

STEPPING OUT OF THE SHADOWS: GENOMIC AND EXPERIMENTAL ILLUMINATION
OF DIVERSITY WITHIN THE CORAL FAMILY AGARICIIDAE

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ABSTRACT

Confidently delimiting species and resolving their evolutionary histories relies on accurate taxonomy and well-supported phylogenies; two things which have been historically challenging in corals. The coral family Agariciidae is composed of species with exceptionally large ranges, and therefore likely contains numerous cryptic species. The aims of this dissertation are to study the phenotypic variation, phylogenomic and geographic diversity of species from the family Agariciidae. To assess the phylogenetics and phylogeography of this family I applied two approaches. First, I used a traditional mitochondrial DNA barcoding approach that focused effort on a taxonomically and geographically broad sampling scheme. I combined 208 new sequences with 191 previously published sequences, representing 31 species. Relationships based on the mtDNA intron revealed considerable discordance between the current taxonomy and recovered clades; just seven species were recovered as monophyletic. Second, I generated RAD libraries for a subset of individuals, which produced far more data from across the genome, albeit from fewer samples (120), which represented twenty nominal taxa. From these libraries I assembled complete mitochondrial genomes, 18 of which are the first recorded for that taxon. I estimated phylogenies from SNPs generated from three different assembly approaches. Both the mitogenome and SNP phylogenies recovered well-supported trees, but they were not fully concordant with one another. I found no evidence of introgression within the SNP datasets, indicating hybridization may not be as prevalent in this family as in some other corals. The SNP trees recovered three well-supported clades, none of which corresponded to a monophyletic *Pavona* or *Leptoseris*. Each phylogenetic data set recovered multiple putative cryptic species associated with the nominal taxa *P. varians* and *L. mycetoseroides*. Both species form similar encrusting, ridged colonies, indicating this morphology may be the ancestral state of this family or may have evolved independently multiple times. Given the evolutionary and ecological success of the ridged morphology, combined with the high variability both within and between species, I examined the extent of light-associated phenotypic plasticity for *P. varians*. A common garden experiment revealed light had a strong effect on both the growth rates and morphology of colonies. This is likely an adaptive response which allows this depth generalist species to tolerate a wide variety of light environments. Overall this work suggests whole genome studies and

further experiments are necessary to fully resolve the species boundaries and evolutionary processes driving speciation in this family.

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CHAPTER 1. INTRODUCTION

INDO-PACIFIC BIOGEOGRAPHY

Diversity is unevenly distributed on Earth. Species richness is highest in the tropics and declines towards the poles in both the marine and terrestrial realms. In the oceans diversity peaks on a single longitudinal point, the Indonesian and Philippine archipelagos, an area known as the Coral Triangle, and declines outwards forming a distinctive “bullseye” pattern of biodiversity (Roberts *et al.* 2002, Bellwood *et al.* 2005, Veron *et al.* 2009). This pattern is pervasive across taxa including fish, corals, benthic foraminifera, and mangroves (Renema *et al.* 2008) and likely reflects the action of multiple biogeographic processes. Three predominant mechanisms have been described to explain this pattern including the Center of Speciation (Ekman 1953), Center of Overlap (Woodland 1986 in Bellwood *et al.* 2012), and Center of Accumulation (Ladd 1960) hypotheses. These processes are not mutually exclusive and a combination of all of them are likely to be generating the distribution of diversity we recognize today (Barber *et al.* 2006; Williams and Duda 2008; Gaither *et al.* 2011; Bowen *et al.* 2013).

The biodiversity of the Indo-Pacific can be further divided into biogeographic provinces based on faunal assemblage or percent endemism (Briggs 1974, Spalding *et al.* 2007, Briggs & Bowen 2013). These provinces are associated with known barriers which limit migration and dispersal, leading to physical and genetic isolation. Within the Indo-Pacific there are four main barriers to dispersal, which can be categorized into oceanographic, and ephemeral barriers. The East Pacific Barrier is a vast expanse (5,000 - 8,000 km) of open ocean which separates the shallow island reefs of the Central Pacific from the fringing reefs of the continental Pacific. This barrier, thought to be impassable by Darwin, has contributed to the low species richness and high endemism in the East Pacific, as few species are able to cross via larval dispersal (Glynn & Ault 2000; Guzman *et al.* 2004; Glynn *et al.* 2017, but see Lessios & Robertson 2006). Similarly the Hawaiian archipelago is separated from the Central Pacific by open ocean, connected via a single stepping stone - Johnston atoll 800 km away. The two ephemeral barriers are linked to reductions in connectivity caused by large drops in sea-level associated with the Plio-Pleistocene glacial cycles. These sea level changes expose continental shelf which reduces the connectivity between

