nominal species and morphology recovered in the study.

Appendix 1.1 A nomenclature for the genus *Porites*, including the authority, the type location for the species, the status of the type material, the museum where the type is held, the accession number of the type, the current taxonomic status at WoRMS and the authority for any synonym. Names followed by (*) indicate species for which the original description was not available. bor = basis of record, was used when Synonymy authority was not identified. The list of museum abbreviations is provided at the end of the table. Numbers in brackets refer to type localities as represented in Appendix 2.2. Species in bold are those included in the morphological and molecular analyses of this study.

Genera and Nominal species	Taxonomic authority	Type locality	Type	Museum	Number	Taxonomic status **WoRMS** **(Hoeksema & Cairns 2019)**	Synonymy	Synonymy authority
Cosmoporites	Duchassaing & Michelotti,1860	Saint Thomas, Virgin Islands	-	MRSN	-	Unaccepted, synonym	*Porites*	Bernard 1905
Madrepora arenosa	Esper, 1797	Unknown	Not recorded	-	-	Unaccepted, synonym	*Porites lutea*	Sheppard 1987
Madrepora conglomerata	Esper, 1797	Madagascar	-	-	-	Unaccepted, synonym	*Porites solida*	Veron & Pichon 1982
Madrepora porites	Pallas, 1766	Curaçao	Not deposited	-	-	Unaccepted, new combination	*Porites porites*	Vaughan 1901
Madrepora rus	Forskål, 1775	Red Sea (1)	Syntype	Zoological Museum of the University of Copenhagen, Denmark	51, 52, 54, 14	Unaccepted, original combination, basionym	*Porites rus*	De Blainville, 1830
Madrepora solida	Forskål 1776	Jeddah, Saudi Arabia (1)	Holotype	Zoological Museum of the University of Copenhagen, Denmark	000535	Unaccepted, original combination, basionym	*Porites solida*	Veron & Pichon 1982 (bor)

Napopora latistellata	Quelch, 1886	Tahiti	-	NHM	-	Unaccepted, previous combination	*Porites latistellata*	Veron & Pichon 1982
Napopora semilunaris	Nemenzo, 1976	Sumilon Island, Phillipines	Syntype	UPZD	SU D-70, SU D-125	Unaccepted, synonym	*Porites vaughani*	Veron & Pichon 1982
Napopora sillimaniana	Nemenzo, 1976	Sumilon Island, Phillipines	Holotype	UPZD	SU D-78	Unaccepted, wrong spelling	*Porites simmilaniani*	Veron & Pichon 1982
Napopora vaughani	Crossland, 1952	Great Barrier Reef, Australia	Holotype	NHM	1934.5.14.491A	Unaccepted, synonym	*Porites vaughani*	Veron & Pichon 1982
Napopora violetae	Nemenzo, 1971	Puerto Galerea, Philippines	Holotype	UPZD/ MTQ (fragment)	G65861 / UP 1345	Unaccepted, synonym	*Porites deformis*	Veron & Hodgson 1989
Neoporites	Duchassaing & Michelotti,1860	-	-	MRSN	-	Unaccepted, synonym	*Porites*	Veron & Pichon 1982
Neoporites astraeoides	Duchassaing & Michelotti,1860	Saint Thomas, Virgin Islands	-	MRSN	-	Unaccepted, new combination	*Porites astreoides*	Zlatarski & Martinez, 1892
Neoporites guadalupensis	Duchassaing & Michelotti,1860	Guadalupe	-	MRSN	-	Unaccepted, new combination	*Porites astreoides*	Zlatarski & Martinez, 1892
Neoporites incerta	Duchassaing & Michelotti,1860	Carribean	-	MRSN	-	Unaccepted, new combination	*Porites astreoides*	Zlatarski & Martinez, 1892

Neoporites littoralis	Duchassaing & Michelotti,1860	Carribean	-	MRSN	-	Unaccepted, new combination	*Porites astreoides*	Zlatarski & Martinez, 1892
Neoporites michelini	Duchassaing & Michelotti,1860	Saint Croix, Virgin Island	-	MRSN	-	Unaccepted, new combination	*Porites astreoides*	Zlatarski & Martinez, 1892
Porites alveolata	Milne Edwards, 1860	Red Sea	Holotype	MNHN	IK-2010-728 form *a* 595 form *b*	accepted		
Porites andrewsi	Vaughan, 1918	Murray Island, Great Barrier Reef, Australia	Syntype	USNM	85761, 45500, 85760, 47231	Unaccepted, synonym	*Porites cylindrica*	Veron & Pichon 1982
Porites angulata	Lamarck, 1816	Australia	-	-	-	Unaccepted, original combination, basionym	*Montipora angulata*	Veron & Wallace 1984
Porites annae	Crossland, 1952	GBR, Australia (10)	-	NHM	-	accepted		
Porites aranetai	Nemenzo, 1955	Liloan, Cebu, Philippines	Types	UPZD	UP C-63, C-176	accepted		
Porites arenacea	Lamarck, 1816	Red Sea, Indian Ocean	-	MNHN	-	taxon inquirendum		
Porites arenosa	(Esper, 1797)	Unknown	Not recorded	-	-	Unaccepted, synonym	*Porites lutea*	Sheppard 1987

Porites arenosa var. parvistella	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	Unaccepted, synonym	*Porites lutea*	Sheppard 1987
Porites astridae	Thiel, 1932	India	-	Zoological Museum Hamburg	-	taxon inquirendum		
Porites armata	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Stylocoeniella armata*	Veron & Pichon 1976
Porites arnaudi	Reyes Bonilla & Carricart Ganivet, 2000	Clipperton Atoll (14)	Holotype	USNM	100261	accepted		
Porites astreoides	Lamarck, 1816	Carrie Bow Cay, Belize	Holotype	MNHN	IK-2010-501	accepted		
Porites attenuata	Nemenzo, 1955	Puerto Galera, Philippines	Holotype	UPZD	UP C-162	accepted		
Porites australiensis	Vaughan, 1918	Murray Island, GBR (10)	Holotype	USNM	47233	accepted		
Porites baueri	Squires, 1959	Puerto Balleto, Maria Madre Island, Mexico	Holotype	AMNH	3348	accepted		
Porites bernardi	Vaughan, 1907	Hawaii	Syntype	USNM	20820	taxon inquirendum		
Porites bernardi	Gravier, 1909	Gabonese Republique	Type	MNHN	IK-2010-591	Unaccepted, homonym	*Porites gabonensis*	Gravier 1910
*Porites branneri**	Rathbun, 1888	Parahyba do Norte, Brazil	Holotype	USNM	10961	accepted		

Porites brighami	Vaughan, 1907	Molokai, Hawaii	Holotype	USNM	21625	accepted		
Porites bulbosa	Quelch, 1886	Honolulu, Hawaii	Holotype	NHM	86.12.9.312	taxon inquirendum		
Porites californica	Verrill, 1869	La Paz, Mexico, Gulf of California	Syntype	YPM	YPM IZ 001599.CN	Unaccepted, synonym	*Porites panamensis*	Reyes-Bonilla 2002
Porites capricornis	Rehberg 1892	Palau	-	Zoological Museum Hamburg	-	Unaccepted, synonym	*Porites cylindrica*	Veron & Pichon 1982
Porites cervina	Lamarck, 1816	Indian Ocean	-	-	-	taxon inquirendum		
Porites circumvallata	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Montipora circumvallata*	Veron & Wallace 1984
Porites clavaria	Lamarck, 1816	Antilles	Holotype	MNHN	IK-2010-508, 482	Unaccepted, synonym	*Porites porites*	Jamenson & Cairns 2012
Porites clavasia	Audouin, 1826	Egypt, Red Sea	-	-	-	taxon inquirendum		
Porites cocosensis	Wells, 1950	Cocos-Keeling Islands	Holotype	USNM	44339	accepted		
Porites colonensis	Zlatarski 1990	Largo Remo, east of Colon, Bahia Las Minas, Panama	Holotype	USNM	82020	accepted		
Porites columnaris	Klunzinger 1879	Red Sea (1)	Holotype	MNB		accepted		

			Type	MNHN	4151			
Porites complanata	Lamarck, 1816					taxon inquirendum		
Porites compressa	Dana, 1846	Hawaii	Syntype	USNM	711, 653	accepted		
Porites conglomerata	(Esper, 1797)	Madagascar	Type	MNHN	IK-2010-558	Unaccepted, synonym	*Porites solida*	Veron & Pichon 1982
Porites conglomerata var. lutea	Quoy & Gaimard, 1833	Tonga	Holotype	MNHN	IK-2010-389	Unaccepted, synonym	*Porites lutea*	Veron & Pichon 1982 (bor)
Porites convexa	(Verrill, 1864)	Society Islands	Type	NHM	1886.12.9.509	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Porites contigua	(Esper, 1794)	Fiji	Syntype	USNM	684	Unaccepted, changed combination	*Psammocora contigua*	Benzoni et al., 2008 (bor)
Porites cribripora	Dana, 1846	Fiji	Holotype	USNM	670	accepted		
Porites crassa	Quelch, 1886	Fiji	Holotype	NHM	1886.12.9.320	taxon inquirendum		
Porites crassistellata	Quelch, 1886	Kadavu, Fiji	Holotype	NHM	1886.12.9.315	taxon inquirendum		
Porites cristagalli	(Ehrenberg, 1834)	Red Sea	-	MNB	-	taxon inquirendum		
Porites cumulatus	Claereboudt, 2006	Gulf of Oman	Not deposited	-	-	nomen nudum		
Porites cumulatus	Nemenzo, 1955	Puerto Galera, Philippines	Holotype	UPZD	UP C-178	accepted		

Porites cylindrica	Dana, 1846	Fiji (11)	Holotype	USNM	708	accepted		
Porites danae	Milne Edwards & Haime, 1851	Fiji	Syntype	USNM	684	Unaccepted, changed combination	*Psammocora contigua*	
*Porites danae**	Studer, 1901* not in this publication	-	-	MNB	-	Unaccepted, homonym, synonym	*Porites rus*	Veron & Pichon 1982
*Porites danai**	Studer, 1901* not in this publication	-	-	MNB	-	Unaccepted, wrong spelling, synonym	*Porites rus*	Veron & Pichon 1982
Porites decasepta	Claereboudt, 2006	Bar Al-Hikman reef, Oman	Holotype	Sultan Qaboos University	SQU05080	accepted		
Porites decipiens	Brüggemann, 1879	Pohnpei Island	-	-	-	taxon inquirendum		
Porites deformis	Nemenzo, 1955	Pinamungajam, Philippines (8)	Holotype	UPZD/MTQ (fragment)	G65860	accepted		
Porites densa	Vaughan, 1918	Murray Island, Australia	Holotype	USNM	47234	accepted		
Porites desilveri	Veron, 2000	Sri Lanka	Holotype	MTQ	G55853	accepted		
Porites discoidea	Studer, 1901	Laysan, Hawaii		NMBE		taxon inquirendum		
Porites divaricata	Le Sueur, 1820	Blue Ground Range, Belize	Neotype	USNM	789920	accepted		

Porites duerdeni	Vaughan, 1907	Kaneohae, Oahu, Hawaii	Holotype	USNM	20954	taxon inquirendum		
Porites echinulata	Klunzinger, 1879	El Qoseir, Egypt, Red Sea	-	MNB	-	accepted		
Porites elongata	Lamarck, 1816	Indian Ocean	-	-	-	taxon inquirendum		
Porites erosa	Dana, 1846	Sulu Sea, Philippines	Holotype	USNM	668	taxon inquirendum		
Porites ericacea	Claereboudt, 2006	Gulf of Oman	Not deposited	-	-	nomen nudum		
Porites eridani	Umbgrove, 1940	Gulf of Tomini, Indonesia	-	-	-	accepted		
Porites evermanni	Vaughan, 1907	Kaneohae, Oahu, Hawaii	Holotype	USMN	21627	accepted		
Porites excavata	Claereboudt, 2006	Gulf of Oman	Not deposited	-	-	nomen nudum, homonym		
Porites excavata	Verrill, 1869	Pearl Island, Gulf of Panama	Syntype	YPM	YPM IZ 001677. CNA	Unaccepted, synonym	*Porites lobata*	Wells 1983
Porites exllis	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	taxon inquirendum		
Porites explanata	Quelch, 1886	Zamboanga, Philippines	Holotype	NHM	1886.12. 9.314	taxon inquirendum		
Porites exserta	Pillai, 1967	Manauli Island, Gulf of	-	-	-	accepted		

		Mannar, India						
Porites farasani	Benzoni & Terraneo, 2019	Farasan Island, Red Sea (1)	Holotype	MNHN	IK-2012-14238	accepted		
Porites faustinoi	Hoffmeister, 1925	Samoa Island	Syntype	USNM	68198, 68201, 85769	Unaccepted, synonym	*Porites rus*	Veron & Hodgson 1989
Porites favosa	Dana, 1846	Fiji	Holotype	USNM	672	taxon inquirendum		
Porites flabelliformis	Le Sueur, 1820	Guadaloupe	Destroyed	-	-	taxon inquirendum		
Porites flavus	Veron, 2000	Milne Bay, Papua New Guinea (9)	Holotype	MTQ	G55830	accepted		
Porites flexuosa	Dana, 1846	Barbados	Type	YPM	YPM IZ 004230. CN	taxon inquirendum		
Porites fontanesii	Benzoni & Stefani, 2012	Balhaf, Yemen (3)	Holotype	MNHN	IK-2009-834	accepted		
Porites fragosa	Dana, 1846	Fiji	Holotype	USNM	643	taxon inquirendum		
Porites furcata	Lamarck, 1816	Western Atlantic	Holotype	MNHN	MNHN 154	accepted		
Porites gaimardi	Milne Edwards & Haime, 1851	Papua New Guinea	Type	MNHN	IK-2010-598, 594	accepted		

Porites galeata	Nemenzo, 1955	Philippines	Holotype	UPZD	UP C-362	Unaccepted, synonym	*Porites cylindrica*	Veron & Hodgson 1989
Porites gabonensis	Gravier, 1910	Gabon	-	-	-	taxon inquirendum, homonym	*Porites bernardi*	Cairns et al., 2008 (bor)
Porites gibsonhilli	Wells, 1950	Cocos-Keeling Islands	Holotype	USNM	44337	taxon inquirendum		
Porites globosa	Nemenzo, 1976	Philippines	Holotype	UPZD	UP C-1400	Unaccepted, synonym	*Porites lobata*	Veron & Hodgson 1989
Porites guadalupensis	Duchassaing & Michelotti, 1860	Guadalupe	-	MRSN	-	Unaccepted, synonym	*Porites astreoides*	Zlatarski & Martinez 1982
Porites haddoni	Vaughan, 1918	Murray Island, Australia	Holotype	USNM	47235	Unaccepted, synonym	*Porites lutea*	Hoffmeister 1925
Porites hadramauti	Benzoni & Terraneo, 2019	Hadramaut, Yemen	Holotype	MNHN	IK-2016-208	accepted		
Porites harrisoni	Veron, 2000	Kuwait (4)	Holotype	MTQ	G55811	accepted		
Porites hawaiiensis	Vaughan, 1907	Kalihi Harbour, Oahu, Hawaii	Holotype	USNM	21624	accepted		
*Porites hentscheli**	Thiel, 1928	West Africa	-	Zoological Museum Hamburg (to verify)	-	Unaccepted, synonym	*Porites astreoides*	Laborel 1974

Porites heronensis	Veron, 1985	Heron Island, Queensland, Australia (10)	Holotype	WAM	162-84	accepted		
*Porites hoffmeisteri**	Faustino, 1927	Philippines	-	-	-	taxon inquirendum		
Porites horizontalata	Hoffmeister, 1925	Pago Pago Harbour, Samoa Island (12)	Syntype	USNM	68202, 68203, 68204	accepted		
Porites informis	Dana, 1846	Fiji	-	-	-	taxon inquirendum		
Porites irregularis	Quelch, 1884	Tahiti	-	NHM	-	taxon inquirendum		
*Porites iwayamaensis**	Eguchi, 1935	Palau	-	-	-	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Porites lanuginosa	Studer, 1901	Laysan, Hawaii	Schizotype	USNM	22233	taxon inquirendum		
Porites latistella	Quelch, 1886	Tahiti	Syntype	NHM	1886.12.9.294 1886.12.9.349 1886.12.9.390	Unaccepted, misspelling	*Porites latistellata*	ICZN 2011
Porites latistellata	Quelch, 1886	Tahiti	Syntype	NHM	1886.12.9.294 1886.12.9.349	accepted		

					1886.12.9.390			
Porites levis	Dana, 1846	Fiji	-	-	-	Unaccepted, synonym	*Porites cylindrica*	Veron & Pichon 1982 (bor)
Porites lichen	(Dana, 1846)	Fiji (11)	Holotype	USNM	666	accepted		
Porites limosa	Dana, 1846	Fiji	Holotype	USNM	673	taxon inquirendum		
Porites lobata	Dana, 1846	Hawaii (13)	Syntype	USNM	646 652	accepted		
Porites lutea	Milne Edwards & Haime, 1851	Tonga (15)	Holotype	MNHN	IK-2010-389	accepted		
Porites macrocephala	Duchassaing & Michelotti, 1864	Antilles	-	MRSN	-	taxon inquirendum		
*Porites mactanensis**	Faustino, 1927	Philippines	-	-	-	taxon inquirendum		
Porites mannarensis	Pillai, 1967	Gulf of Mannar, India	-	-	-	accepted		
Porites mauritiensis	Bernard, 1905	Mauritius	-	NHM	-	taxon inquirendum		
Porites mayeri	Vaughan, 1918	Murray, Island, Australia	Holotype	USNM	47236	accepted		
Porites meandrina	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Montipora meandrina*	Veron &Wallace 1984

Porites minicoiensis	Pillai, 1967	Minicoy Island, India	-	-	-	accepted		
Porites mirabilis	Quelch, 1886	Mactan Island, Philippines	Holotype	NHM	1886.12.301	taxon inquirendum		
Porites monticulosa	Dana, 1846	Fiji (11)	Holotype	USNM	664	accepted		
Porites mordax	Dana, 1846	Hawaii	Holotype	USNM	710	taxon inquirendum		
Porites murrayensis	Vaughan, 1918	Murray Island, Australia	Holotype	USNM	47237	accepted		
Porites myrmidonensis	Veron, 1985	Magdelaine Cay, Coral Sea, Australia	Holotype	WAM	WAM 163-84	accepted		
Porites napopora	Veron, 2000	Western Australia	Holotype	WAM	Z12914	accepted		
Porites negrosensis	Veron, 1990	Negros Island, Philippines (8)	Holotype	MTQ	G32478	accepted		
Porites nigrescens	Dana, 1846	Fiji	Syntype	USNM	690, 691	accepted		
Porites nodifera	Klunzinger, 1879	Red Sea	Holotype	MNB	921	accepted		
Porites nodulosa	Verrill, 1869	La Paz, Mexico, Gulf of California	Syntype	YPM	YPM IZ 006844.CNA	Unaccepted, synonym	*Porites panamensis*	Reyes-Bonilla 2002
Porites okinawensis	Veron, 1990	Japan	Holotype	MTQ	G32495	accepted		

Porites ornata	Nemenzo, 1971	Philippines	Holotype	UPZD	UP C-1108	accepted		
*Porites pacifica**	Brüggemann, 1877* not in this publication			NHM		taxon inquirendum		
Porites palmata	Dana, 1846	Sulu Sea, Philippines	Holotype	USNM	689	accepted		
Porites panamensis	Verrill, 1866	Pearl Island, Gulf of Panama	Syntype	YPM	YPM IZ 000585. CNA	accepted		
Porites parvistellata	Quelch, 1886	Vanuatu	Holotype	NHM	1886.12. 9.318	taxon inquirendum		
Porites paschalensis	Vaughan, 1906	Easter Island	Syntype	USNM	68279	Unaccepted, synonym	*Porites lobata*	Wells 1972
Porites phrygiana	Milne Edwards & Haime, 1851	Unknown	-	-	-	taxon inquirendum		
Porites pistillata	(Esper, 1797)		Not recorded	-	-	Unaccepted, previous combination	*Stylophora pistillata*	Veron & Pichon 1976
Porites planocella	Nemenzo, 1955	Cebu, Philippines	Holotype	UPZD	897A	Unaccepted, synonym	*Porites cylindrica*	Veron & Hodgson 1989
Porites plumieri	Duchassaing & Michelotti, 1866	Antilles	-	MRSN	-	taxon inquirendum		
Porites polymorphus	Link, 1807	Unknown	-	-	-	Unaccepted, synonym	*Porites porites*	Zlatarski & Martinez 1982
Porites porites	(Pallas, 1766)	Antilles	Neotype	MNHN	150	accepted		

Porites porosa	Verrill, 1869	La Paz, Mexico, Gulf of California	Syntype	YPM	YPM IZ 004068. CN	Unaccepted, synonym	*Porites panamensis*	Reyes-Bonilla 2002
Porites profundus	Rehberg, 1892	Nosy Be, Madagascar	-	Hamburg Museum	-	accepted		
Porites pukoensis	Vaughan, 1907	Molokai Island, Hawaii	Paratype	USNM	22236	accepted		
Porites punctata	(Linnaeus, 1758)	Unknown	-	-	-	Unaccepted, previous combination	*Stylaraea punctata*	Veron & Pichon 1982 (bor)
Porites purpurea	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	Unaccepted, synonym	*Porites lichen*	Veron & Pichon 1982
Porites quelchii	Studer, 1901	Molokai, Hawaii	-	MNB	-	taxon inquirendum		
Porites randalli	Forsman & Birkeland, 2009	American Samoa	Holotype	SC	4161	accepted		
Porites recta	Le Sueur, 1820	Saint-Barthélemy, Carribean	Destroyed	-	-	taxon inquirendum		
Porites reticulosa	Dana, 1846	Fiji	Syntype	USNM	662, 663	Unaccepted, synonym	*Porites lichen*	Wells, 1954
Porites reticulum	Ortmann, 1892	Dar es Salaam, Tanzania (6)	lost	-	-	taxon inquirendum		
Porites rosacea	Lamarck, 1816	Indian Ocean	-	-	-	taxon inquirendum		

Porites rugosa	Veron & Fenner, 2000	Indonesia	Holotype	MTQ	G55808	Unaccepted, wrong spelling	*Porites rugosus*	ICZN 2011
Porites rugosus	Fenner & Veron, 2000	Indonesia	Holotype	MTQ	G55808	accepted		
Porites rus	(Forskål, 1775)	Red Sea (1)	Syntype	Zoological Museum of the University of Copenhagen, Denmark	51, 52, 54, 14	accepted		
Porites saccharata	Brüggemann, 1878	Singapore	-	NHM or MNB	-	Unaccepted, synonym	*Porites nigrescens*	Veron & Pichon 1982 (bor)
Porites schauinslandi	Studer, 1901	Laysan, Hawaii	-	MNB	-	taxon inquirendum		
Porites semilunaris	Nemenzo, 1976	Sumilon Island, Phillipines	Syntype	UPZD	SU D-70, SU D-125	Unaccepted, synonym	*Porites vaughani*	Veron & Pichon 1982
Porites sillimaniana	Nemenzo, 1976	Sumilon Island, Phillipines (8)	Holotype	UPZD	SU D-78	accepted		
Porites solanderi	Duchassaing & Michelotti, 1861	Antilles	-	MRSN	-	taxon inquirendum		
Porites solida	(Forskål, 1775)	Red Sea (1)	Holotype	Zoological Museum of the University of Copenha	17	accepted		

				gen, Denmark				
Porites somaliensis	Gravier, 1910	Djibouti (2)	-	-	-	accepted		
Porites spongiosa	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Montipora spongiosa*	Veron & Wallace 1984
Porites spumosa	Lamarck, 1816	Unknown	-	-	-		*Montipora spumosa*	Veron & Wallace 1984 (bor)
Porites stephensoni	Crossland, 1952	Great Barrier Reef, Australia	Syntype	NHM	1434.5.14.235, 1434.5.14.233	accepted		
Porites stilosa	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Montipora stilosa*	
Porites studeri	Vaughan, 1907	Hawaii	Holotype	USNM	21623	taxon inquirendum		
Porites subdigitata	Lamarck, 1816	Indian Ocean	-	-	-	Unaccepted synonym	*Stylophora pistillata*	Veron & Pichon 1976
Porites subseriata	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, new combination, basionym	*Stylophora subseriata*	Milne Edwards & Haime, 1857
Porites superfusa	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	accepted		

Porites suppressa	Crossland, 1952	Great Barrier Reef, Australia	Holotype	NHM	731	Unaccepted, synonym	*Porites nigrescens*	Veron & Pichon 1982 (bor)
Porites sverdrupi	Durham, 1947	Carmen Island, Mexico	Holotype	USNM	M547362	accepted		
Porites tenuis	Verrill, 1866	Ryukyu Island, Japan	Holotype	USNM	407	Unaccepted, synonym	*Porites lutea*	Scheer & Pillai 1983
Porites trimurata	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	taxon inquirendum		
Porites tuberculosa	Lamarck, 1816	Australia (not verified)	-	-	-	Unaccepted, original combination, basionym	*Montipora tuberculosa*	
Porites tuberculosa	Veron, 2000	Indonesia	Holotype	MTQ	G55804	Unaccepted, wrong spellig	*Porites tuberculosus*	ICZN 2011
Porites tuberculosus	Veron, 2000	Indonesia	Holotype	MTQ	G55804	accepted		
Porites tumida	Brüggemann, 1879	Pohnpei Island	-	MNB	-	taxon inquirendum		
Porites umbellifera	Gardiner, 1898	Funafuti, Tuvalu	-	NHM	-	taxon inquirendum		
Porites undulata	(Verrill, 1864)	Red Sea	-	NHM	-	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Porites vaughani	Crossland, 1952	Great Barrier Reef, Australia (10)	Holotype	NHM	1934.5.14.491A	accepted		

Porites venosa	(Ehrenberg, 1834)	Red Sea	-	MNB	-	Unaccepted, changed combination	*Montipora venosa*	Veron & Wallace 1984
Porites verrillii	Rehberg, 1892	Abrolhos reefs, Brazil	Holotype	YPM	YPM IZ 004539	Unaccepted, synonym	*Porites astreoides*	Laborel 1967
Porites verrucosa	Lamarck, 1816		-	-	-	Unaccepted, original combination, basionym	*Montipora verrucosa*	Veron & Wallace 1984 (bor)
Porites violetae	Nemenzo, 1955	Puerto Galerea, Philippines	Holotype	UPZD/ MTQ (fragment)	G65861 / UP 1345	Unaccepted, synonym	*Porites deformis*	Veron & Hodgson 1989
Porites viridis	Gardiner, 1898	Solkope Island, Fiji	-	NHM	-	Unaccepted, synonym	*Porites lichen*	Veron & Pichon 1982
Synaraea	Verrill 1864		-	-	-	Unaccepted, synonym	*Porites*	
Synaraea convexa	(Verrill, 1864)	Society Islands, French Polynesia	Type	NHM	1886.12. 9.509	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Synaraea faustinoi	Hoffmeister, 1925	Samoa Island	Syntype	USNM	68198, 68201, 85769	Unaccepted, synonym	*Porites rus*	Veron & Hodgson, 1989
Synaraea irregularis	(Verrill, 1864)	Hawaii	Syntype	MCZ	SCOR-1059 SCOR-1060	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982

Synaraea iwayamaensis	(Eguchi, 1935)	Palau	-	-	-	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Synaraea monticulosa	Dana, 1846	Fiji	Holotype	USNM	664	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982
Synaraea undulata	(Klunzinger, 1879)	Koseir, Egypt, Red Sea	Type	MNHN	16-4151	Unaccepted, synonym	*Porites rus*	Veron & Pichon 1982

Museum Abbreviations

AMNH = American Museum of Natural History, New York, USA

MNB = Museum für Naturkunde, Berlin, Germany

NMBE = Naturhistorisches Museum Bern, Swtizerland

MCZ = Museum of Comparative Zoology, Harvard, USA

MNHN = Muséum National d' Histoire Naturelle, Paris, France

MRSN = Museo Regionale di Scienze Naturali, Torino, Italy

MTQ = Museum of Tropical Queensland, Townsville, QLD, Australia

NHM = Natural History Museum, London, UK

WAM = Western Australian Museum, Perth Australia

UPZD = University of the Philippines Zoology Department, Quezon City, Phiilippines

USNM = Smithsonian National Museum of Natural History, Washington D.C., USA

YPM = Yale Paabody Museum of Natural History, Yale, USA

SC = Bishop Museum, Ohau, Hawaii

SMF = Forschungsinstitut Senckenberg, Senckenberg Museum, Frankfurt, Germany

SU = Silliman University Marine Laboratory, Dumanguete City, Philippines

Appendix 2.1 List of coral specimens examined in the present study. For each sample, voucher number, species identification based on morphology, sampling locality and body of water (Locality), collector, and latitude and longitude (GPS) are provided. FB is Francesca Benzoni, TIT is Tullia Isotta Terraneo, RA is Roberto Arrigoni, JB is Jessica Bouwmeester, DC is Darren Coker, MT is Matthew Tietbhol, MLB is Michael L Berumen, AM is Alison Monroe

Voucher number	Species	Locality	Collector	GPS
AD30	*Porites* sp 9	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD32	*Porites annae*	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD33	*Porites annae*	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD49	*Porites* sp 9	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD57	*Porites columnaris*	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD58	*Porites rus*	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD6	*Porites columnaris*	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AD60	*Porites* sp 9	Aden, Yemen - Gulf of Aden	FB	12.751, 45.027
AU076	*Porites* sp 8	Solitary Islands, Australia	FB	-29.677, 153.518
AU092	*Porites* sp 8	Solitary Islands, Australia	FB	-30.128, 153.500
AU096	*Porites* sp 8	Solitary Islands, Australia	FB	-30.128, 153.500
AU099	*Porites* sp 8	Solitary Islands, Australia	FB	-30.128, 153.500
AU106	*Porites* sp 8	Solitary Islands, Australia	FB	-28.095, 153.483
AU114	*Porites* sp 8	Solitary Islands, Australia	FB	-28.095, 153.483
AU128	*Porites* sp 8	Solitary Islands, Australia	FB	-31.537, 159.308
AU140	-	Lord Howe Island, Australia	FB	-31.612, 159.2
AU165	*Porites lichen*	Lord Howe Island, Australia	FB	-31.629, 159.309

AU167	*Porites lichen*	Lord Howe Island, Australia	FB	-31.629, 159.309
AU195	*Porites lichen*	Lord Howe Island, Australia	FB	-31.516, 159.278
AU222	-	Lord Howe Island, Australia	FB	-31.693, 159.168
AU238	*Porites lichen*	Lord Howe Island, Australia	FB	-31.81, 159.271
AU43	*Porites* sp 8	Solitary Islands, Australia	FB	-30.322, 153.518
AU68	*Porites* sp 8	Solitary Islands, Australia	FB	-30.322, 153.518
AU73	*Porites* sp 8	Solitary Islands, Australia	FB	-30.322, 153.518
AU75	*Porites* sp 8	Solitary Islands, Australia	FB	-30.322, 153.518
BA109	*Porites rus*	Bir Ali, Yemen – Gulf of Aden	FB	13.929, 48.386
BA135	*Porites* sp 9	Bir Ali, Yemen – Gulf of Aden	FB	13.929, 48.386
BA74	*Porites lutea*	Bir Ali, Yemen – Gulf of Aden	FB	13.929, 48.386
BA87	*Porites columnaris*	Bir Ali, Yemen – Gulf of Aden	FB	13.929, 48.386
BA98	*Porites lutea*	Bir Ali, Yemen – Gulf of Aden	FB	13.929, 48.386
BU38	*Porites* sp 9	Burum, Yemen – Gulf of Aden	FB	14.307, 48.967
BU70	*Porites hadramauti*	Burum, Yemen – Gulf of Aden	FB	14.307, 48.967
DJ134	*Porites fontanesii*	Musha, Djibouti – Gulf of Tadjoura	FB	11.743, 43.168
DJ179	*Porites annae*	Musha, Djibouti – Gulf of Tadjoura	FB	11.704, 43.219
DJ200	*Porites rus*	Ankali, Djibouti – Gulf of Tadjoura	FB	11.726, 43.326
DJ228	*Porites annae*	Obock, Djibouti – Gulf of Tadjoura	FB	11.967, 43.313
DJ29	*Porites columnaris*	Ras Ali, Djibouti – Gulf of Tadjoura	FB	11.772, 42.954
DJ3	*Porites rus*	Ras Douan, Djibouti – Gulf of Tadjoura	FB	11.788, 42.967

DJ30	*Porites fontanesii*	Ras Ali, Djibouti – Gulf of Tadjoura	FB	11.772, 42.954
DJ306	*Porites solida*	Parrot Island, Djibouti – Gulf of Tadjoura	FB	11.493, 42.571
DJ5	*Porites solida*	Ras Douan, Djibouti – Gulf of Tadjoura	FB	11.788, 42.967
DJ63	*Porites lobata*	Oblal, Djibouti, Djibouti – Gulf of Tadjoura	FB	11.861, 43.108
DJ75	*Porites* sp 4	Oblal, Djibouti, Djibouti – Gulf of Tadjoura	FB	11.811, 43.057
DJ76	*Porites somaliensis*	Oblal, Djibouti – Gulf of Tadjoura	FB	11.811, 43.057
DJ78	*Porites columnaris*	Oblal, Djibouti – Gulf of Tadjoura	FB	11.811, 43.057
DJ79	*Porites fontanesii*	Oblal, Djibouti – Gulf of Tadjoura	FB	11.811, 43.057
DJ80	*Porites annae*	Oblal, Djibouti – Gulf of Tadjoura	FB	11.811, 43.057
DJ89	*Porites solida*	Kalaf, Djibouti – Gulf of Tadjoura	FB	11.729, 42.773
DJ90	*Porites rus*	Kalaf, Djibouti – Gulf of Tadjoura	FB	11.729, 42.773
DJ91	*Porites rus*	Kalaf, Djibouti – Gulf of Tadjoura	FB	11.729, 42.773
DJ92	*Porites solida*	Kalaf, Djibouti – Gulf of Tadjoura	FB	11.729, 42.773
DJ93	*Porites lutea*	Kalaf, Djibouti – Gulf of Tadjoura	FB	11.729, 42.773
GA140	-	Gambier	FB	-23.103, -134.989
GA34	-	Gambier	FB	-23.185, -134.925
HS3342	-	New Caledonia	FB	-21.668, 167.858
HS3373	*Porites flavus*	New Caledonia	FB	-21.512, 168.162
HS3397	*Porites lichen*	New Caledonia	FB	-21.154, 168.013
HS3449	*Porites monticulosa*	New Caledonia	FB	-20.925, 167.228
HS3585	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.638, 167.466

HS3597	*Porites* sp 1	Île de Pins, New Caledonia	TIT	-22.672, 167.241
HS3598	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.672, 167.241
HS3600	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.672, 167.241
HS3602	*Porites cylindrica*	Île de Pins, New Caledonia	TIT	-22.672, 167.241
HS3603	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.672, 167.241
HS3611	*Porites* sp 12	Île de Pins, New Caledonia	FB	-22.759, 167.701
HS3612	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3615	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3616	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3617	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3618	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3620	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3621	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3622	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.759, 167.701
HS3629	*Porites lichen*	Île de Pins, New Caledonia	FB	-22.717, 167.514
HS3630	*Porites* sp 12	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3631	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3632	*Porites cylindrica*	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3635	*Porites cylindrica*	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3636	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3637	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.717, 167.514

HS3638	*Porites* sp 12	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3639	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.717, 167.514
HS3640	*Porites* sp 7	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3641	*Porites* sp 7	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3645	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3646	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3648	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3649	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3650	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.588, 167.721
HS3651	*Porites flavus*	Île de Pins, New Caledonia	FB	-22.588, 167.721
HS3660	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.669, 167.568
HS3662	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.669, 167.568
HS3664	*Porites solida*	Île de Pins, New Caledonia	TIT	-22.669, 167.568
HS3676	*Porites flavus*	Île de Pins, New Caledonia	FB	-22.771, 167.454
HS3687	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.771, 167.454
HS3693	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.771, 167.454
HS3694	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.771, 167.454
HS3698	*Porites cylindrica*	Île de Pins, New Caledonia	FB	-22.780, 167.480
HS3700	*Porites lichen*	Île de Pins, New Caledonia	FB	-22.780, 167.480
HS3707	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.780, 167.480
HS3709	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.780, 167.480

HS3710	*Porites cylindrica*	Île de Pins, New Caledonia	TIT	-22.780, 167.480
HS3711	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.780, 167.480
HS3712	*Porites cylindrica*	Île de Pins, New Caledonia	TIT	-22.780, 167.480
HS3713	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.931, 167.606
HS3715	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.931, 167.606
HS3716	*Porites* sp 7	Île de Pins, New Caledonia	TIT	-22.931, 167.606
HS3717	*Porites lichen*	Île de Pins, New Caledonia	TIT	-22.931, 167.606
HS3723	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.699, 167.484
HS3724	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.699, 167.484
HS3725	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.699, 167.484
HS3750	*Porites* sp 2	Île de Pins, New Caledonia	FB	-22.678, 167.392
HS3755	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.678, 167.392
HS3761	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.678, 167.392
HS3763	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.678, 167.392
HS3764	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.678, 167.392
HS3766	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.678, 167.392
HS3794	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.852, 167.463
HS3796	*Porites lobata*	Île de Pins, New Caledonia	TIT	-22.852, 167.463
HS3799	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.852, 167.463
HS3800	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.852, 167.463
HS3801	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.852, 167.463

HS3808	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.668, 167.438
HS3810	*Porites lobata*	Île de Pins, New Caledonia	TIT	-22.668, 167.438
HS3811	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.668, 167.438
HS3815	*Porites lobata*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3816	*Porites australiensis*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3817	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3818	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3819	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3820	*Porites lobata*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3821	*Porites* cf *lobata*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3823	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3824	*Porites flavus*	Île de Pins, New Caledonia	TIT	-22.822, 167.453
HS3832	*Porites* sp 2	Île de Pins, New Caledonia	FB	-22.822, 167.453
HS3835	*Porites lutea*	Île de Pins, New Caledonia	TIT	-22.686, 167.445
HS3840	*Porites* sp 3	Île de Pins, New Caledonia	FB	-22.686, 167.445
HS3847	*Porites solida*	Île de Pins, New Caledonia	TIT	-22.538, 167.471
HS3848	*Porites solida*	Île de Pins, New Caledonia	TIT	-22.538, 167.471
HS3860	*Porites deformis*	Île de Pins, New Caledonia	FB	-22.721, 167.558
HS3863	*Porites deformis*	Île de Pins, New Caledonia	TIT	-22.721, 167.558
HS3864	*Porites deformis*	Île de Pins, New Caledonia	TIT	-22.721, 167.558
HS3866	*Porites deformis*	Île de Pins, New Caledonia	TIT	-22.721, 167.558

HS3867	*Porites deformis*	Île de Pins, New Caledonia	TIT	-22.721, 167.558
HS3872	*Porites* sp 7	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3873	*Porites* sp 7	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3874	*Porites* sp 7	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3875	*Porites monticulosa*	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3876	*Porites cylindrica*	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3877	*Porites cylindrica*	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3879	*Porites cylindrica*	Île Ouen, New Caledonia	TIT	-22.549, 167.077
HS3890	*Porites lichen*	Île Ouen, New Caledonia	FB	-22.572, 167.037
HS3892	*Porites lichen*	Île Ouen, New Caledonia	FB	-22.572, 167.037
HS3894	*Porites rus*	Île Ouen, New Caledonia	TIT	-22.572, 167.037
HS3895	*Porites rus*	Île Ouen, New Caledonia	TIT	-22.572, 167.037
HS3929	*Porites cylindrica*	Île Ouen, New Caledonia	TIT	-22.626, 166.875
HS3963	*Porites solida*	Bampton North East, New Caledonia	FB	-18.947833, 158.754167
HS3978	*Porites flavus*	Ilot Reynard, New Caledonia	FB	-19.947833, 158.9468
HS3979	*Porites* sp 8	Ilot Reynard, New Caledonia	FB	-19.947833, 158.9468
HS3980	*Porites lobata*	Ilot Reynard, New Caledonia	FB	-19.947833, 158.9468
HS3981	*Porites lutea*	Ilot Reynard, New Caledonia	FB	-19.947833, 158.9468
HS3982	*Porites lichen*	Ilot Reynard, New Caledonia	FB	-19.947833, 158.9468
HS4012	*Porites* sp 8	Caye Skeleton, New Caledonia	FB	-19.437583, 158.912033
HS4013	*Porites solida*	Caye Skeleton, New Caledonia	FB	-19.437583, 158.912033

HS4014	*Porites flavus*	Caye Skeleton, New Caledonia	FB	-19.437583, 158.912033
HS4024	*Porites lichen*	Caye Skeleton, New Caledonia	FB	-19.437583, 158.912033
HS4037	*Porites flavus*	Îlots du Mouillage, New Caledonia	FB	-19.975, 158.590
HS4038	*Porites lichen*	Îlots du Mouillage, New Caledonia	FB	-19.975, 158.590
HS4039	*Porites annae*	Les trios llots du Mouillage, New Caledonia	FB	-19.8105, 158.44275
HS4041	*Porites* sp 7	Les trios llots du Mouillage, New Caledonia	FB	-19.8105, 158.44275
HS4078	*Porites solida*	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4079	*Porites lichen*	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4082	*Porites annae*	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4084	*Porites* sp 7	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4092	*Porites* sp 7	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4093	*Porites* sp 2	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4097	*Porites* sp 8	Olry Reef, New Caledonia	FB	-21.641, 159.661
HS4098	*Porites columnaris*	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4104	*Porites cf tuberculosus*	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4105	*Porites flavus*	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4106	*Porites lichen*	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4107	*Porites cf lichen*	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4108	*Porites* sp 7	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4109	*Porites flavus*	Bellona Reef, New Caledonia	FB	-21.882, 159.597

HS4112	*Porites* sp 7	Bellona Reef, New Caledonia	FB	-21.882, 159.597
HS4127	*Porites cf tuberculosus*	Millieu Reef, New Caledonia	FB	-21.43935, 159.01585
HS4138	*Porites* sp 7	North-West Reef, New Caledonia	FB	-20.43935, 158.470283
HS4149	*Porites lichen*	Ilot du Passage, New Caledonia	FB	-19.910317, 158.361867
HS4152	*Porites lutea*	Ilot du Passage, New Caledonia	FB	19.910317, 158.361867
HS4154	*Porites lutea*	Ilot du Passage, New Caledonia	FB	19.910317, 158.361867
HS4155	*Porites lutea*	Ilot du Passage, New Caledonia	FB	19.910317, 158.361867
HS4170	*Porites cf columnaris*	Ilot Loop, New Caledonia	FB	19.910317, 158.361867
HS4182	*Porites* sp 7	Îlots du Mouillage New Caledonia	FB	-19.975, 158.590
HS4191	*Porites* sp 8	Îlot Avon, New Caledonia	FB	-19.840, 158.265
HS4193	*Porites* sp 8	Îlot Avon, New Caledonia	FB	-19.840, 158.265
HS4196	*Porites lichen*	Îlot Avon, New Caledonia	FB	-19.840, 158.265
HS4198	*Porites cf australiensis*	Îlot Avon, New Caledonia	FB	-19.840, 158.265
HS4234	*Porites lichen*	New Caledonia	TIT	-21.951, 166.773
HS4235	*Porites lobata*	New Caledonia	TIT	-21.951, 166.773
HS4236	*Porites* sp 1	New Caledonia	TIT	-21.951, 166.773
HS4239	*Porites lichen*	New Caledonia	TIT	-22.114, 166.805
HS4240	*Porites lichen*	New Caledonia	TIT	-22.114, 166.805
HS4242	*Porites lichen*	New Caledonia	TIT	-22.356, 166.825
HS4243	*Porites* cf *horizontalata*	New Caledonia	TIT	-22.356, 166.825
HS4244	*Porites cylindrica*	New Caledonia	TIT	-22.356, 166.825

HS4255	*Porites* sp 3	New Caledonia	TIT	-18.267, 162.969
HS4256	*Porites tuberculosus*	New Caledonia	TIT	-18.267, 162.969
KA103	*Porites annae*	TiqfashIsland, Yemen – Red Sea	FB	15.700, 42.386
MA246	*Porites rus*	Mayotte Island	F. Seguin	-
MA487	*Porites rus*	Mayotte Island	FB	-13.079, 46.791
MD004	*Porites profundus*	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD005	*Porites profundus*	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD006	*Porites* sp 6	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD007	*Porites monticulosa*	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD102	*Porites lobata*	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD103	*Porites rus*	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD104	*Porites somaliensis*	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD105	*Porites* sp 4	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD106	*Porites lobata*	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD107	-	Baie Andovobazaha, Diego Suarez, Madagascar	FB	-12.271, 49.341
MD118	*Porites columnaris*	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD12	*Porites* sp 6	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD120	*Porites profundus*	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD121	*Porites profundus*	Nosy Hara, Madagascar	FB	-12.242, 49.017

MD136	*Porites profundus*	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD137	-	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD138	*Porites* sp 10	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD140	*Porites lobata*	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD142	*Porites columnaris*	Nosy Hara, Madagascar	FB	-12.242, 49.017
MD146	*Porites* sp 5	Nosy Hao, Madagascar	FB	-12.097, 49.034
MD147	*Porites columnaris*	Nosy Hao, Madagascar	FB	-12.097, 49.034
MD151	*Porites cf lutea*	Nosy Hao, Madagascar	FB	-12.097, 49.034
MD162	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.882, 48.547
MD163	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.882, 48.547
MD165	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.882, 48.547
MD166	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.882, 48.547
MD167	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.882, 48.547
MD207	*Porites* cf *reticulum*	Nosy Mitsio, Madagascar	FB	-12.934, 48.536
MD22	*Porites columnaris*	Île aux Nattes, Madagascar	FB	-17.119, 49.819
MD231	*Porites rus*	Nosy Ovy, Madagascar	FB	-13.977, 47.776
MD248	*Porites* sp 10	Nosy Antaiamora, Madagascar	FB	-14.111, 47.680
MD25	*Porites* sp 5	Île aux Nattes, Madagascar	FB	-17.134, 49.790
MD253	*Porites* sp 10	Nosy Antaiamora, Madagascar	FB	-14.111, 47.680
MD254	*Porites* sp 10	Nosy Antaiamora, Madagascar	FB	-14.111, 47.680
MD255	*Porites* cf *horizontalata*	Nosy Antaiamora, Madagascar	FB	-14.111, 47.680

MD256	*Porites* cf *horizontalata*	Nosy Antaiamora, Madagascar	FB	-14.111, 47.680
MD26	*Porites profundus*	Île aux Nattes, Madagascar	FB	-17.134, 49.790
MD27	*Porites lutea*	Île aux Nattes, Madagascar	FB	-17.134, 49.790
MD49	*Porites* cf *lutea*	Île Sainte Marie, Madagascar	FB	-16.873, 49.885
MD66	*Porites* sp 6	Cap Masoala, Madagascar	FB	-16.013, 50.151
MD68	*Porites* sp 6	Cap Masoala, Madagascar	FB	-16.013, 50.151
MD69	*Porites lobata*	Cap Masoala, Madagascar	FB	-16.013, 50.151
MQ135	-	Marquesas Islands	FB	-10.496, -138.678
MQ150	*Porites arnaudi*	Marquesas Islands	FB	-10.458, -138.672
MQ16	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.251
MQ163	*Porites arnaudi*	Marquesas Islands	FB	-9.888, -139.078
MQ164	*Porites arnaudi*	Marquesas Islands	FB	-9.888, -139.078
MQ168	*Porites* cf *hawaiiensis*	Marquesas Islands	FB	-9.890, -139.075
MQ17	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.251
MQ170	*Porites arnaudi*	Marquesas Islands	FB	-9.890, -139.075
MQ178	*Porites* cf *hawaiiensis*	Marquesas Islands	FB	-9.836, -139.118
MQ18	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.251
MQ183	*Porites* cf *hawaiiensis*	Marquesas Islands	FB	-9.790, -139.157
MQ30	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.248