the Indian and Pacific oceans to a narrow sea, forming the Sunda Shelf Barrier (Gaither & Rocha 2013). And, in the Red Sea, a similar narrowing of the connecting passages between the Red Sea and the Indian Ocean occurs during low sea level stands (DiBattista et al. 2016). The isolation caused by these barriers generated the endemic species recovered in peripheral isolated provinces (Fenner 2005; Palacios-Salgado et al. 2012; Glynn et al. 2017; Bogorodsky & Randall 2019). And, the marginal and novel habitats in these outermost areas also likely contributes to the many endemics found in these regions (DiBattista et al. 2016; Budd & Pandolfi 2010).

THE AGARICIDS

The coral family Agariciidae (Gray 1847) is comprised of species which exhibit a myriad of unusual biogeographic patterns: few species are geographically confined to the coral triangle, multiple nominal species persist across the entire IP, they are well-represented in the typically depauperate East Pacific, and the isolated Red Sea has equivalent species richness as the Coral Triangle. This trend can be summarized as an over-representation of pandemics, and fewer-than-expected Coral Triangle endemics (Hughes et al. 2002).

The molecular studies conducted on this group thus far have indicated the presence of unrecognized cryptic diversity (Luck et al. 2013; Waheed et al. 2015; Bongaerts et al. 2015; Terraneo et al. 2017). The exceptionally large ranges of these species, combined with the general inaccuracy of coral taxonomy, and the specific indications of unrecognized diversity in this family, suggest that cryptic species are likely to be concealed within large ranging nominal species. Previous molecular studies have been limited in geographic scope, and so would not have been able to detect such cryptics associated with the known biogeographic barriers discussed earlier.

The Agariciidae family is moderately diverse, and is comprised of four genera in the Indo-Pacific, two of which are monotypic. The two species rich genera, *Pavona* and *Leptoseris*, are predominantly associated with shallow water and mesophotic reefs environments respectively. Each of these genera contains 13-19 species depending on the taxonomic source, and these species are diverse in form. Colony morphology ranges from delicate fronds such as

those found in *P. cactus* and *L. papyracea*, to large mounding colonies of *P. explanulata* and *P. clavus*, to the distinctive rounded lobes of *P. duerdeni*, and the tube-forming plates of *L. tubulifera*. Despite this diversity, one morphological feature is pervasive across the family: ridges. In *L. mycetoseroides*, ridges form parallel to the edge of growth, and in *P. varians*, *P. venosa*, and *P. chiriquiensis* ridges form perpendicular to the edge of growth. Colonies of *L. yabei* form both directions of ridges, such that it looks like a hybrid of *P. varians* and *L. mycetoseroides*.

A species of particular interest is the widely distributed, very common *P. varians* (Verrill 1864; Veron et al. 2015; DeVantier & Turak 2017; Dietzel et al. 2021). In addition to having a broad geographical distribution, this species is also a depth generalist (Roberts et al. 2019; Montgomery et al. 2021), found from shallow reef flats to mesophotic depths of more than 80 m (Luck et al. 2013). This species, as the name suggests, is morphologically diverse with respect to colony morphology (ranging from foliose to encrusting to plating), skeletal characters (shape, extent, and pattern of ridge formation), as well as soft tissue traits (polyp extension, fluorescence, and color). The original description encompasses this variation and as such this morphological diversity has been lumped into a single species, with the exception of the recently described *P. chiriquinesis* (Glynn et al. 2001).

CORAL PHYLOGENETICS AND TAXONOMY

Detecting and identifying endemic species relies on accurate taxonomic identification, and well-supported phylogenies; two things which have been historically challenging in corals. The morphology of corals is notoriously tricky, species exhibit considerable phenotypic plasticity and intraspecific variation, and there is extensive homoplasy across even distantly related scleractinians (Todd 2008; Budd et al. 2010; Schmidt-Roach et al. 2014). The introduction of molecular techniques revealed inaccurate classification across all taxonomic levels of the scleractinian tree (Romano & Palumbi 1996). Initial progress to delimit species was hampered by the slow evolution of the anthozoan mitogenome, which prevented widespread use of traditional barcoding techniques to assess diversity in this group (Shearer et al. 2002; Hellberg 2006; Chen et al. 2009). But substantial progress has been made revising the taxonomy and

classification of corals (Romano & Palumbi 1996; Kerr et al. 2005; Fukami et al. 2008; Kitahara et al. 2010; Budd et al. 2012; Huang et al. 2016; Arrigoni et al. 2014; 2016; Terraneo et al. 2016).