MQ31	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.248
MQ32	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.248
MQ52	*Porites arnaudi*	Marquesas Islands	FB	-8.820, -140.248
MQ6	*Porites arnaudi*	Marquesas Islands	FB	-8.929, -140.226
MQ82	*Porites arnaudi*	Marquesas Islands	FB	-7.896, -140.562
MQ94	*Porites arnaudi*	Marquesas Islands	FB	-7.955, -140.661
MY104	*Porites* sp 11	Mayotte Island	FB	-13.079, 45.301
MY113	*Porites rus*	Mayotte Island	FB	-13.037, 45.121
MY115	*Porites monticulosa*	Mayotte Island	FB	-13.037, 45.121
MY116	*Porites profundus*	Mayotte Island	FB	-13.037, 45.121
MY117	*Porites lutea*	Mayotte Island	FB	-13.037, 45.121
MY118	*Porites* sp 5	Mayotte Island	FB	-13.037, 45.121
MY128	*Porites solida*	Mayotte Island	FB	-13.015, 45.498
MY162	*Porites lichen*	Mayotte Island	FB	-13.135, 45.414
MY170	-	Mayotte Island	FB	-12.825, 45.198
MY172	-	Mayotte Island	FB	-12.825, 45.198
MY177	-	Mayotte Island	FB	-12.937, 45.273
MY182	-	Mayotte Island	FB	-12.815, 45.322
MY185	*Porites rus*	Mayotte Island	FB	-12.815, 45.322
MY194	-	Mayotte Island	FB	-12.815, 45.322
MY20	*Porites rus*	Mayotte Island	FB	-12.832, 45.371

MY206	-	Mayotte Island	FB	-12.8, 45.352
MY209	-	Mayotte Island	FB	-12.8, 45.352
MY21	*Porites rus*	Mayotte Island	FB	-12.832, 45.371
MY214	-	Mayotte Island	FB	-12.605, 45.003
MY22	*Porites cylindrica*	Mayotte Island	FB	-12.832, 45.371
MY220	-	Mayotte Island	FB	-12.737, 45.105
MY23	*Porites* cf *horizontalata*	Mayotte Island	FB	-12.832, 45.371
MY249	*Porites profundus*	Mayotte Island	FB	-12.832, 44.994
MY274	*Porites lutea*	Mayotte Island	FB	-13.021, 45.172
MY275	*Porites solida*	Mayotte Island	FB	-13.021, 45.172
MY276	-	Mayotte Island	FB	-13.021, 45.172
MY285	-	Mayotte Island	FB	-13.154, 45.225
MY291	-	Mayotte Island	FB	-13.154, 45.225
MY292	-	Mayotte Island	FB	-13.154, 45.225
MY309	*Porites rus*	Mayotte Island	FB	-13.093, 45.358
MY317	-	Mayotte Island	FB	-13.093, 45.358
MY324	-	Mayotte Island	FB	-12.864, 45.333
MY37	-	Mayotte Island	FB	-12.726, 45.246
MY58	*Porites lutea*	Mayotte Island	FB	-12.609, 45.093
MY75	-	Mayotte Island	FB	-12.722, 45.122
MY80	-	Mayotte Island	FB	-12.722, 45.122

MY86	*Porites* cf *lobata*	Mayotte Island	FB	-12.809, 45.178
MY99	*Porites* sp 5	Mayotte Island	FB	-13.079, 45.291
P1	*Porites* sp 4	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P10	*Porites lobata*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P12	*Porites solida*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P13	*Porites columnaris*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P14	*Porites somaliensis*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P15	*Porites* sp 4	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P16	*Porites solida*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P17	*Porites* sp 9	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P2	*Porites solida*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P4	*Porites solida*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P5	*Porites somaliensis*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P6	*Porites* sp 4	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
P9	*Porites columnaris*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.175
PFB283	*Porites negrosensis*	Papua New Guinea	FB	-5.222, 146.073
PFB284	*Porites lichen*	Papua New Guinea	FB	-5.222, 146.073
PFB285	*Porites lichen*	Papua New Guinea	FB	-5.222, 146.073
PFB295	*Porites monticulosa*	Papua New Guinea	FB	-5.081, 145.826
PFB354	-	Papua New Guinea	FB	-5.106, 145.814
PFB375	*Porites tuberculosus*	Papua New Guinea	FB	-5.111, 145.822

PFB462	*Porites negrosensis*	Papua New Guinea	FB	-2.641, 150.772
PFB479	*Porites lichen*	Papua New Guinea	FB	-2.641, 150.772
PFB490	*Porites cylindrica*	Papua New Guinea	FB	-2.623, 150.793
PFB496	*Porites negrosensis*	Papua New Guinea	FB	-2.623, 150.793
PFB673	*Porites monticulosa*	Papua New Guinea	FB	-2.753, 150.719
PFB674	*Porites tuberculosus*	Papua New Guinea	FB	-2.753, 150.719
PFB676	*Porites* cf *horizontalata*	Papua New Guinea	FB	-2.753, 150.719
PFB679	*Porites cylindrica*	Papua New Guinea	FB	-2.753, 150.719
PFB689	*Porites lichen*	Papua New Guinea	FB	-2.753, 150.719
PFB695	*Porites columnaris*	Papua New Guinea	FB	-2.753, 150.719
PFB697	*Porites tuberculosus*	Papua New Guinea	FB	-2.753, 150.719
QA1	*Porites harrisoni*	Fasht al Udayd, Qatar – Arabian Gulf	JB	24.779, 51.767
QA104	*Porites harrisoni*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA105	*Porites harrisoni*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA17	*Porites lutea*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA5	*Porites harrisoni*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA6	*Porites harrisoni*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA60	*Porites harrisoni*	Maydan Mahzam, Qatar – Arabian Gulf	JB	25.507, 52.516
QA69	*Porites harrisoni*	Maydan Mahzam, Qatar – Arabian Gulf	JB	25.507, 52.516
QA7	*Porites harrisoni*	Fasht al Dibal, Qatar – Arabian Gulf	JB	26.276, 50.980
QA91	*Porites lutea*	Bulhambar, Qatar – Arabian Gulf	JB	25.969, 51.877

SA1028	*Porites columnaris*	Aqaba, Saudi Arabia – Red Sea	FB	28.403, 34.740
SA12	*Porites fontanesii*	Farasan Banks, Saudi Arabia – Red Sea	FB	19.570, 40.008
SA1444	*Porites rus*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1448	*Porites solida*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1449	*Porites lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1488	*Porites* cf *lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1490	*Porites solida*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1491	*Porites lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA1493	*Porites lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.770, 42.464
SA150	*Porites fontanesii*	Farasan Banks, Saudi Arabia – Red Sea	FB	18.220, 41.324
SA151	*Porites lutea*	Farasan Banks, Saudi Arabia – Red Sea	FB	18.220, 41.324
SA1516	*Porites farasani*	Farasan Islands, Saudi Arabia – Red Sea	FB	17.110, 42.067
SA1574	*Porites lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	17.467, 41.787
SA1581	*Porites* sp 9	Farasan Islands, Saudi Arabia – Red Sea	FB	17.467, 41.787
SA1609	*Porites lobata*	Farasan Islands, Saudi Arabia – Red Sea	FB	17.467, 41.787
SA1612	*Porites lobata*	Farasan Islands, Saudi Arabia – Red Sea	FB	17.467, 41.787
SA1647	*Porites lobata*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.978, 41.384
SA1703	*Porites lutea*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.872, 41.440
SA1704	*Porites columnaris*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.872, 41.440
SA1705	*Porites solida*	Farasan Islands, Saudi Arabia – Red Sea	FB	16.872, 41.440

SA172	*Porites farasani*	Farasan Banks, Saudi Arabia – Red Sea	FB	18.220, 41.324
SA180	*Porites farasani*	Farasan Banks, Saudi Arabia – Red Sea	FB	18.220, 41.324
SA2080	*Porites columnaris*	Yanbu, Saudi Arabia – Red Sea	TIT	24.101, 38.009
SA2136	*Porites solida*	Yanbu, Saudi Arabia – Red Sea	TIT	24.101, 38.009
SA2148	*Porites annae*	Yanbu, Saudi Arabia – Red Sea	TIT	24.021, 37.969
SA2163	*Porites lutea*	Yanbu, Saudi Arabia – Red Sea	TIT	24.021, 37.969
SA2195	*Porites luteea*	Yanbu, Saudi Arabia – Red Sea	TIT	24.021, 37.969
SA2196	*Porites monticulosa*	Yanbu, Saudi Arabia – Red Sea	TIT	24.021, 37.969
SA2332	*Porites annae*	Al Wajh, Saudi Arabia – Red Sea	MT	25.345, 36.891
SA2432	*Porites lutea*	Al Wajh, Saudi Arabia – Red Sea	FB	25.345, 36.891
SA308	*Porites monticulosa*	Farasan Islands, Saudi Arabia – Red Sea	FB	18.281, 41.445
SA309	*Porites annae*	Farasan Islands, Saudi Arabia – Red Sea	FB	18.281, 41.445
SA310	*Porites fontanesii*	Farasan Islands, Saudi Arabia – Red Sea	FB	18.281, 41.445
SA363	*Porites lutea*	Thuwal, Saudi Arabia – Red Sea	FB	22.607, 38.918
SA383	*Porites monticulosa*	Thuwal, Saudi Arabia – Red Sea	FB	22.607, 38.918
SA388	*Porites lutea*	Thuwal, Saudi Arabia – Red Sea	FB	22.607, 38.918
SA389	*Porites lutea*	Thuwal, Saudi Arabia – Red Sea	FB	22.607, 38.918
SA438	*Porites fontanesii*	Thuwal, Saudi Arabia – Red Sea	FB	22.426, 38.996
SA55	*Porites somaliensis*	Farasan Banks, Saudi Arabia – Red Sea	FB	19.005, 40.148
SA57	*Porites monticulosa*	Farasan Banks, Saudi Arabia – Red Sea	FB	19.005, 40.148
SA771	*Porites rus*	Duba, Saudi Arabia – Red Sea	FB	27.638, 35.306

SA876	*Porites annae*	Duba, Saudi Arabia – Red Sea	FB	27.905, 35.059
SA92	*Porites lobata*	Farasan Banks, Saudi Arabia – Red Sea	FB	18.659, 40.826
SA970	*Porites columnaris*	Aqaba, Saudi Arabia – Red Sea	FB	28.403, 34.740
SI111	-	Singapore	RA	1.1682, 103.7458
SI112	-	Singapore	RA	1.1682, 103.7458
SI113	*Porites monticulosa*	Singapore	RA	1.1682, 103.7458
SI114	*Porites* cf *horizontalata*	Singapore	RA	1.1682, 103.7458
SI115	*Porites* sp 11	Singapore	RA	1.1682, 103.7458
SI116	*Porites* sp 11	Singapore	RA	1.1682, 103.7458
SI117	*Porites rus*	Singapore	RA	1.1682, 103.7458
SI118	*Porites* sp 11	Singapore	RA	1.1682, 103.7458
SI119	*Porites* sp 11	Singapore	RA	1.1682, 103.7458
SI23	-	Singapore	RA	1.2488, 103.7304
SI29	*Porites lutea*	Singapore	RA	1.232, 103.8627
SI3	-	Singapore	RA	1.2488, 103.7304
SI30	*Porites* sp 11	Singapore	RA	1.232, 103.8627
SI31	*Porites* sp 11	Singapore	RA	1.232, 103.8627
SI32	*Porites* sp 11	Singapore	RA	1.232, 103.8627
SI33	*Porites* sp 11	Singapore	RA	1.232, 103.8627
SI35	*Porites rus*	Singapore	RA	1.232, 103.8627
SI36	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627

SI37	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI38	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI4	-	Singapore	RA	1.2488, 103.7304
SI5	-	Singapore	RA	1.2488, 103.7304
SI53	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI6	-	Singapore	RA	1.2488, 103.7304
SI68	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI69	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI71	*NO PIC*	Singapore	RA	1.232, 103.8627
SI72	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI73	*Porites* cf *horizontalata*	Singapore	RA	1.232, 103.8627
SI74	*Porites* sp 11	Singapore	RA	1.232, 103.8627
SI75	*Porites lutea*	Singapore	RA	1.232, 103.8627
SI78	*Porites cylindrica*	Singapore	RA	1.232, 103.8627
SI79	*Porites cylindrica*	Singapore	RA	1.232, 103.8627
SO114	*Porites fontanesii*	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433
SO120	*Porites* sp 3	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433
SO140	*Porites* cf *annae*	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433
SO154	*Porites* cf *reticulum*	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433
SO155	*Porites lutea*	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433
SO156	*Porites solida*	Socotra Island, Yemen – Gulf of Aden	FB	12.582, 54.433

TAU001	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU003	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU004	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU005	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU006	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU007	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU008	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU009	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5214, 159.0468
TAU013	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5390, 159.0654
TAU014	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5390, 159.0654
TAU015	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5390, 159.0654
TAU016	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5390, 159.0654
TAU017	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5305, 159.0534
TAU018	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5305, 159.0534
TAU019	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5305, 159.0534
TAU020	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5305, 159.0534
TAU023	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5425, 159.0618
TAU024	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5425, 159.0618
TAU025	*Porites heronensis*	Lord Howe Island, Australia	TIT	-31.5425, 159.0618
TAU034	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.4874, 159.0719
TAU037	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.4987, 159.0659

TAU038	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.4987, 159.0659
TAU039	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.4987, 159.0659
TAU041	*Porites lichen*	Lord Howe Island, Australia	TIT	-31.5665, 159.1016
TAU043	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.5665, 159.1016
TAU044	*Porites* sp 8	Lord Howe Island, Australia	TIT	-31.5665, 159.1016
TAU046	*Porites* lichen	Lord Howe Island, Australia	TIT	-31.5665, 159.1016
TAU047	*Porites* sp 1	Lord Howe Island, Australia	TIT	-31.5738, 159.0597
TAU049	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU051	*Porites lichen*	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU056	*Porites lutea*	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU058	*Porites flavus*	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU059	*Porites* lichen	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU060	*Porites lutea*	Great Barrier Reef, Australia	TIT	-18.748, 147.54
TAU061	*Porites lutea*	Great Barrier Reef, Australia	TIT	-18.742, 147.51
TAU063	*Porites lutea*	Great Barrier Reef, Australia	TIT	-18.742, 147.51
TAU066	*Porites lichen*	Great Barrier Reef, Australia	TIT	-18.742, 147.51
TAU068	*Porites lichen*	Great Barrier Reef, Australia	TIT	-18.742, 147.51
TAU070	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-18.742, 147.51
TAU071	*Porites lobata*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU072	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU073	*Porites australiensis*	Great Barrier Reef, Australia	TIT	-18.49, 146.88

TAU075	*Porites tuberculosus*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU077	*Porites tuberculosus*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU078	*Porites lichen*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU079	*Porites lobata*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU080	*Porites lichen*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU081	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU082	*Porites rus*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU083	*Porites rus*	Great Barrier Reef, Australia	TIT	-18.49, 146.88
TAU086	*Porites* sp 8	Great Barrier Reef, Australia	TIT	-17.096, 146.2
TAU087	*Porites lichen*	Great Barrier Reef, Australia	TIT	-17.096, 146.2
TAU090	*Porites lichen*	Great Barrier Reef, Australia	TIT	-17.096, 146.2
TAU091	*Porites lutea*	Great Barrier Reef, Australia	TIT	-17.096, 146.2
TAU093	*Porites australiensis*	Great Barrier Reef, Australia	TIT	-17.062, 146.18
TAU094	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-17.062, 146.18
TAU096	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-17.062, 146.18
TAU100	*Porites lichen*	Great Barrier Reef, Australia	TIT	-17.062, 146.18
TAU101	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-16.713, 145.98
TAU102	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-16.713, 145.98
TAU105	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-16.713, 145.98
TAU106	*Porites* cf lobata	Great Barrier Reef, Australia	TIT	-16.713, 145.98
TAU107	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-16.713, 145.98

TAU109	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU110	*Porites lichen*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU112	*Porites rus*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU115	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU116	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU117	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU118	*Porites lutea*	Great Barrier Reef, Australia	TIT	-15.91, 145.66
TAU123	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-15.409, 145.79
TAU125	*Porites lutea*	Great Barrier Reef, Australia	TIT	-15.409, 145.79
TAU131	*Porites solida*	Great Barrier Reef, Australia	TIT	-15.017, 145.7
TAU134	*Porites lobata*	Great Barrier Reef, Australia	TIT	-15.017, 145.7
TAU141	*Porites columnaris*	Great Barrier Reef, Australia	TIT	-14.992, 145.7
TAU143	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-14.992, 145.7
TAU144	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-14.992, 145.7
TAU145	*Porites neegrosensis*	Great Barrier Reef, Australia	TIT	-14.6596, 145.4533
TAU146	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-14.6596, 145.4533
TAU147	*Porites lutea*	Great Barrier Reef, Australia	TIT	-14.6596, 145.4533
TAU149	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-14.6596, 145.4533
TAU154	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-14.6245, 145.4533
TAU155	*Porites australiensis*	Great Barrier Reef, Australia	TIT	-14.6245, 145.4533
TAU156	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-14.6162, 145.6175

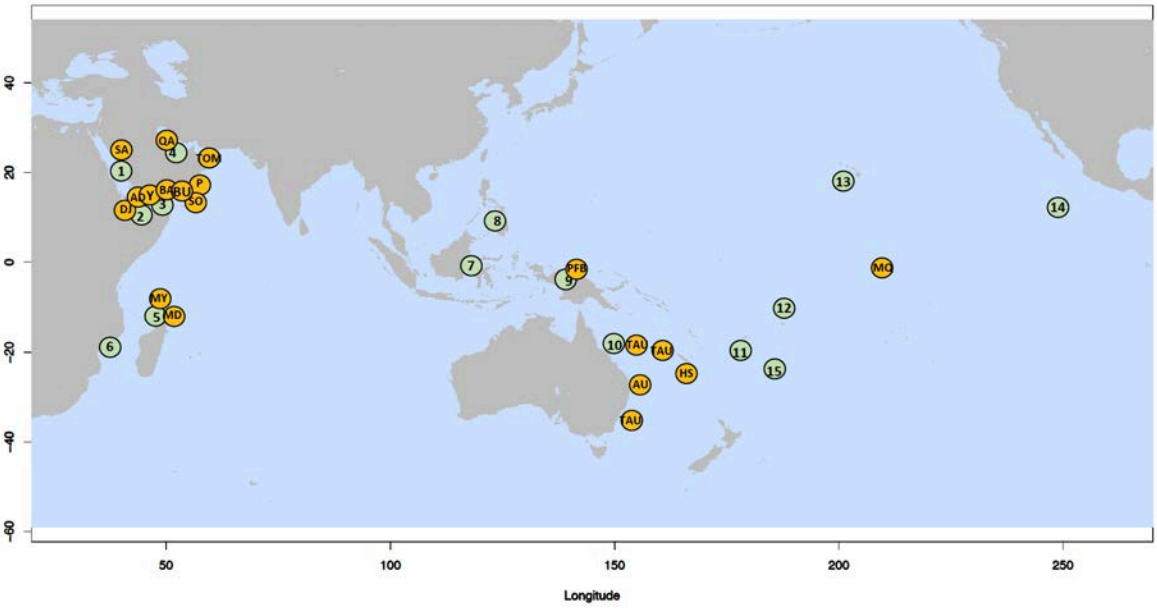
TAU158	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-14.6162, 145.6175
TAU161	*Porites tuberculosus*	Great Barrier Reef, Australia	TIT	-14.6162, 145.6175
TAU168	*Porites columnaris*	Great Barrier Reef, Australia	TIT	-14.4875, 145.6175
TAU171	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-14.4711, 145.5230
TAU172	*Porites lichen*	Great Barrier Reef, Australia	TIT	-14.4711, 145.5230
TAU175	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-14.4678, 145.4753
TAU179	*Porites lobata*	Great Barrier Reef, Australia	TIT	-14.3700, 144.7756
TAU180	*Porites rus*	Great Barrier Reef, Australia	TIT	-14.3700, 144.7756
TAU182	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-14.3483, 144.7362
TAU189	*Porites tuberculosus*	Great Barrier Reef, Australia	TIT	-14.3483, 144.7362
TAU191	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-14.3483, 144.7362
TAU197	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-13.8989, 144.0174
TAU207	*Porites sillimaniana*	Great Barrier Reef, Australia	TIT	-12.7693, 143.6022
TAU209	*Porites lutea*	Great Barrier Reef, Australia	TIT	-12.7693, 143.6022
TAU213	*Porites lichen*	Great Barrier Reef, Australia	TIT	-12.7643, 143.6063
TAU214	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-12.7643, 143.6063
TAU218	*Porites lutea*	Great Barrier Reef, Australia	TIT	-12.3489, 143.8040
TAU220	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-12.3489, 143.8040
TAU221	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-12.3489, 143.8040
TAU222	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-12.3259, 143.8464
TAU223	*Porites* cf *horizontalata*	Great Barrier Reef, Australia	TIT	-12.3259, 143.8464

TAU225	*Porites lichen*	Great Barrier Reef, Australia	TIT	-12.3259, 143.8464
TAU227	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-12.3271, 143.8659
TAU228	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-12.1361, 143.8074
TAU229	*Porites lichen*	Great Barrier Reef, Australia	TIT	-11.9924, 143.8959
TAU230	*Porites lichen*	Great Barrier Reef, Australia	TIT	-11.9924, 143.8959
TAU231	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-11.9924, 143.8959
TAU232	*Porites* cf *lobata*	Great Barrier Reef, Australia	TIT	-11.9924, 143.8959
TAU234	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-11.9672, 143.8754
TAU235	*Porites sillimaniana*	Great Barrier Reef, Australia	TIT	-11.9565, 143.8613
TAU236	*Porites monticulosa*	Great Barrier Reef, Australia	TIT	-11.9565, 143.8613
TAU237	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-11.9565, 143.8613
TAU240	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-11.8116, 143.8676
TAU241	*Porites sillimaniana*	Great Barrier Reef, Australia	TIT	-11.8116, 143.8676
TAU243	*Porites vaughani*	Great Barrier Reef, Australia	TIT	-11.8116, 143.8676
TAU247	*Porites rus*	Great Barrier Reef, Australia	TIT	-11.8127, 143.8695
TAU248	*Porites tuberculosus*	Great Barrier Reef, Australia	TIT	-11.8132, 143.9826
TAU250	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-11.7706, 143.9843
TAU251	*Porites negrosensis*	Great Barrier Reef, Australia	TIT	-11.7706, 143.9843
TAU252	*Porites lutea*	Great Barrier Reef, Australia	TIT	-11.7706, 143.9843
TAU253	*Porites lobata*	Great Barrier Reef, Australia	TIT	-11.7706, 143.9843
TAU255	*Porites cylindrica*	Great Barrier Reef, Australia	TIT	-11.7706, 143.9843

TAU264	*Porites sillimaniana*	Great Barrier Reef, Australia	TIT	-10.5685, 143.2454
TAU273	*Porites australiensis*	Great Barrier Reef, Australia	TIT	-9.3354, 142.7237
TAU274	*Porites cylindrica*	Coral Sea, Australia	TIT	-
TAU275	*Porites solida*	Coral Sea, Australia	TIT	-
TAU277	*Porites lutea*	Coral Sea, Australia	TIT	-
TAU279	*Porites monticulosa*	Coral Sea, Australia	TIT	-
TAU280	*Porites australiensis*	Coral Sea, Australia	TIT	-
TAU281	*Porites tuberculosus*	Coral Sea, Australia	TIT	-
TAU283	*Porites flavus*	Coral Sea, Australia	TIT	-
TAU286	*Porites monticulosa*	Coral Sea, Australia	TIT	-
TAU287	*Porites* sp 2	Coral Sea, Australia	TIT	-
TAU288	*Porites lichen*	Coral Sea, Australia	TIT	-
TAU289	*Porites australiensis*	Coral Sea, Australia	TIT	-
TAU292	*Porites tuberculosus*	Coral Sea, Australia	TIT	-
TAU295	*Porites tuberculosus*	Coral Sea, Australia	TIT	-
TAU296	*Porites* cf *australiensis*	Coral Sea, Australia	TIT	-
TAU297	*Porites flavus*	Coral Sea, Australia	TIT	-
TAU299	*Porites flavus*	Coral Sea, Australia	TIT	-
TAU302	*Porites flavus*	Coral Sea, Australia	TIT	-
TAU304	*Porites tubreculosus*	Coral Sea, Australia	TIT	-
TAU305	*Porites flavus*	Coral Sea, Australia	TIT	-
TAU309	*Porites lutea*	Coral Sea, Australia	TIT	-
TAU310	*Porites tuberculosus*	Coral Sea, Australia	TIT	-
TAU311	*Porites* cf *lobata*	Coral Sea, Australia	TIT	-
TAU313	*Porites flavus*	Coral Sea, Australia	TIT	-

TOM14	*Porites annae*	Banda Khayran, Oman – Gulf of Oman	DC	23.522, 58.740
TOM15	*Porites lutea*	Banda Khayran, Oman – Gulf of Oman	DC	23.522, 58.740
TOM18	*Porites lutea*	Banda Khayran, Oman – Gulf of Oman	DC	23.522, 58.740
TOM2	*Porites* sp 4	Fahal, Oman – Gulf of Oman	DC	23.678, 58.501
TOM3	*Porites* sp 4	Fahal, Oman – Gulf of Oman	DC	23.678, 58.501
Y359	*Porites fontanesii*	Balhaf, Yemen – Gulf of Aden	FB	13.969, 48.182
Y360	*Porites fontanesii*	Balhaf, Yemen – Gulf of Aden	FB	13.969, 48.182
Y694	*Porites annae*	Balhaf, Yemen – Gulf of Aden	FB	13.971, 48.205
Y719	*Porites annae*	Balhaf, Yemen – Gulf of Aden	FB	13.972, 48.194
Y734	*Porites rus*	Balhaf, Yemen – Gulf of Aden	FB	13.980, 48.176
Y747	*Porites columnaris*	Balhaf, Yemen – Gulf of Aden	FB	13.973, 48.175
Y760	*Porites columnaris*	Balhaf, Yemen – Gulf of Aden	FB	13.969, 48.178

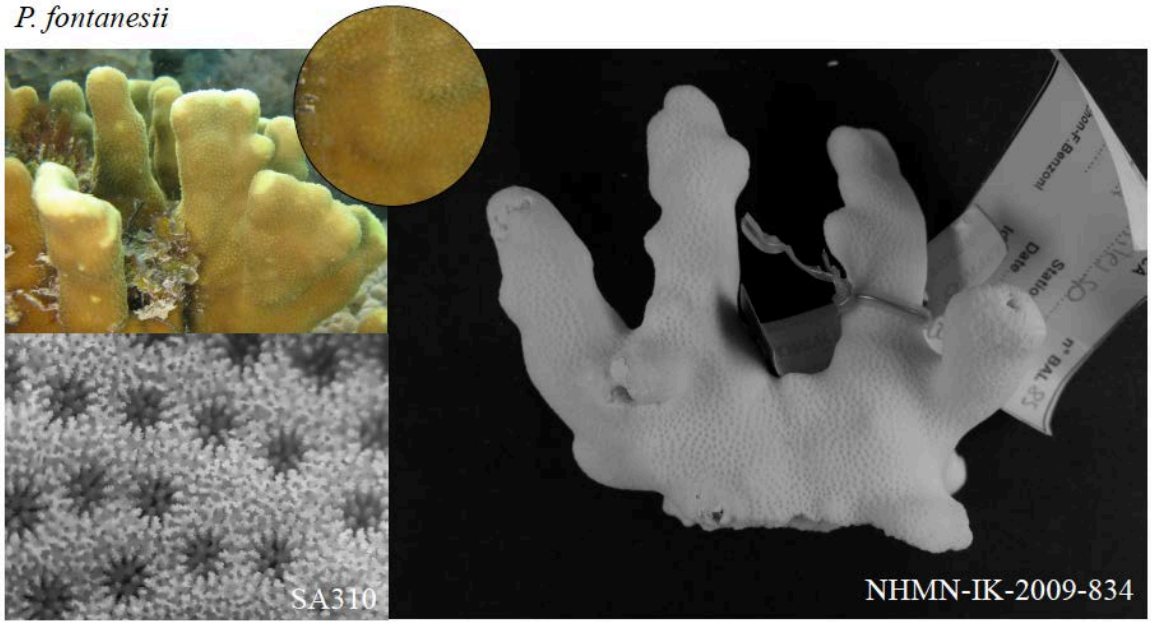
Appendix 2.2 Map showing type localities (numbered dots) of the examined nominal species and sampling localities (yellow circles) of the specimens collected for this study (Appendix 1.1). Code for sampling localities: SA = Saudi Arabia; DJ = Djibouti; AD = Aden; Y = Yemen; BA = Bir ali-Yemen; BU = Burum-Yemen; SO = Socotra Island-Yemen; P = Balhaf-Yemen; TOM = Gulf of Oman; QA = Qatar MY = Mayotte Island; MD = Madagascar; PFB = Papua New Guinea; TAU = Eastern-Australia (Great Barrier Reef, Coral Sea, Lord Howe Island); AU = Solitary Islands; HS = New Caledonia; MQ = Marquesas Islands. Numbers in the stars refer to type localities in Appendix 1.1.



Appendix 2.3 Images of each nominal species recovered in this study. For each species we reported: (a) an *in situ* image of a typical morphology with a close up; (b) a zoom in of the dry skeletal stuctures of the same specimen; when available (c) the species holotype with a close up

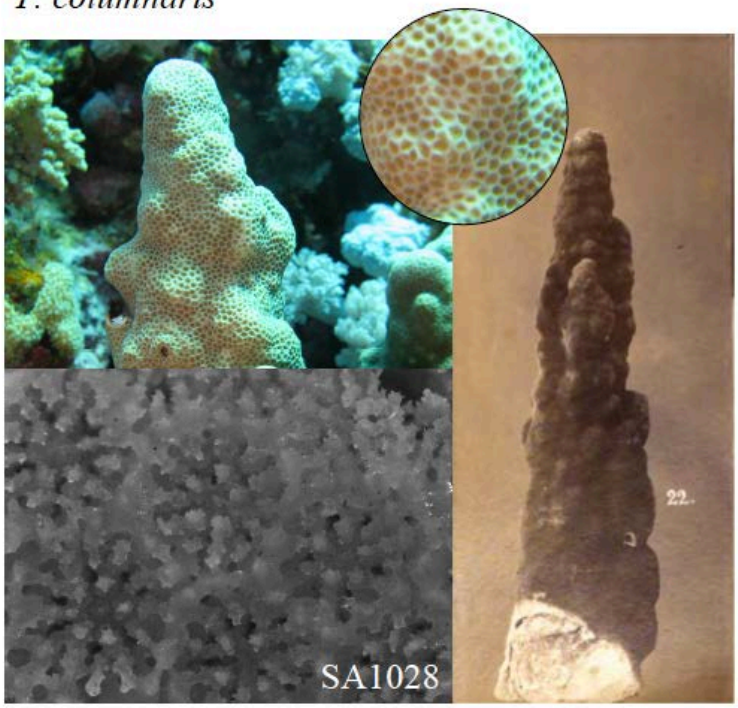
CLADE I

P. fontanesii

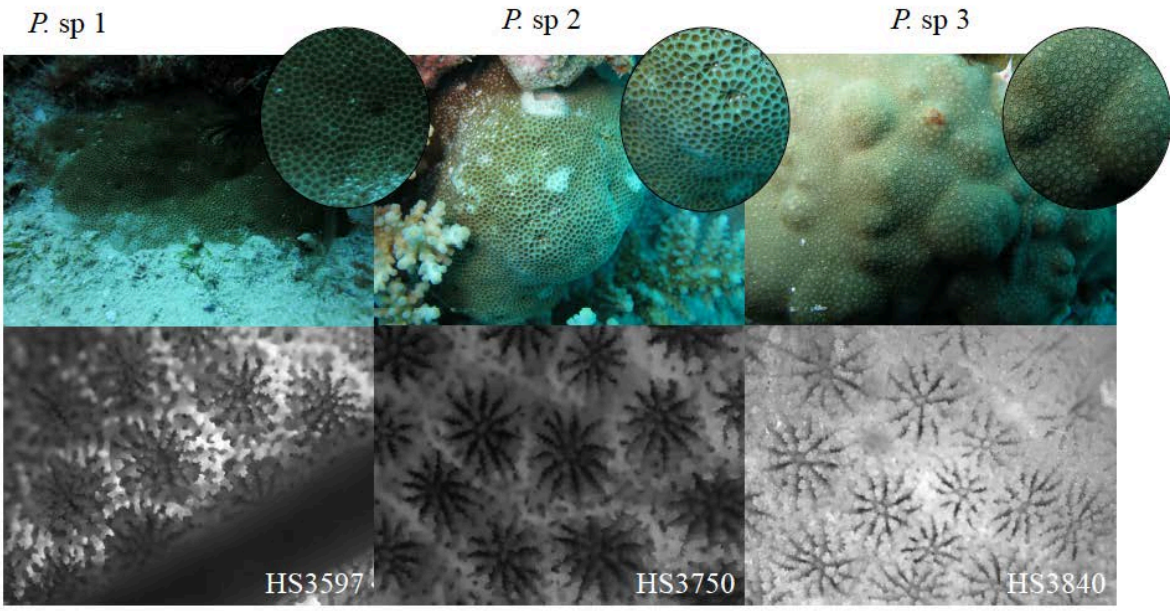


CLADE II

P. columnaris

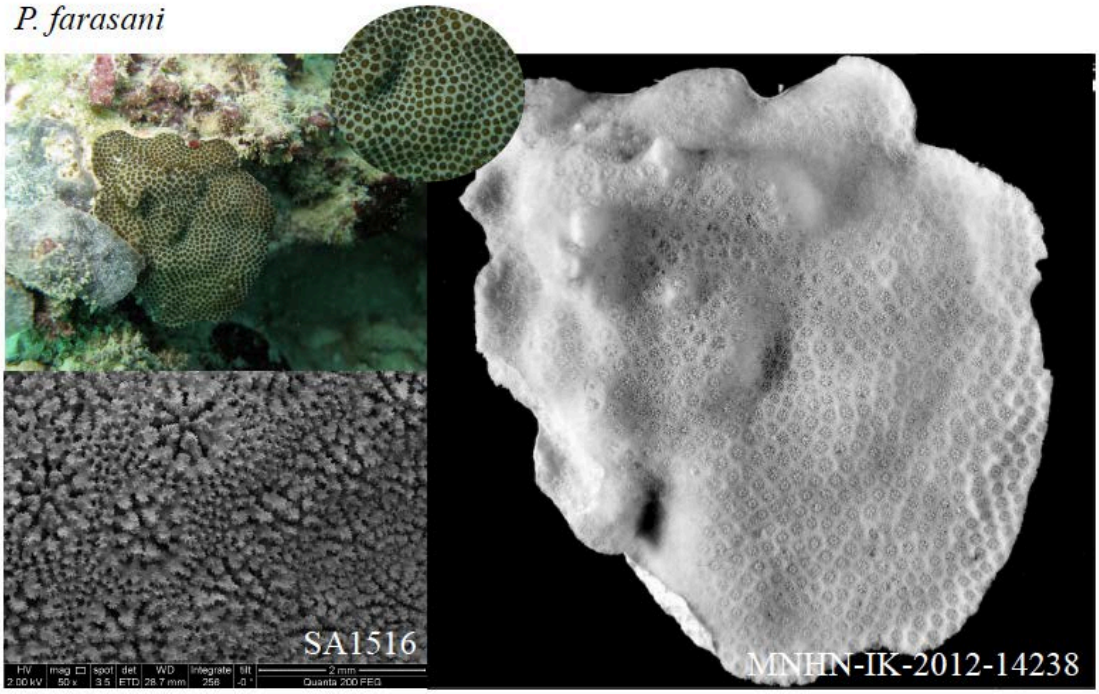


CLADE II



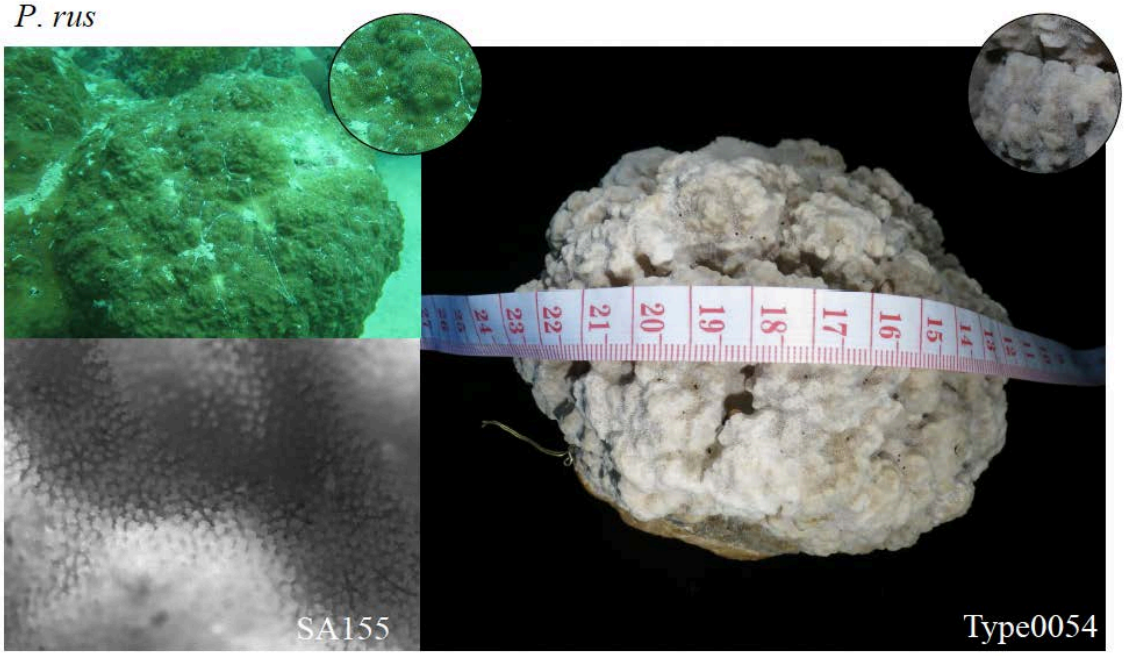
CLADE III

P. farasani



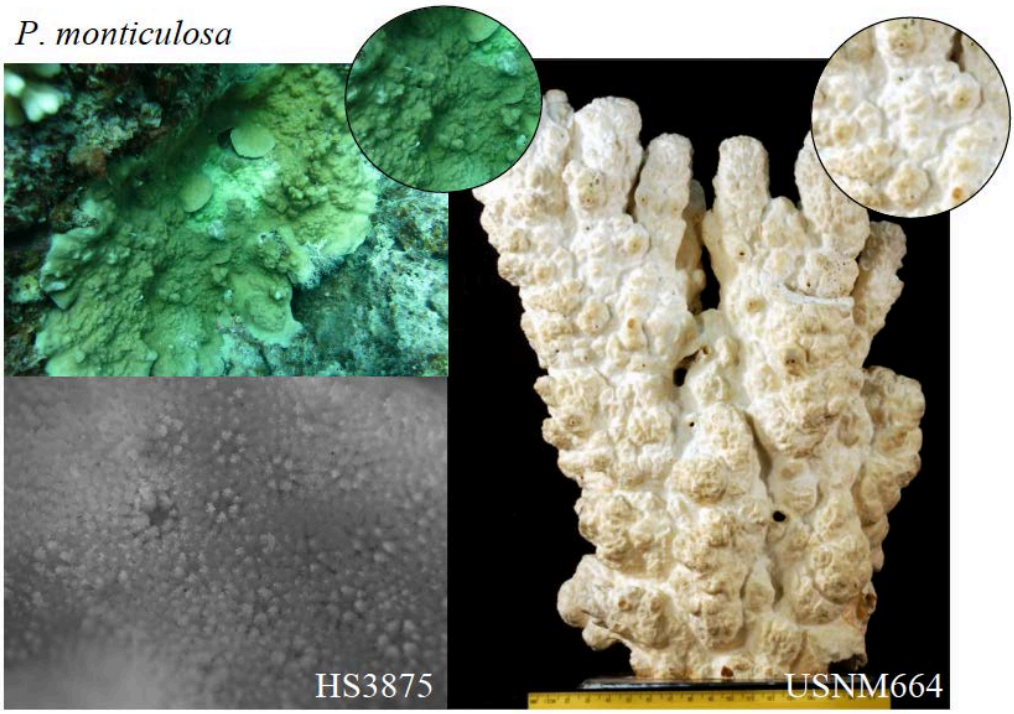
CLADE IV

P. rus

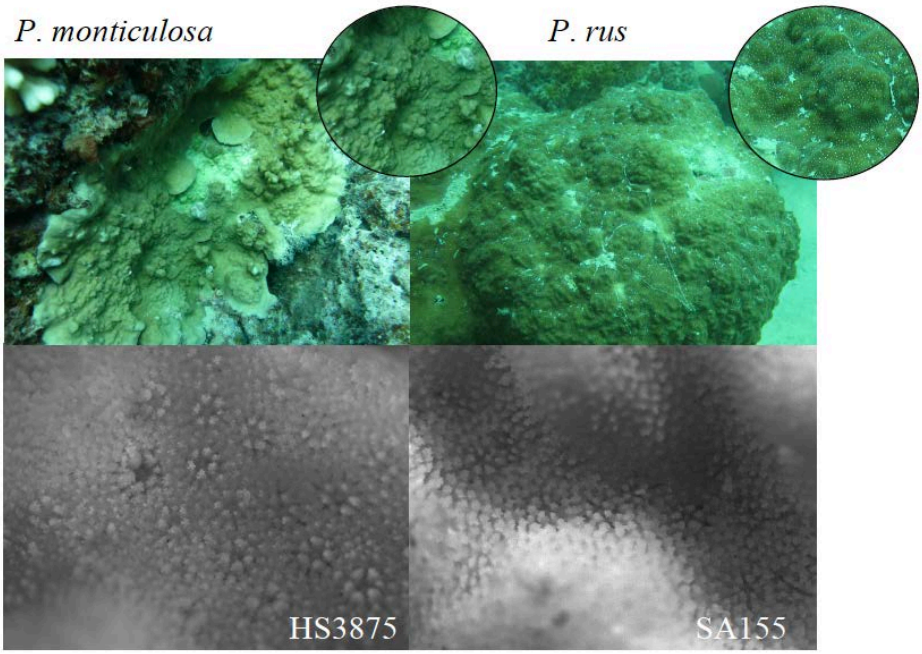


CLADE IV

P. monticulosa

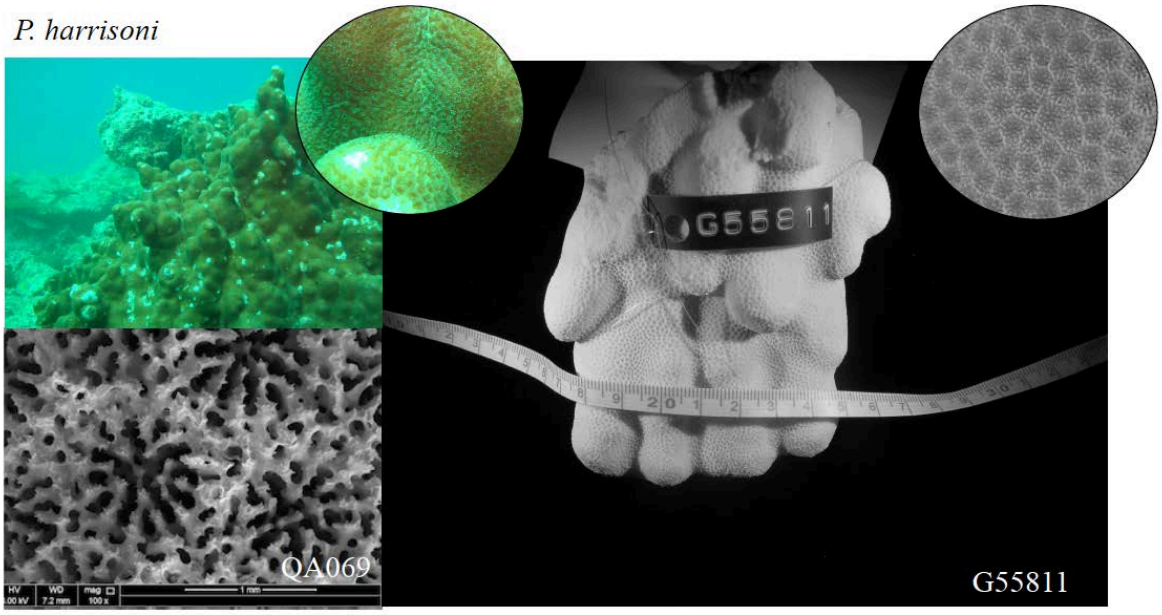


CLADE IV



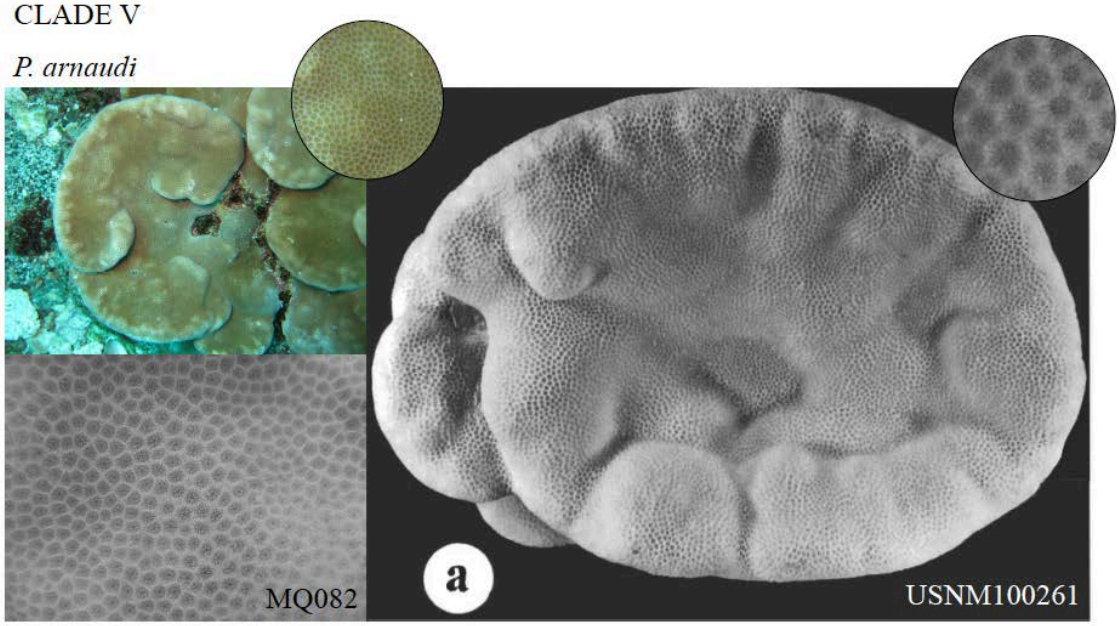
CLADE V

P. harrisoni



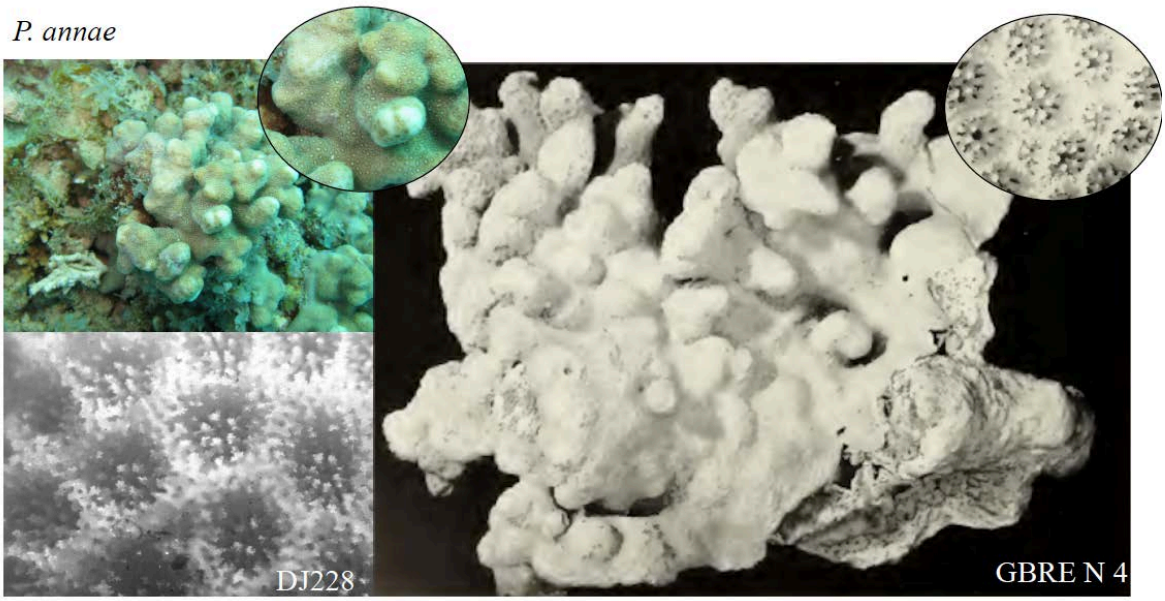
CLADE V

P. arnaudi



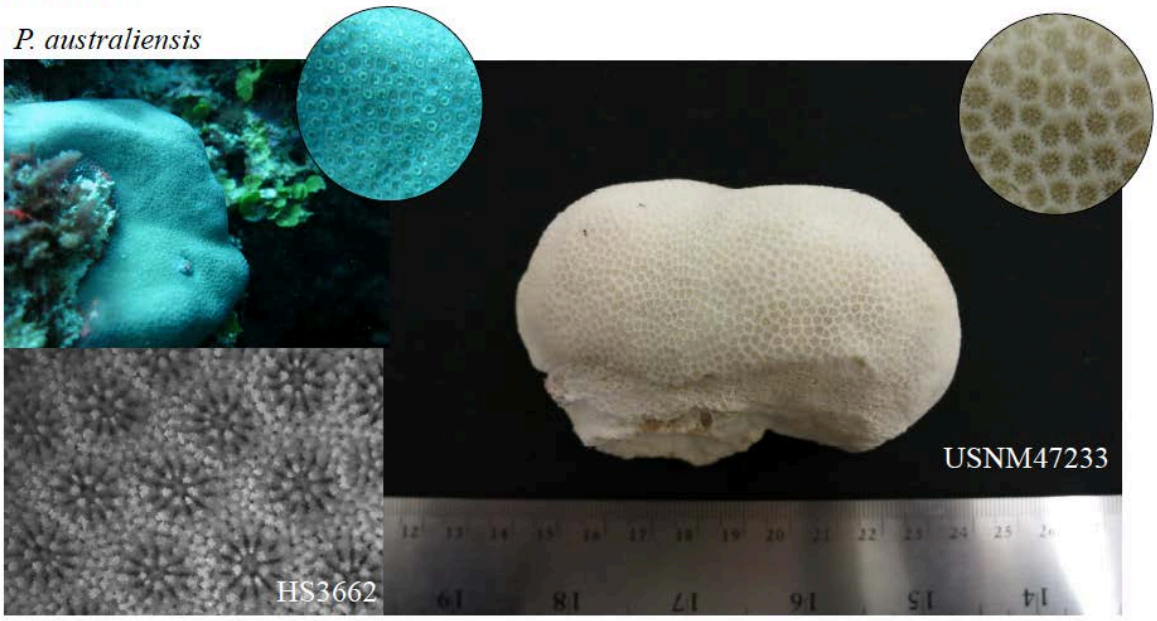
CLADE V

P. annae



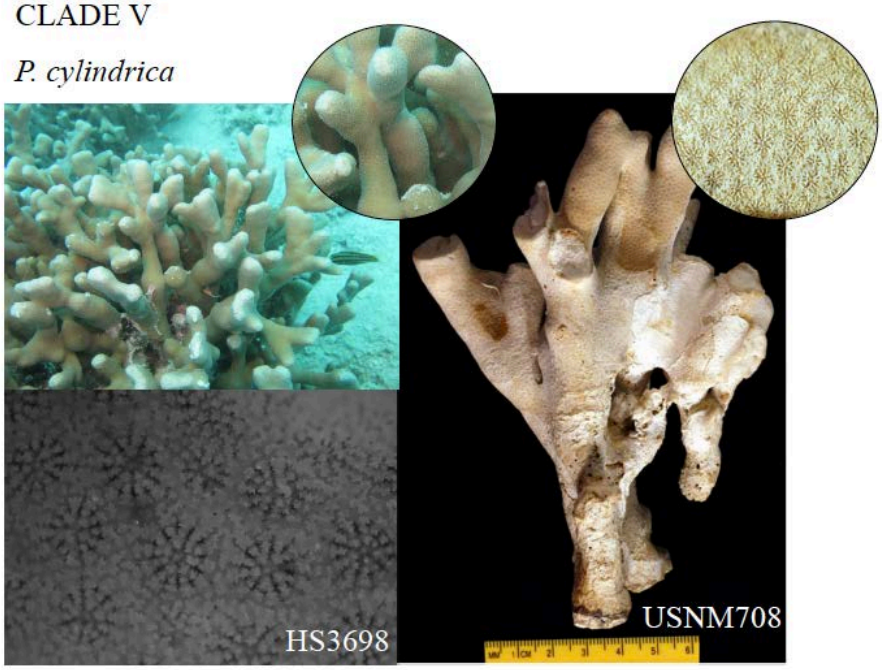
CLADE V

P. australiensis



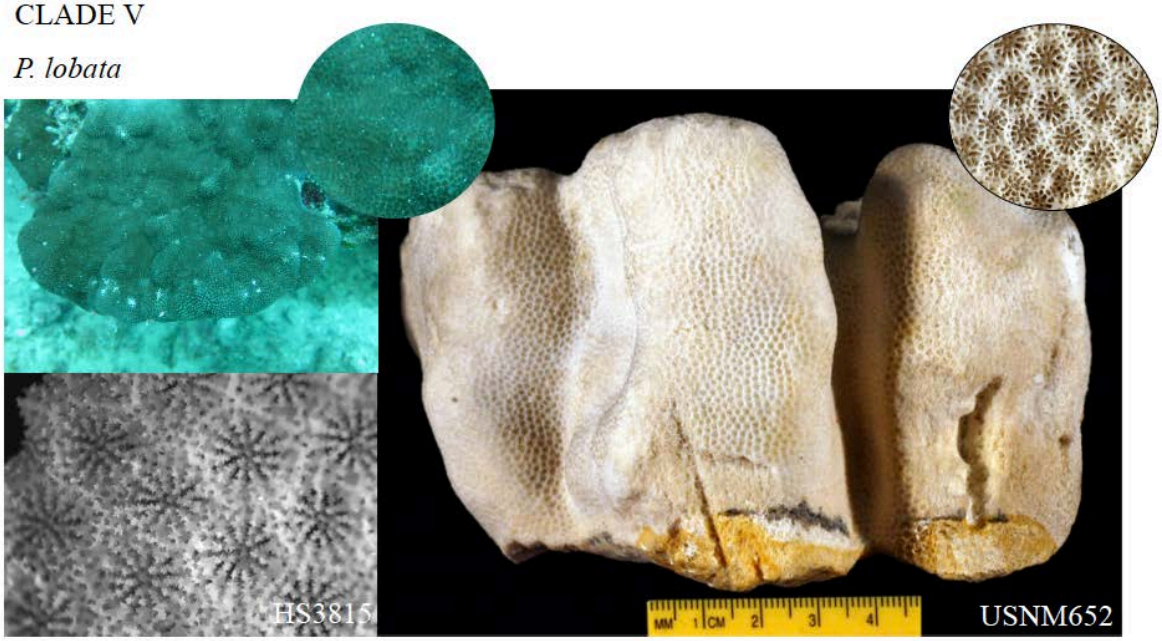
CLADE V

P. cylindrica



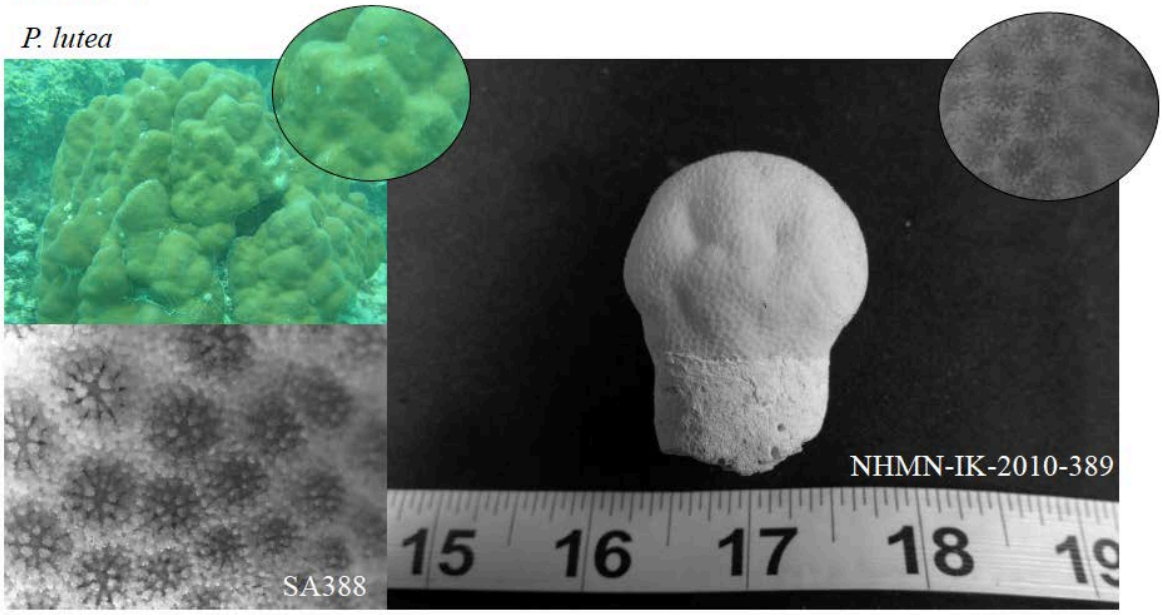
CLADE V

P. lobata



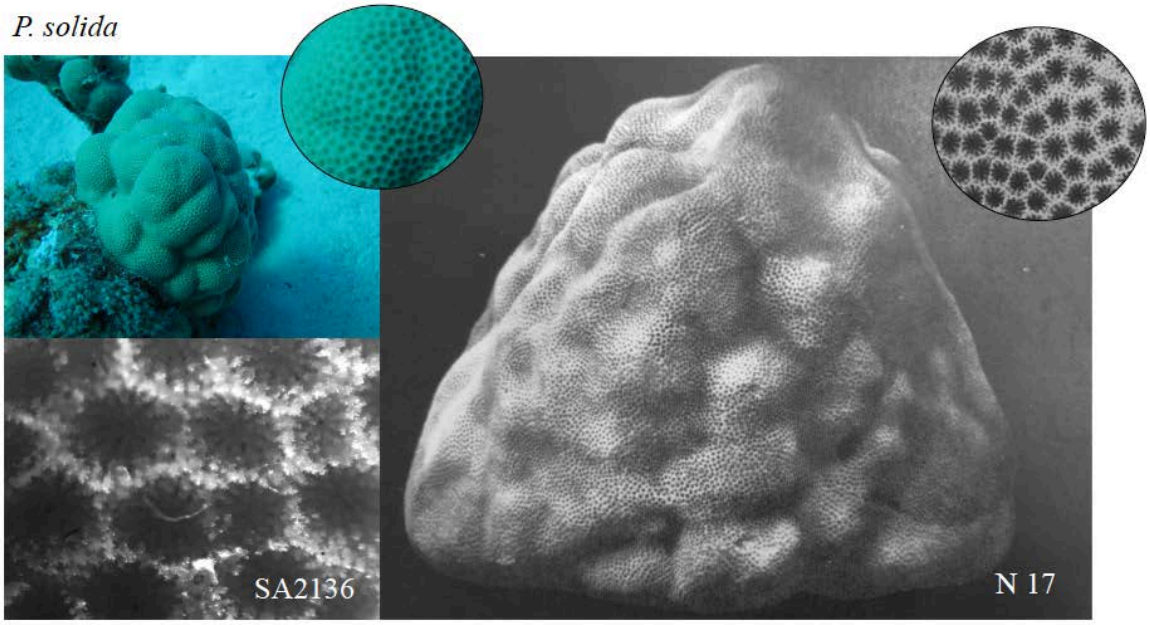
CLADE V

P. lutea



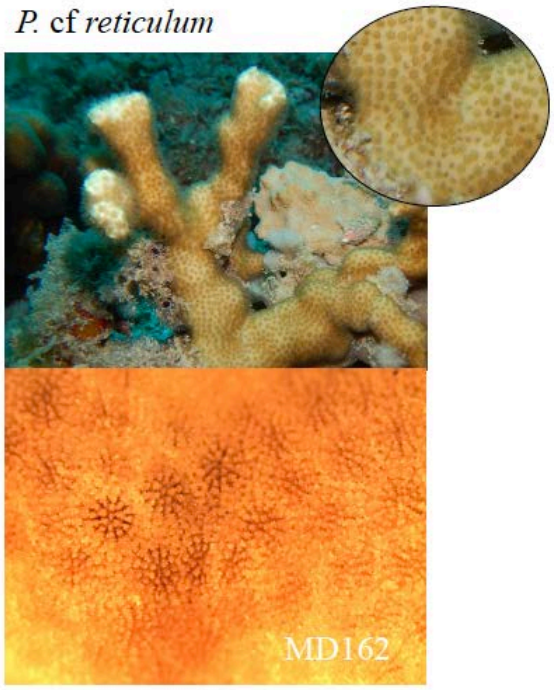
CLADE V

P. solida



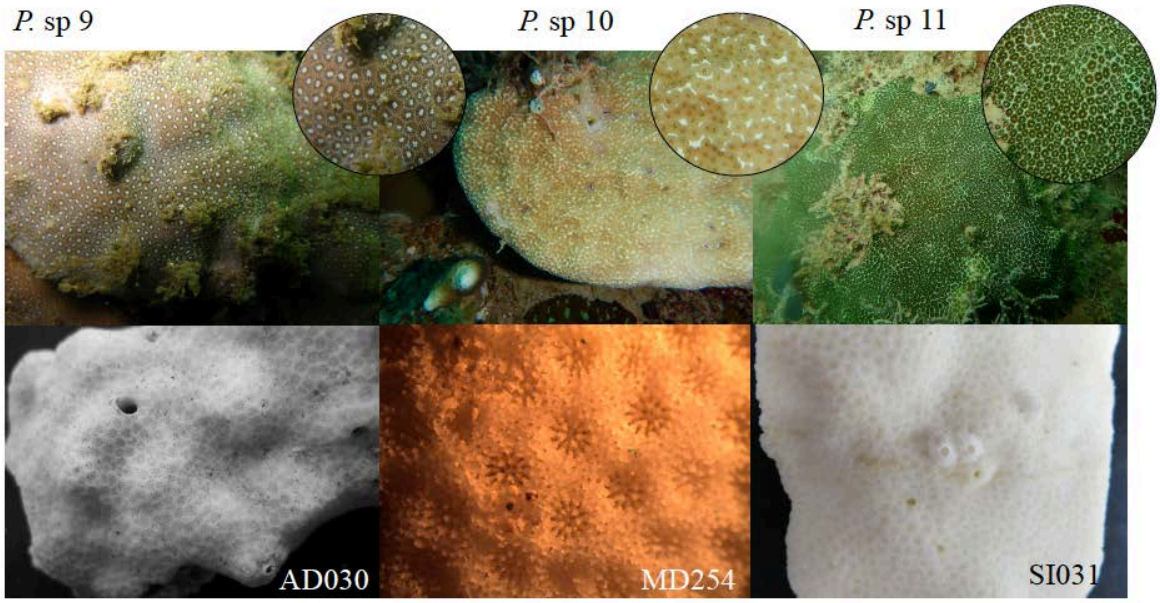
CLADE V

P. cf *reticulum*



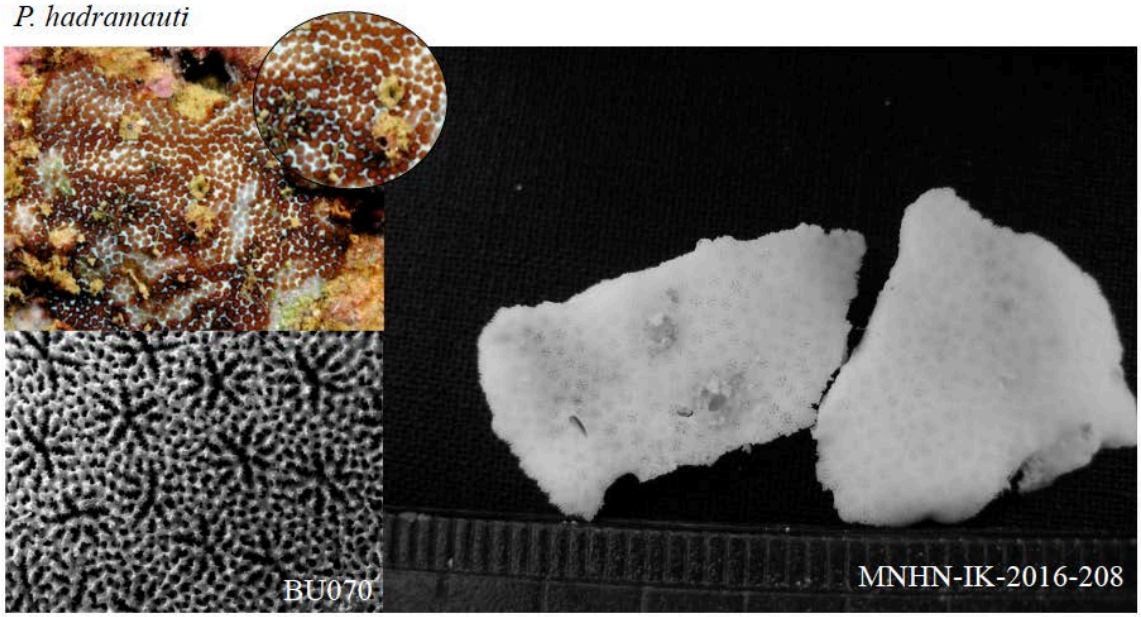
CLADE V

P. sp 9 *P.* sp 10 *P.* sp 11



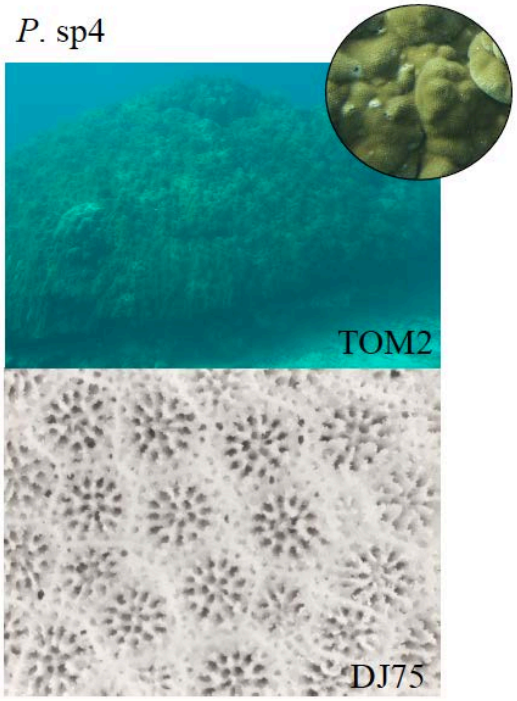
CLADE VI

P. hadramauti



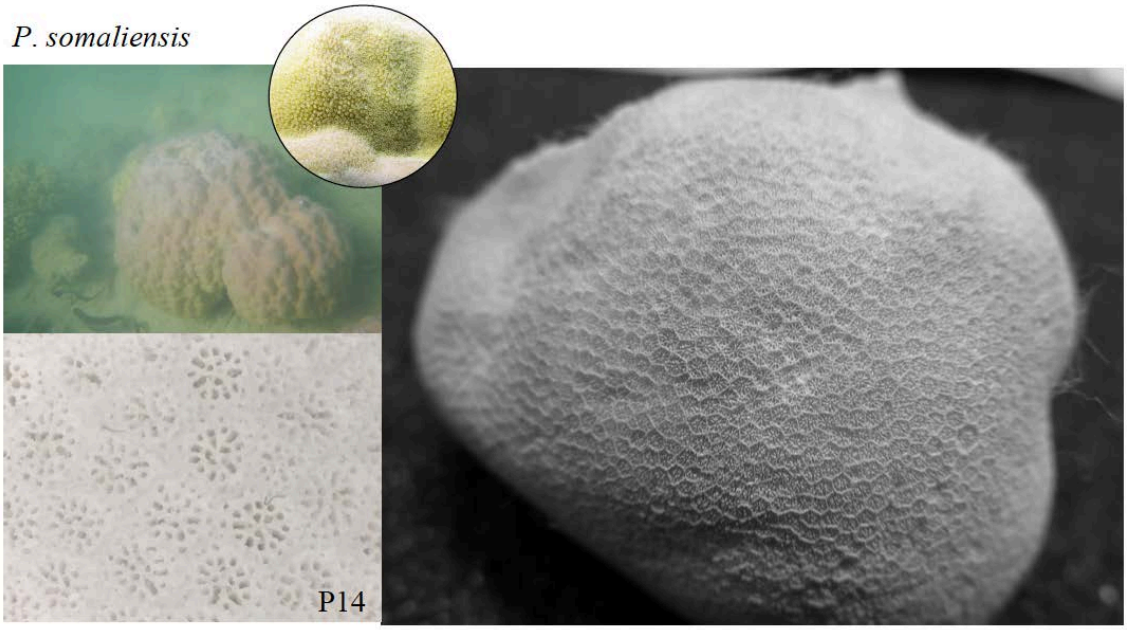
CLADE VII

P. sp4

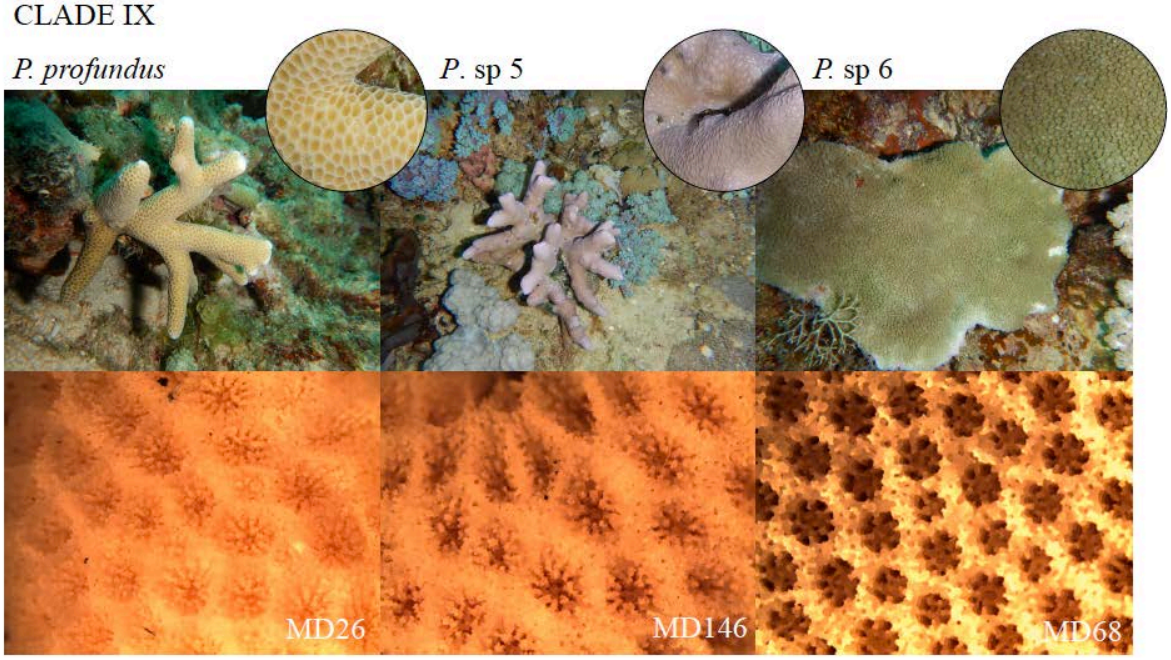


CLADE VIII

P. somaliensis

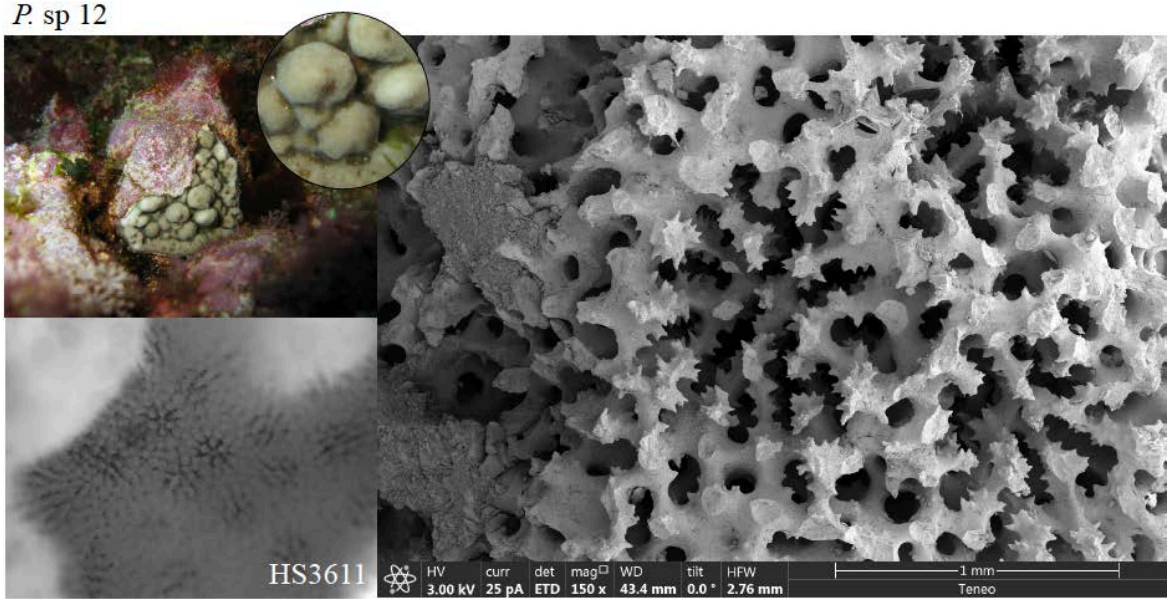


CLADE IX



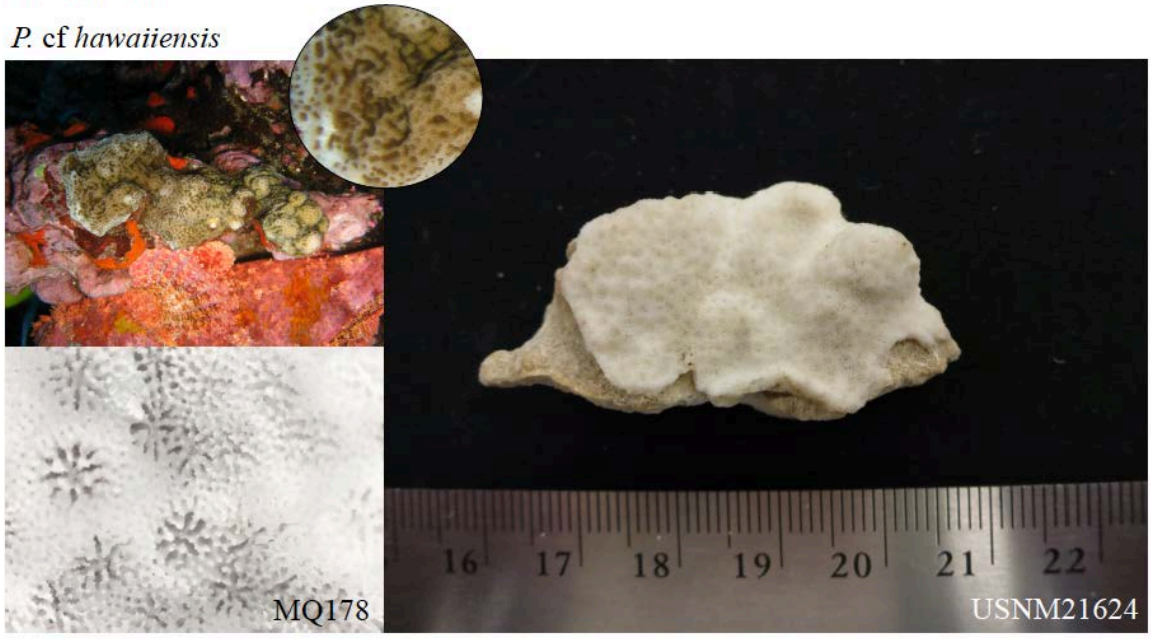
CLADE X

P. sp 12



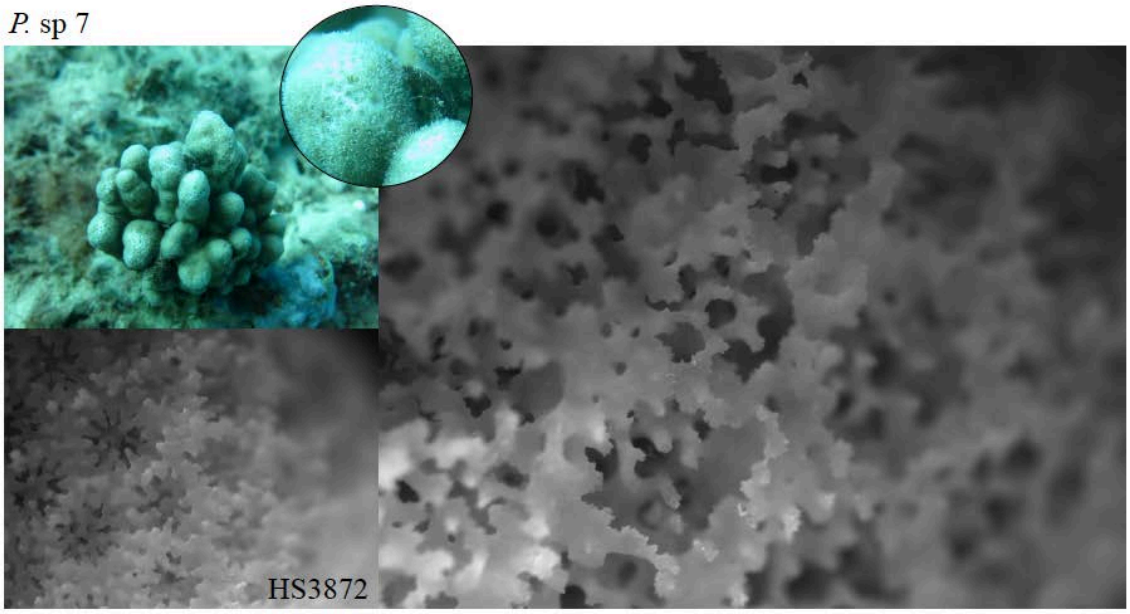
CLADE XI

P. cf *hawaiiensis*



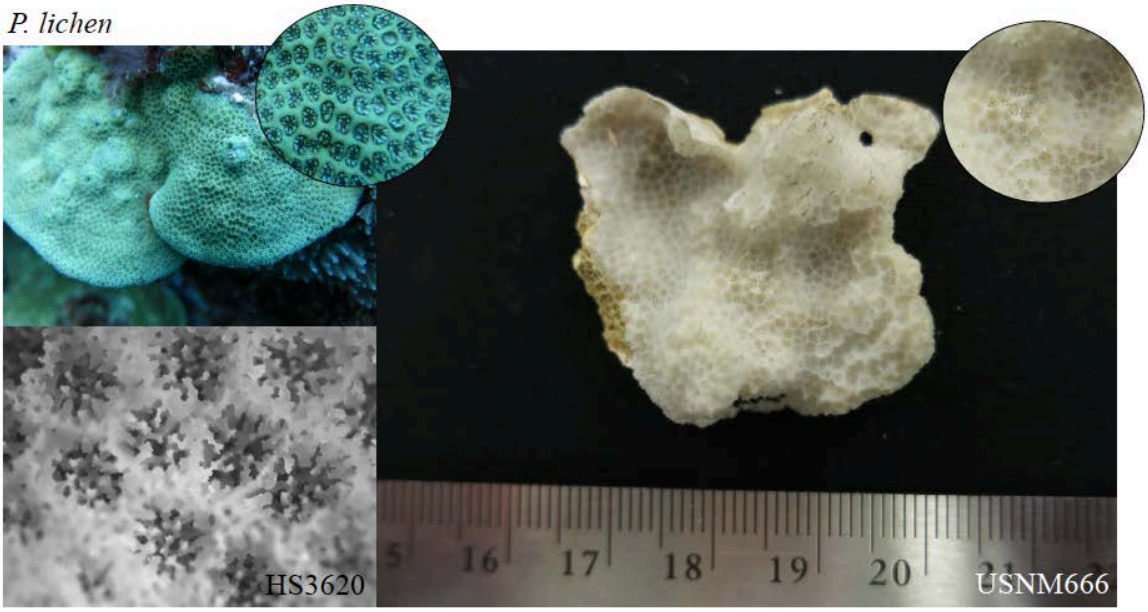
CLADE XII

P. sp 7



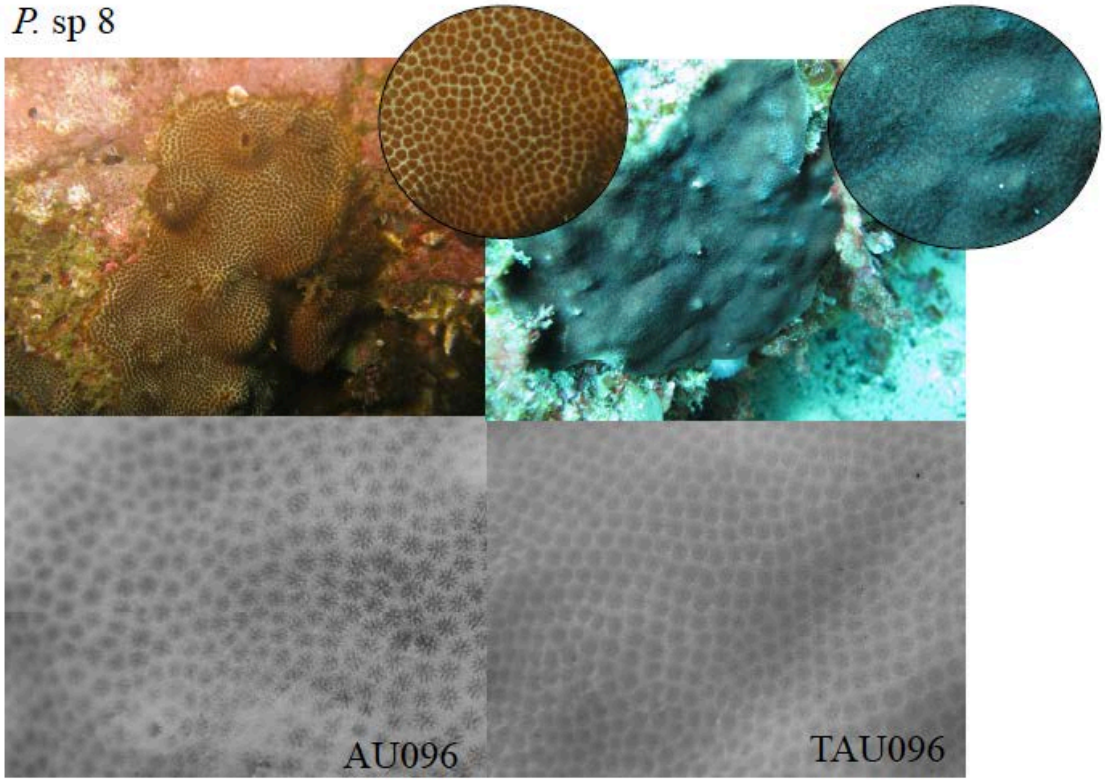
CLADE XIII

P. lichen



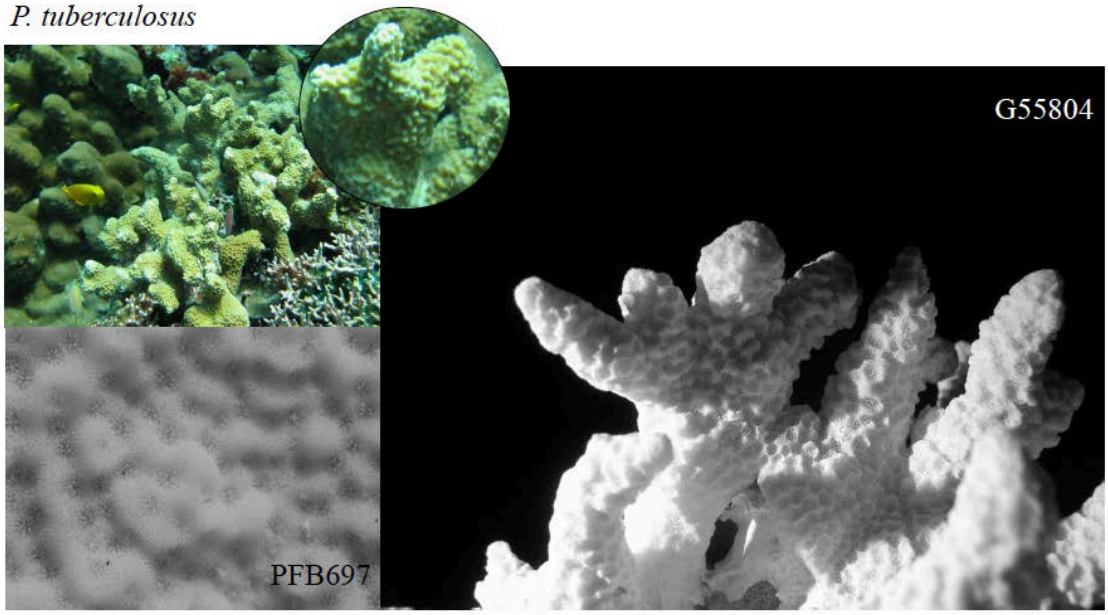
CLADE XIII

P. sp 8



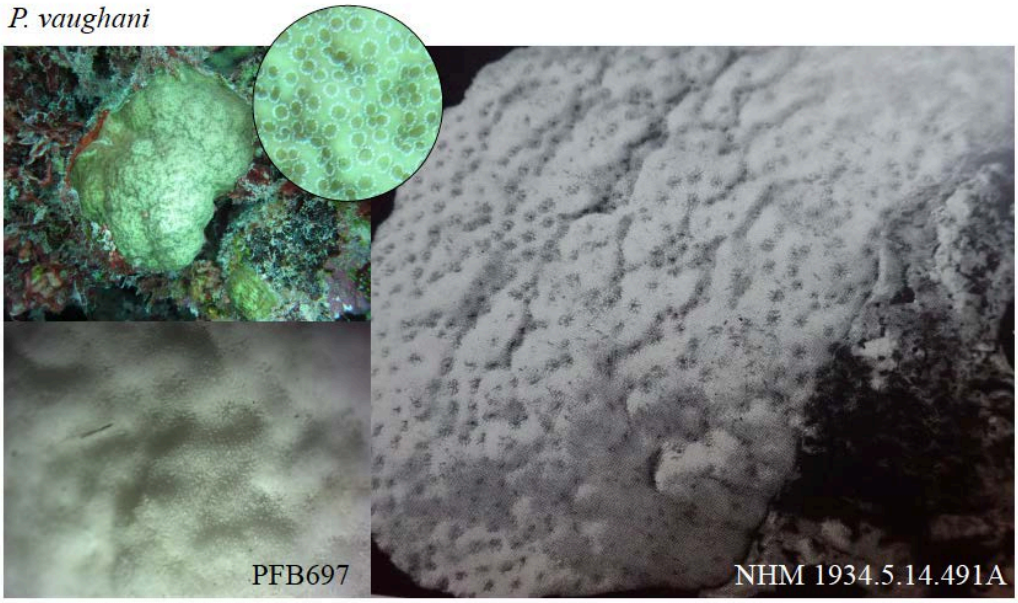
CLADE XIII

P. tuberculosus



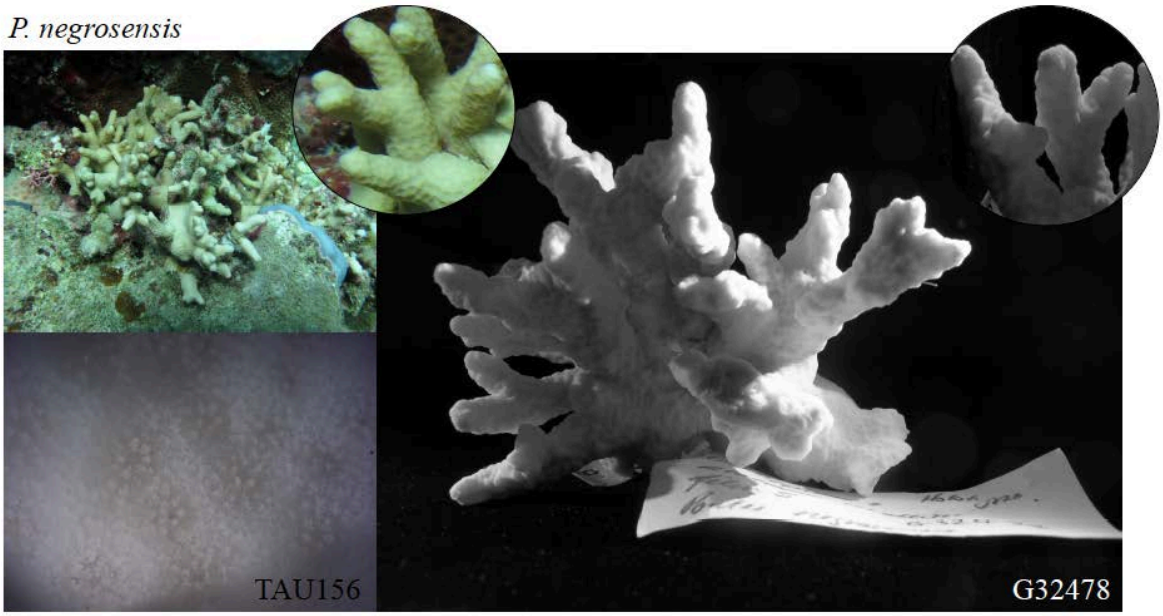
CLADE XIII

P. vaughani



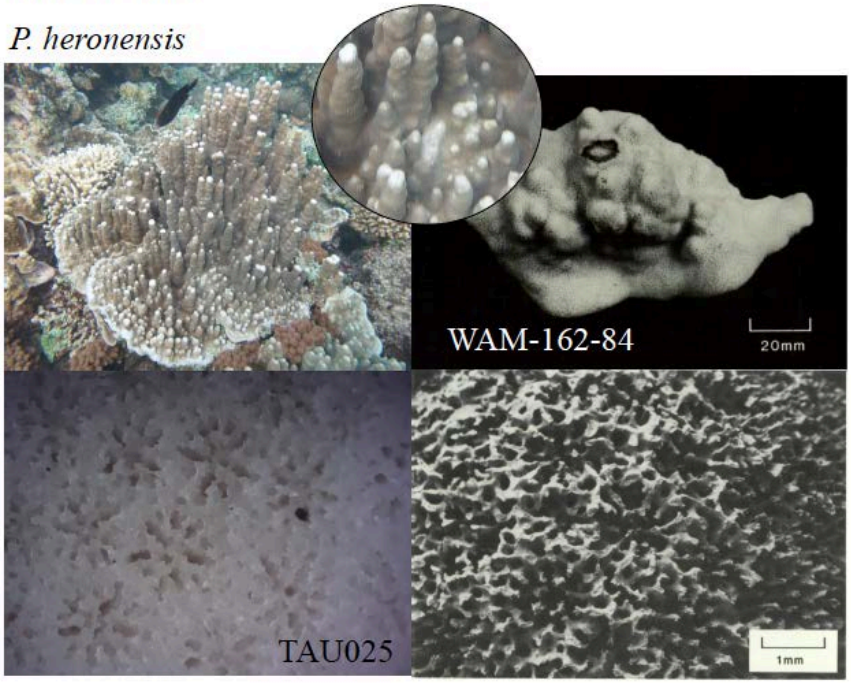
CLADE XIII

P. negrosensis



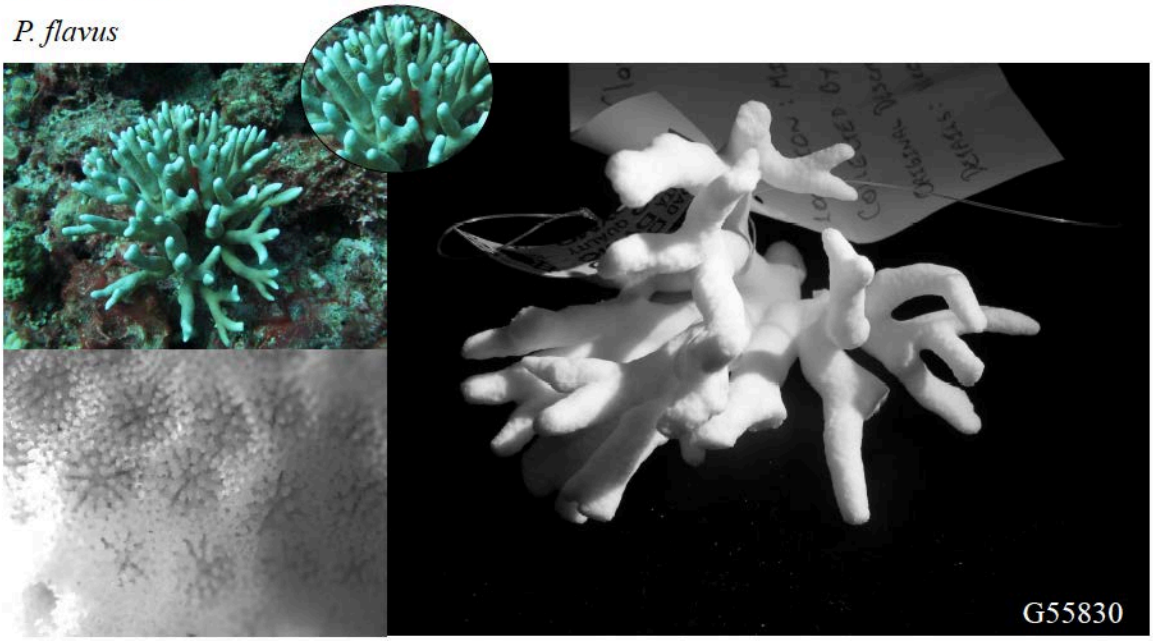
CLADE XIII

P. heronensis



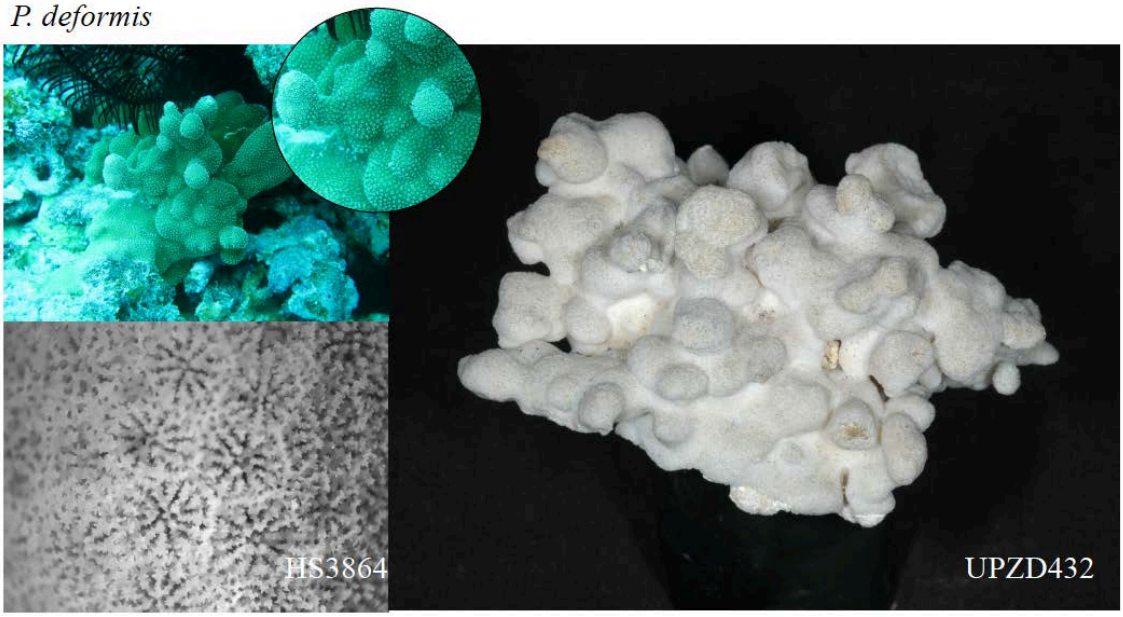
CLADE XIV

P. flavus



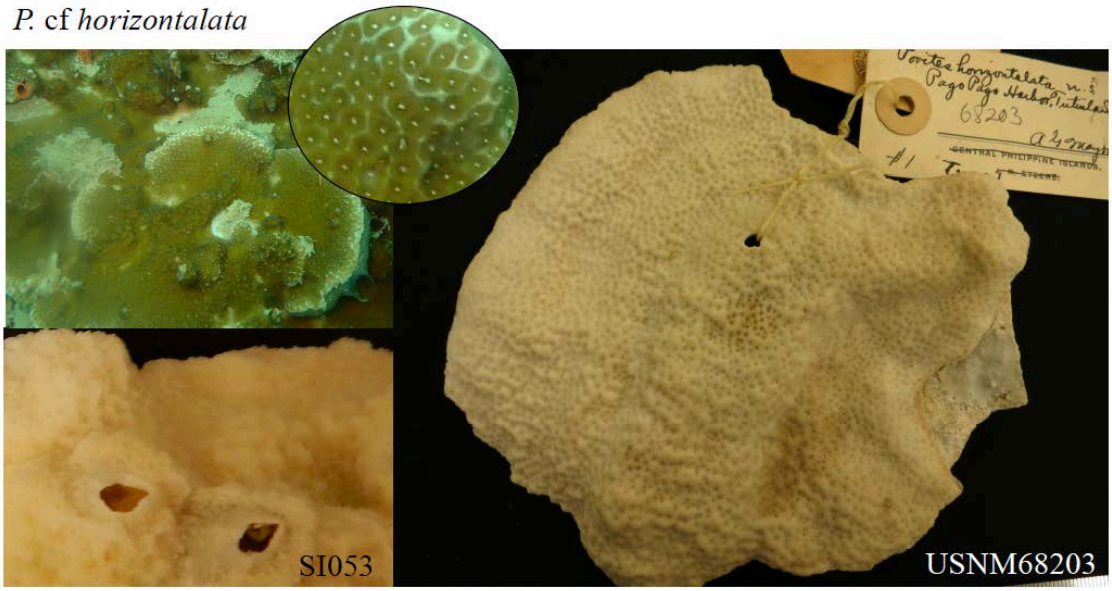
CLADE XV

P. deformis

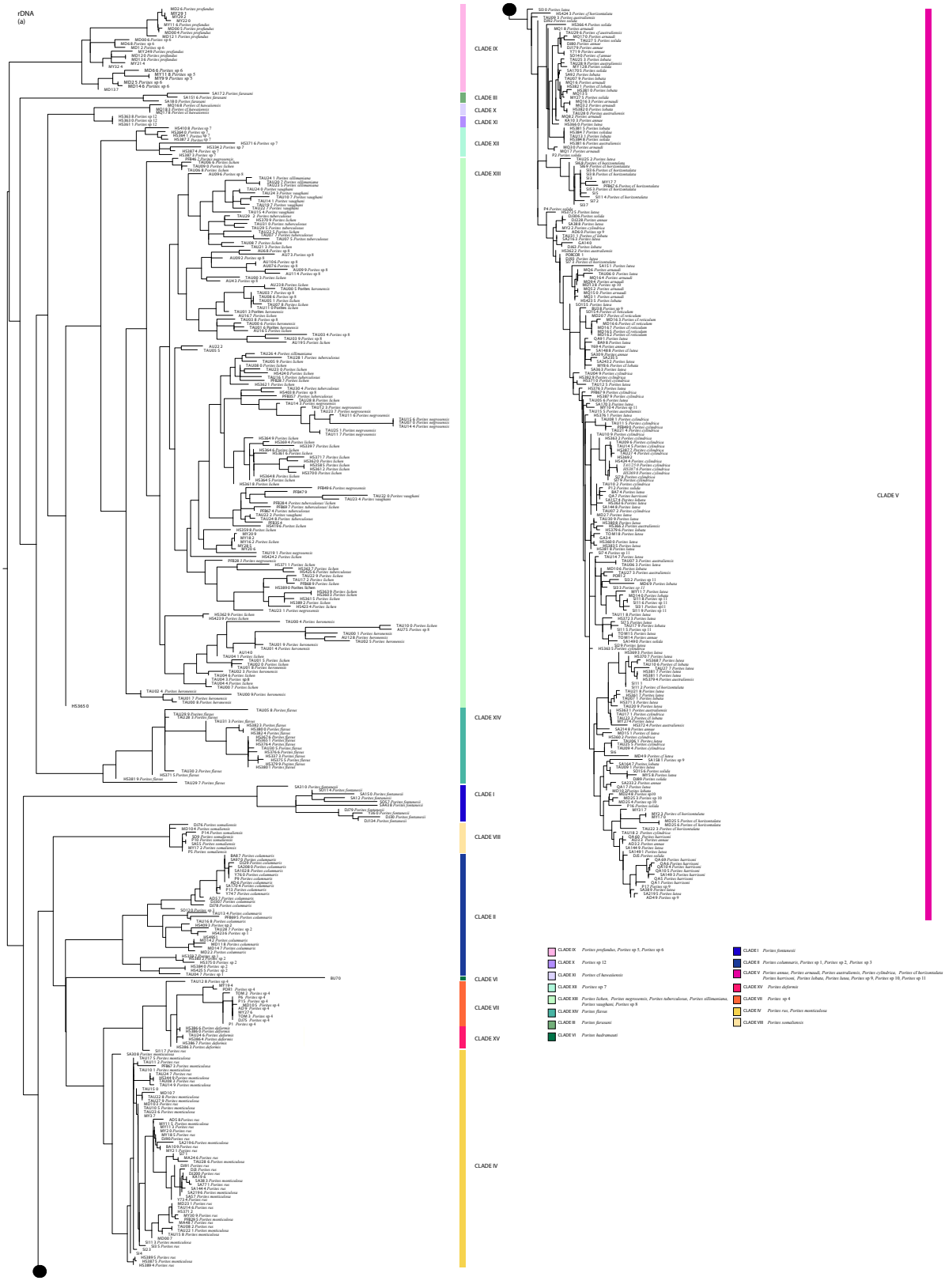


CLADE XV

P. cf *horizontalata*

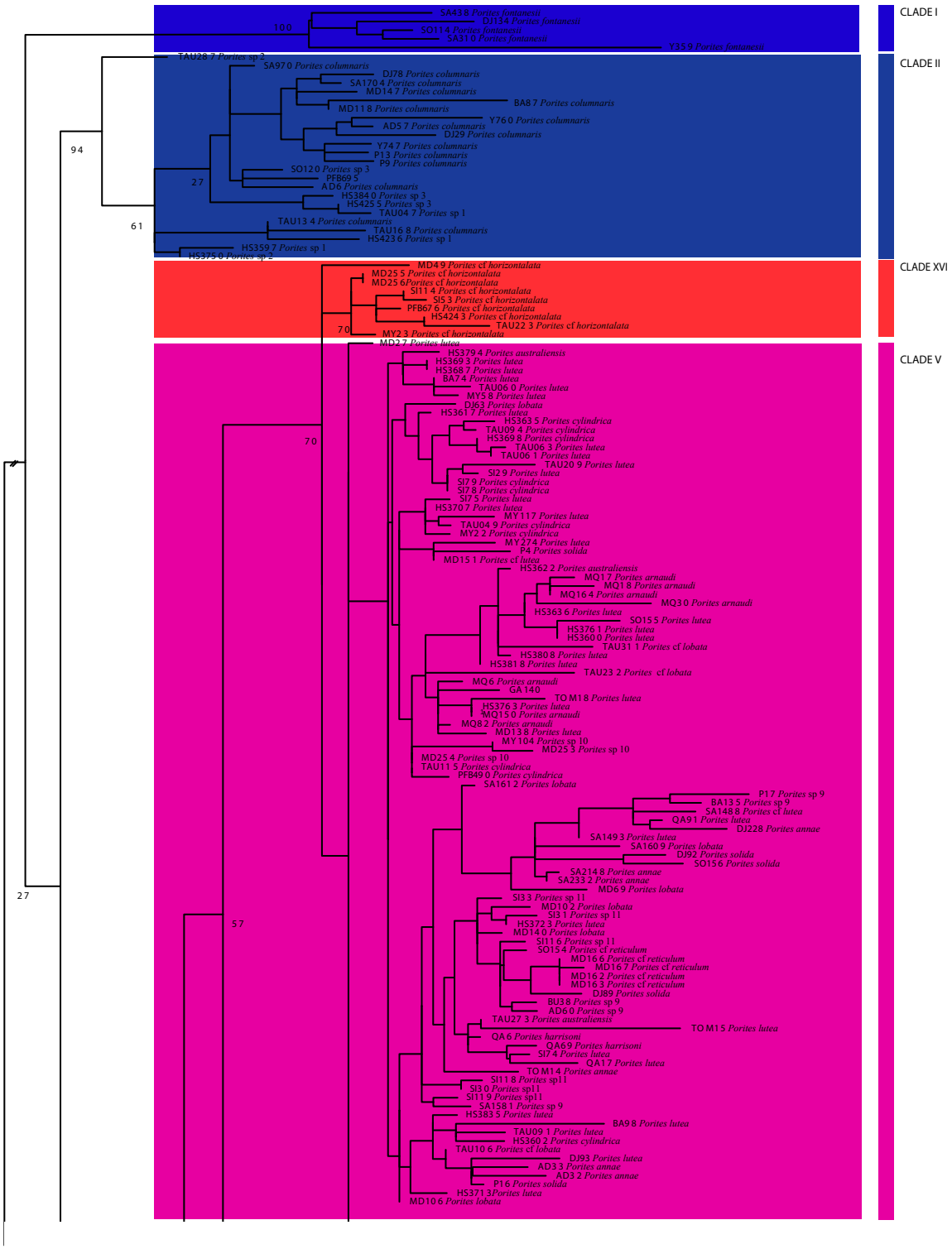


Appendix 2.4 Phylogeny reconstruction based on rDNA region. Node values represent BI posterior probabilities and ML bootstrap supports. Roman numbers from I to XVI refer to the assigned clade numbers. Colour codes are explained in the legend

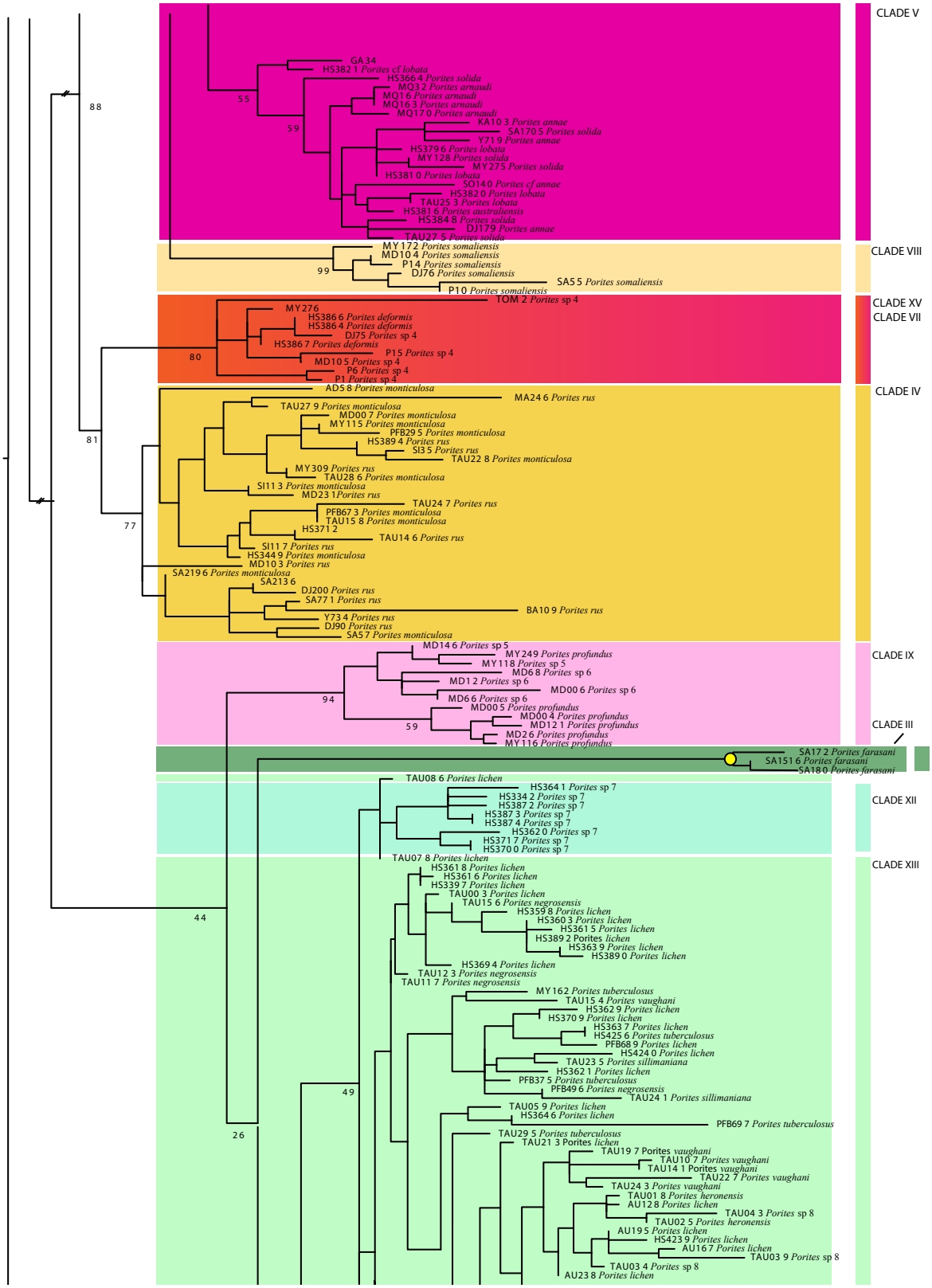


Appendix 2.5 RAxML tree based on “coral-min” dataset, that allowed for 50% missing data, and consted of 1,637 SNPs. Values at nodes represent ML bootstrap supports. Roman numbers from I to XVI refer to the assigned molecular clade numbers. Colour codes are explained in the legend

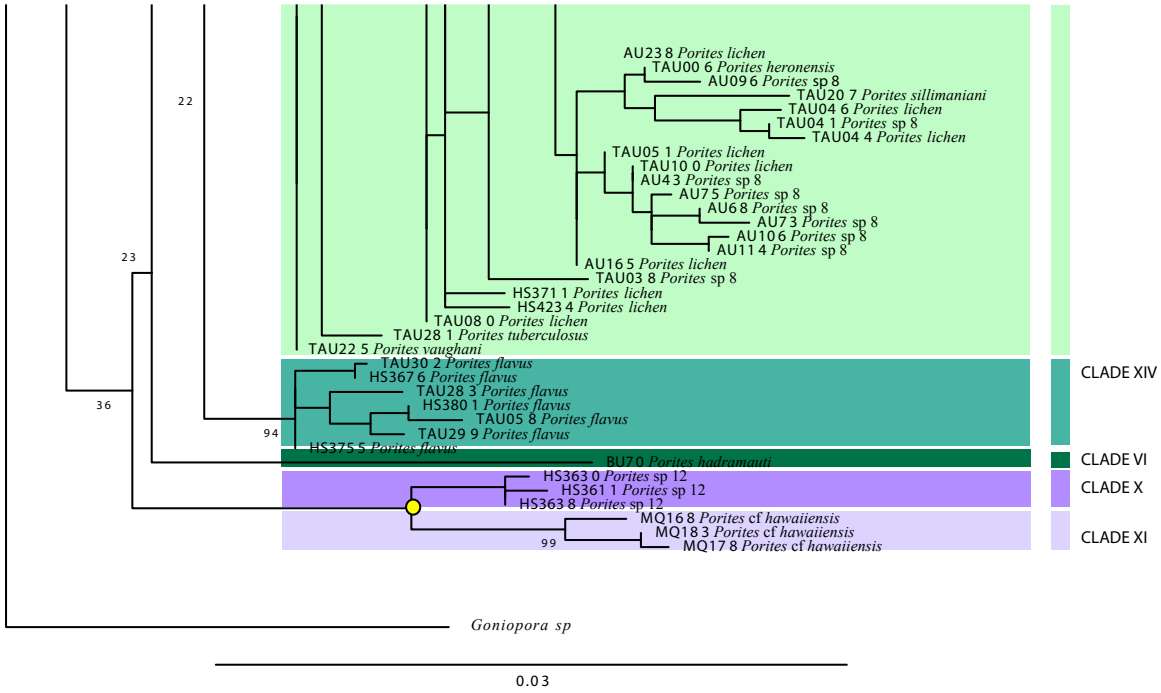
Coral Min 10_156_5
(a)



Coral Min 10_156_5
(b)



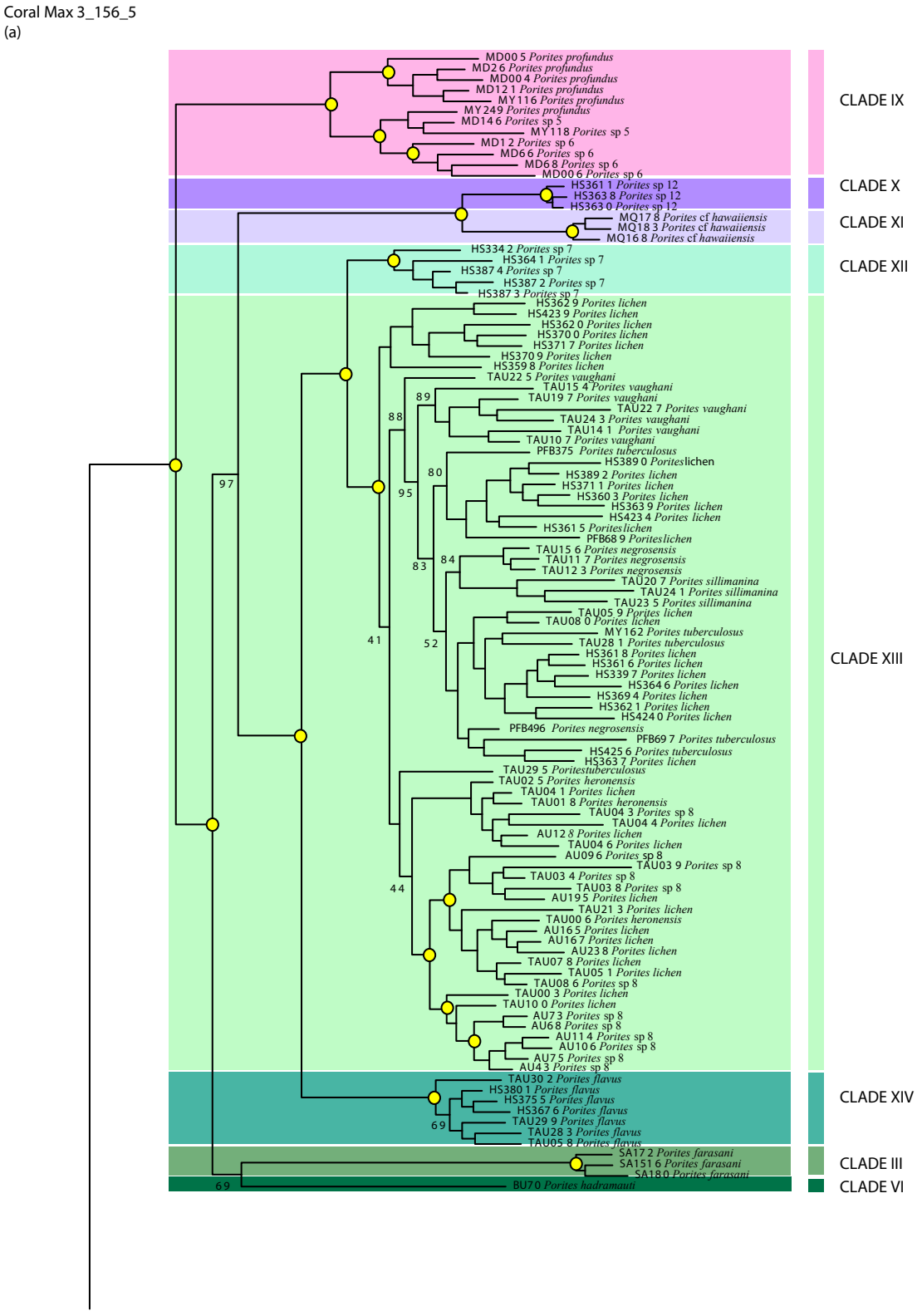
Coral Min 10_156_5
(c)

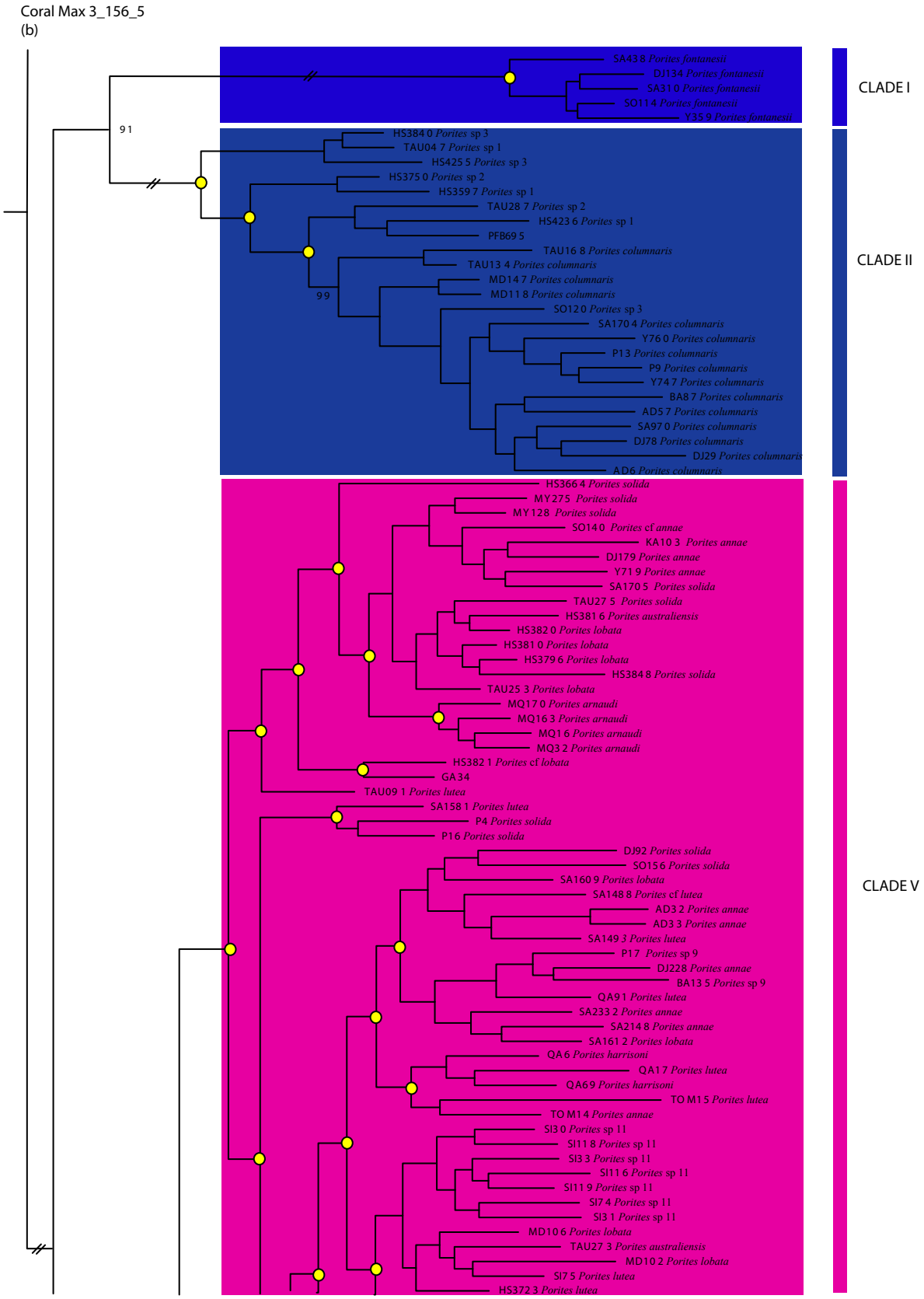


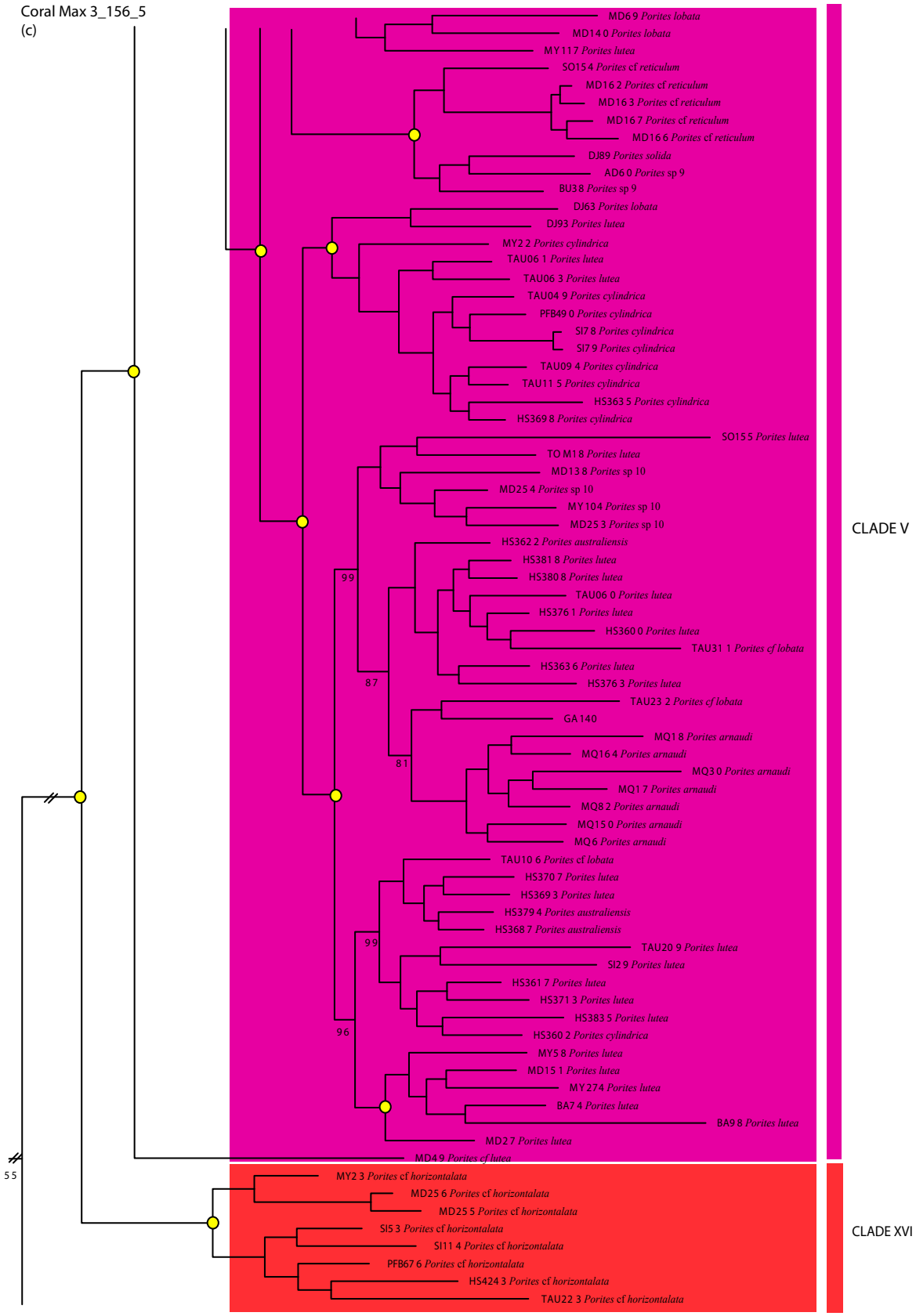
CLADE IX *Porites profundus*, *Porites* sp 5, *Porites* sp 6
CLADE X *Porites* sp 12
CLADE XI *Porites* cf *hawaiiensis*
CLADE XII *Porites* sp 7
CLADE XIII *Porites lichen*, *Porites negrosensis*, *Porites tuberculosus*, *Porites sillimaniana*, *Porites vaughani*, *Porites* sp 8
CLADE XIV *Porites flavus*
CLADE III *Porites farasani*
CLADE VI *Porites hadramauti*

CLADE I *Porites fontanesii*
CLADE II *Porites columnaris*, *Porites* sp 1, *Porites* sp 2, *Porites* sp 3
CLADE V *Porites annae*, *Porites arnaudi*, *Porites australiensis*, *Porites cylindrica*, *Porites harrisoni*, *Porites lobata*, *Porites lutea*, *Porites* sp 9, *Porites* sp 10, *Porites* sp 11
CLADE XV *Porites deformis*
CLADE XVI *Porites* cf *horizontalata*
CLADE VII *Porites* sp 4
CLADE IV *Porites rus*, *Porites monticulosa*
CLADE VIII *Porites somaliensis*

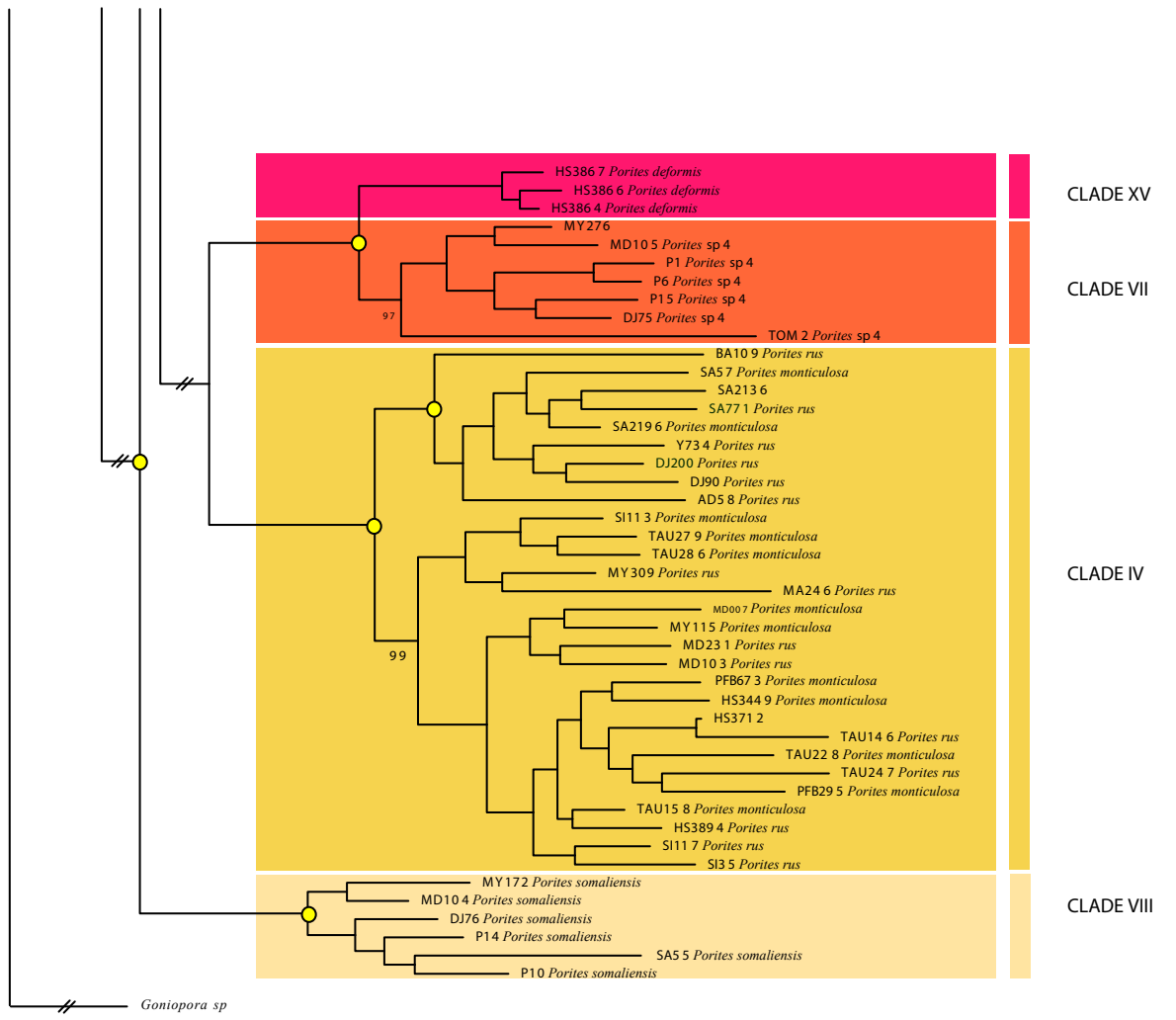
Appendix 2.6 RAxML tree based on "coral-max" dataset, that allowed for 50% missing data and consisted of 163,637 SNPs. Values at nodes represent ML bootstrap supports. Roman numbers from I to XVI refer to the assigned molecular clade numbers. Colour codes are explained in the legend




Coral Max 3_156_5
(b)
91
99
SA438 Porites fontanesii
DJ134 Porites fontanesii
SA310 Porites fontanesii
SO114 Porites fontanesii
Y359 Porites fontanesii
HS3840 Porites sp 3
TAU047 Porites sp 1
HS4255 Porites sp 3
HS3750 Porites sp 2
HS3597 Porites sp 1
TAU287 Porites sp 2
HS4236 Porites sp 1
PFB695
TAU168 Porites columnaris
TAU134 Porites columnaris
MD147 Porites columnaris
MD118 Porites columnaris
SO120 Porites sp 3
SA1704 Porites columnaris
Y760 Porites columnaris
P13 Porites columnaris
P9 Porites columnaris
Y747 Porites columnaris
BA87 Porites columnaris
AD57 Porites columnaris
SA970 Porites columnaris
DJ78 Porites columnaris
DJ29 Porites columnaris
AD6 Porites columnaris
HS3664 Porites solida
MY275 Porites solida
MY128 Porites solida
SO140 Porites cf annae
KA103 Porites annae
DJ179 Porites annae
Y719 Porites annae
SA1705 Porites solida
TAU275 Porites solida
HS3816 Porites australiensis
HS3820 Porites lobata
HS3810 Porites lobata
HS3796 Porites lobata
HS3848 Porites solida
TAU253 Porites lobata
MQ170 Porites arnaudi
MQ163 Porites arnaudi
MQ16 Porites arnaudi
MQ32 Porites arnaudi
HS3821 Porites cf lobata
GA34
TAU091 Porites lutea
SA1581 Porites lutea
P4 Porites solida
P16 Porites solida
DJ92 Porites solida
SO156 Porites solida
SA1609 Porites lobata
SA1488 Porites cf lutea
AD32 Porites annae
AD33 Porites annae
SA1493 Porites lutea
P17 Porites sp 9
DJ228 Porites annae
BA135 Porites sp 9
QA91 Porites lutea
SA2332 Porites annae
SA2148 Porites annae
SA1612 Porites lobata
QA6 Porites harrisoni
QA17 Porites lutea
QA69 Porites harrisoni
TOM15 Porites lutea
TOM14 Porites annae
SI30 Porites sp 11
SI118 Porites sp 11
SI33 Porites sp 11
SI116 Porites sp 11
SI119 Porites sp 11
SI74 Porites sp 11
SI31 Porites sp 11
MD106 Porites lobata
TAU273 Porites australiensis
MD102 Porites lobata
SI75 Porites lutea
HS3723 Porites lutea
CLADE I
CLADE II
CLADE V


Coral Max 3_156_5
(c)
MD69 Porites lobata
MD140 Porites lobata
MY117 Porites lutea
SO154 Porites cf reticulum
MD162 Porites cf reticulum
MD163 Porites cf reticulum
MD167 Porites cf reticulum
MD166 Porites cf reticulum
DJ89 Porites solida
AD60 Porites sp 9
BU38 Porites sp 9
DJ63 Porites lobata
DJ93 Porites lutea
MY22 Porites cylindrica
TAU061 Porites lutea
TAU063 Porites lutea
TAU049 Porites cylindrica
PFB490 Porites cylindrica
SI78 Porites cylindrica
SI79 Porites cylindrica
TAU094 Porites cylindrica
TAU115 Porites cylindrica
HS3635 Porites cylindrica
HS3698 Porites cylindrica
SO155 Porites lutea
TOM18 Porites lutea
MD138 Porites sp 10
MD254 Porites sp 10
MY104 Porites sp 10
MD253 Porites sp 10
HS3622 Porites australiensis
HS3818 Porites lutea
HS3808 Porites lutea
TAU060 Porites lutea
HS3761 Porites lutea
HS3600 Porites lutea
TAU311 Porites cf lobata
HS3636 Porites lutea
HS3763 Porites lutea
TAU232 Porites cf lobata
GA140
MQ18 Porites arnaudi
MQ164 Porites arnaudi
MQ30 Porites arnaudi
MQ17 Porites arnaudi
MQ82 Porites arnaudi
MQ150 Porites arnaudi
MQ6 Porites arnaudi
TAU106 Porites cf lobata
HS3707 Porites lutea
HS3693 Porites lutea
HS3794 Porites australiensis
HS3687 Porites australiensis
TAU209 Porites lutea
SI29 Porites lutea
HS3617 Porites lutea
HS3713 Porites lutea
HS3835 Porites lutea
HS3602 Porites cylindrica
MY58 Porites lutea
MD151 Porites lutea
MY274 Porites lutea
BA74 Porites lutea
BA98 Porites lutea
MD27 Porites lutea
MD49 Porites cf lutea
MY23 Porites cf horizontalata
MD256 Porites cf horizontalata
MD255 Porites cf horizontalata
SI53 Porites cf horizontalata
SI114 Porites cf horizontalata
PFB676 Porites cf horizontalata
HS4243 Porites cf horizontalata
TAU223 Porites cf horizontalata
99
87
81
99
96
55
CLADE V
CLADE XVI

Coral Max 3_156_5
(d)



CLADE IX *Porites profundus*, *Porites* sp 5, *Porites* sp 6

CLADE X *Porites* sp 12

CLADE XI *Porites* cf *hawaiiensis*

CLADE XII *Porites* sp 7

CLADE XIII *Porites lichen*, *Porites negrosensis*, *Porites tuberculosus*, *Porites sillimaniana*, *Porites vaughani*, *Porites* sp 8

CLADE XIV *Porites flavus*

CLADE III *Porites farasani*

CLADE VI *Porites hadramauti*

CLADE I *Porites fontanesii*

CLADE II *Porites columnaris*, *Porites* sp 1, *Porites* sp 2, *Porites* sp 3

CLADE V *Porites annae*, *Porites arnaudi*, *Porites australiensis*, *Porites cylindrica*, *Porites harrisoni*, *Porites lobata*, *Porites lutea*, *Porites* sp 9, *Porites* sp 10, *Porites* sp 11

CLADE XV *Porites deformis*

CLADE XVI *Porites* cf *horizontalata*

CLADE VII *Porites* sp 4

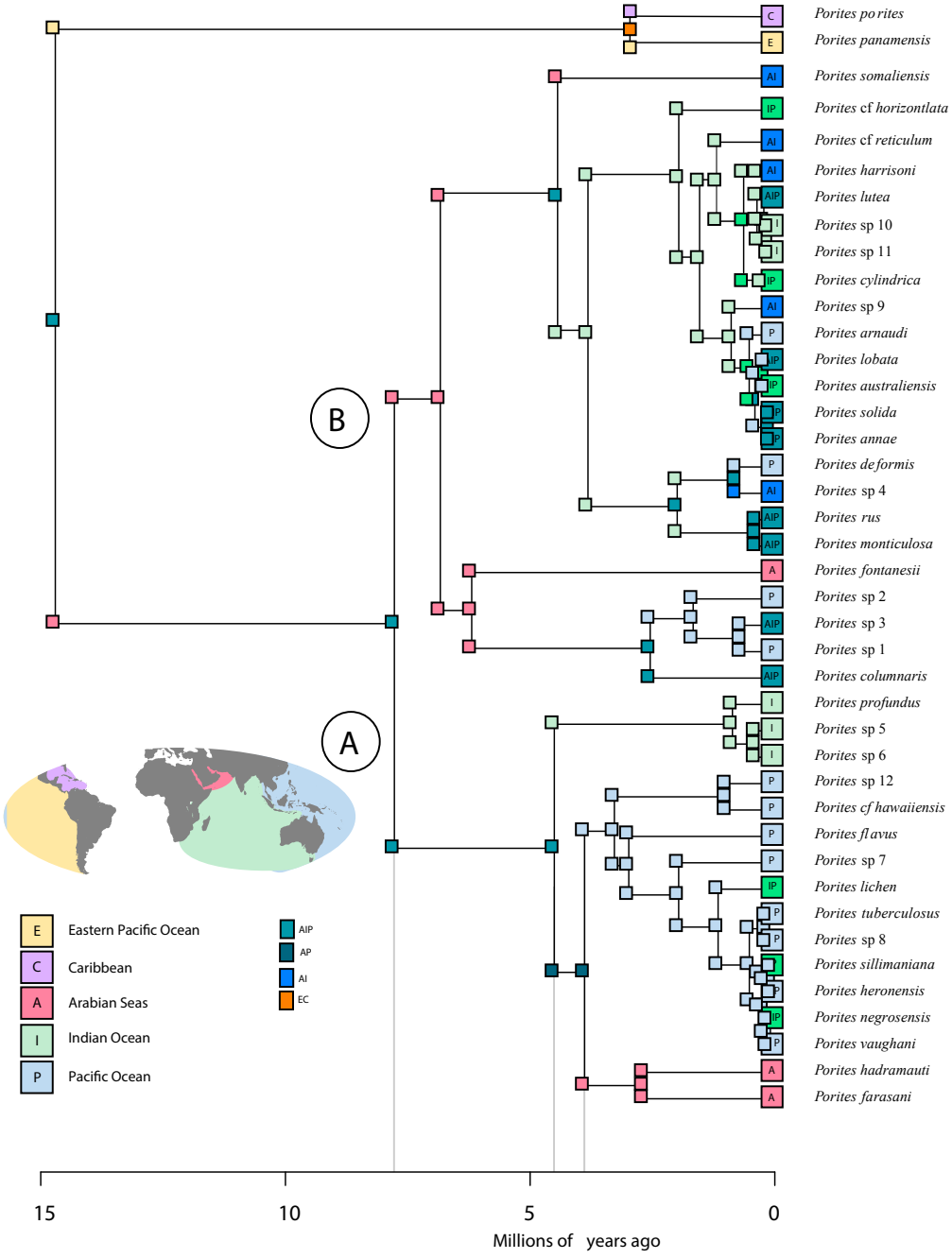
CLADE IV *Porites rus*, *Porites monticulosa*

CLADE VIII *Porites somaliensis*

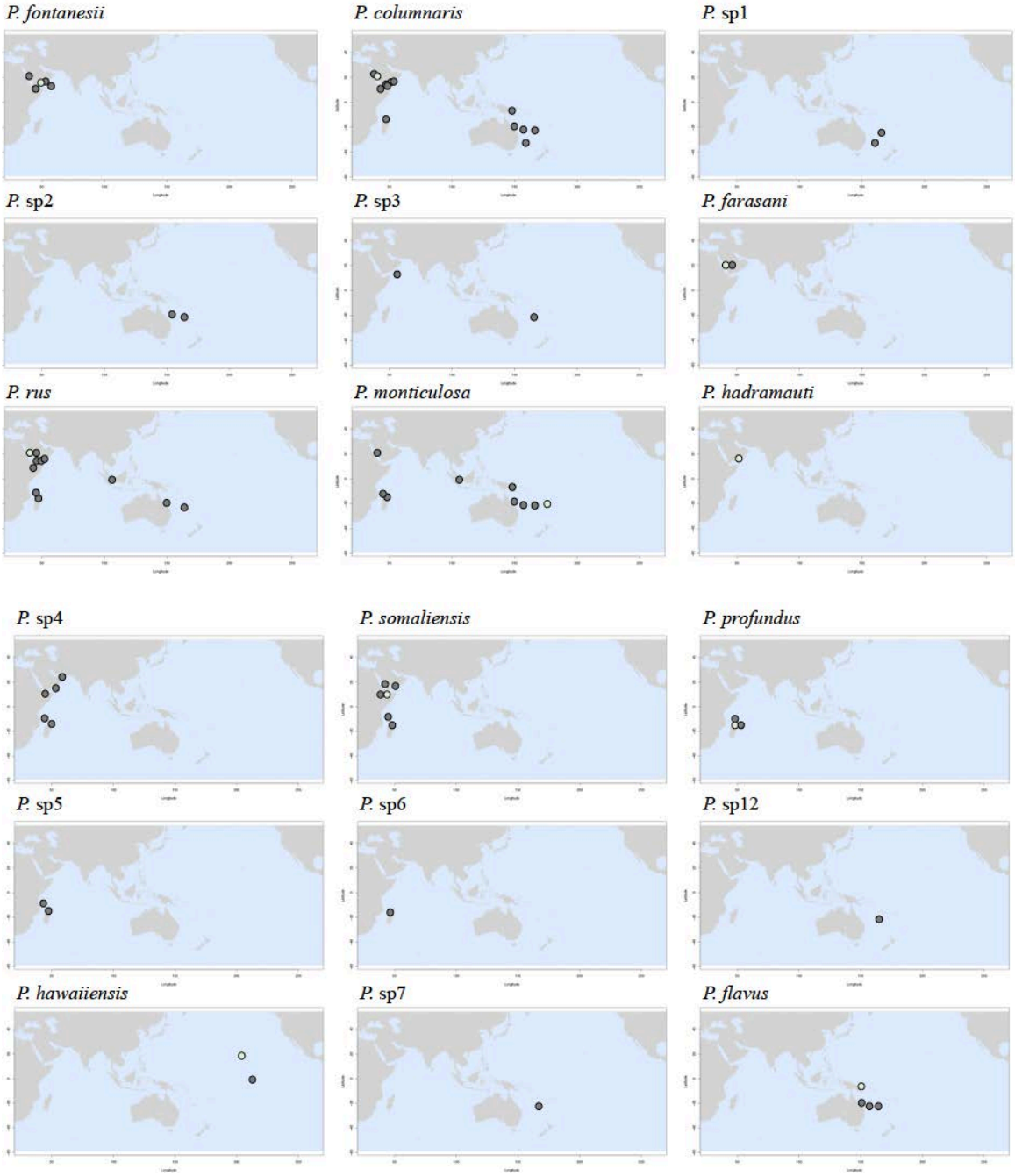
Appendix 2.7 Results of BioGeoBEARS Likelihood Ratio Tests (LRT) for the two pairs of nested models (DEC vs. DEC+J, DIVALIKE vs. DIVALIKE+J).

Alternative model	Null model	LnL alternative model	LnL null model	P value
DEC+J	DEC	-127.2	127.2005	0.97
DIVALIKE+J	DIVALIKE	-135.0496	135.0489	1

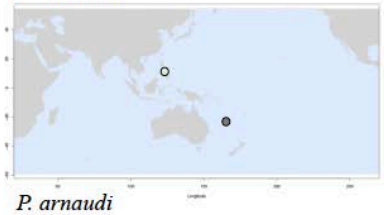
Appendix 2.8 Ancestral area reconstruction of *Porites* using BioGeoBEARS on the same topology as the phylogenetic tree presented in Fig. 3.3. Coloured boxes at each node and corner are colour coded for the area with the highlest ML probability. Areas are illustrated on the map to the left. Caption refers to colours of areas in the map and boxes.



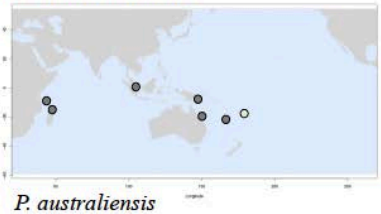
Appendix 2.9 Distribution maps for each nominal species and morphology recovered in the study



P. deformis



P. cf *horizontalata*

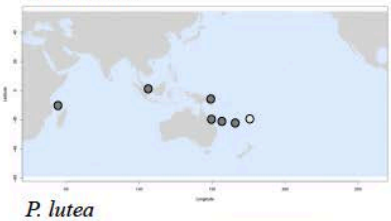


P. annae

P. arnaudi

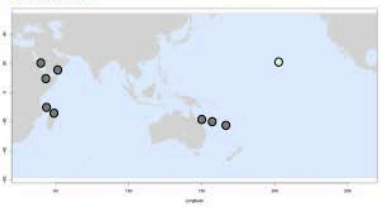
P. australiensis

P. cylindrica



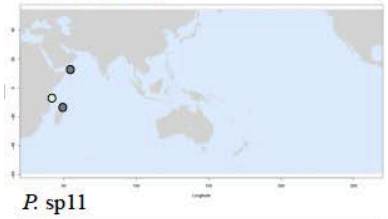
P. harrisoni

P. lobata



P. lutea

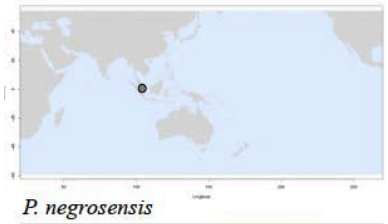
P. cf *reticulum*



P. sp9

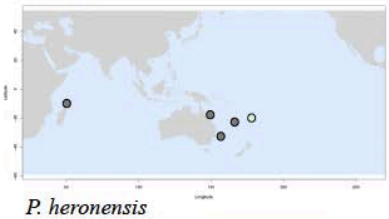
P. sp10

P. sp11



P. solida

P. lichen



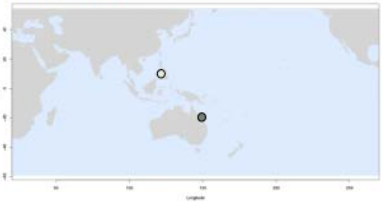
P. negrosensis

P. sp8

P. heronensis

P. tuberculosus

P. sillimaniani



P. vaughani