The advances in molecular data generation and adoption of phylogenomic techniques has increased our understanding of coral systematics considerably in the past five years (Quek & Huang 2021). A multitude of approaches have been employed to resolve coral phylogenies, including genome skimming to assemble whole mitochondrial genomes (Liu et al. 2015; Niu et al. 2018; Tong et al. 2019; Seiblitiz et al. 2020), reduced representation approaches to generate SNP and locus datasets (Combosch & Vollmer 2015; Forsman et al. 2017; 2020; Johnston et al. 2017; Rosser et al. 2017; Cunha et al. 2019; Arrigoni et al. 2020; Wepfer et al. 2020; Bongaerts et al. 2021), ultra conserved element bait sets to recover thousands of neutral loci (Cowman et al. 2020; Ramírez-Portilla et al. 2022), and even whole genomes and transcriptomes (Bhattacharya et al. 2016; Mao et al. 2018; Zhang et al. 2019). These datasets are not only recovering well-supported topologies and delimiting species confidently and accurately, they are illuminating the processes driving coral evolution.

AIMS

The aims of this dissertation are to investigate the phenotypic variation, phylogenomic and geographic diversity of species from the coral family Agariciidae. The unusually large ranges of species in this group indicate a high likelihood of cryptic species, which I expect to be associated with known biogeographic barriers. I will use two approaches to assess the diversity of this family. In Chapter 2 I will combine 208 sequences of a mitochondrial intron with 191 previously published sequences to generate a dataset which represent over 80% of known Indo-Pacific agaricid species, from across the Indo-Pacific.

In Chapter 3 I will exchange taxonomic sampling for genomic data, and generate 120 RAD libraries. These will enable me to assemble whole mitochondrial genomes and 100s of nuclear SNPs. Together these two approaches will reveal the relationships of species in the

family, and the effect of known barriers on species formation. The genomic data will also facilitate statistical tests to determine if introgression is occurring between species.

In Chapter 4 I will use a common garden experimental approach to investigate the extent of phenotypic plasticity in *P. varians*. I will combine cutting edge techniques, such as 3D photogrammetry, symbiont community metabarcoding, laser scanning confocal microscopy and biochemical analysis of functional lipid ratio to understand the role of light in shaping morphology and growth in this species. I will be particularly focusing on the plasticity of ridge formation, because this trait may be facilitating the large range, depth generalism and high abundance of this species.

Together, I hope this work will shed light on this cosmopolitan and underexplored group of corals.

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CHAPTER 2. DIVERSITY AND DISTRIBUTION OF INDO-PACIFIC STONY CORALS OF THE FAMILY AGARICIIDAE

ABSTRACT

Coral taxonomy is a famously challenging field, confounded by high levels of morphological variation within species. Molecular assays have provided some clarity in defining species boundaries, but the slow rate of evolution at mtDNA and high variation in nuclear loci has resulted in few informative markers. Here we resolve members of the coral family Agariciidae, focusing on two dominant genera in the Indo-Pacific that are segregated primarily by depth: mesophotic *Leptoseris* and shallow-water *Pavona*. We obtained specimens at 26 sites including five biogeographic provinces from the East Pacific to the Red Sea, and contribute *cox1-1-rRNA* intron sequence data from 208 corals to augment 191 previously published sequences. Both Maximum Likelihood and Bayesian phylogenies resolved the same overall topology, which confirmed the polyphyly of both *Pavona* and *Leptoseris*, with little correspondence between clades (32) and nominal Indo-West Pacific agaricid species (31). Only seven of 31 nominal species were monophyletic, and several morphologically distinct taxa were not phylogenetically distinct. Most of the cryptic genetic diversity was associated with two nominal species, *P. varians* and *L. mycetoseroides*. *Pavona varians* included six cryptic lineages, two of which were detected across the entire Indo-Pacific, likely indicating undescribed species. Clarifying the taxonomy and identification of these putative new species is essential to accurately manage them.

INTRODUCTION

Accurate identification and delimitation of species is a foundational component of many fields of biology, including biogeography, restoration, and conservation. The incorporation of molecular sequence data has revolutionized species delimitation efforts in many groups, but for corals the use of DNA sequences have revealed considerable knowledge gaps at all taxonomic levels (Romano and Palumbi 1996, Kitahara et al. 2010). As with many plants and macroalgae,

extensive phenotypic plasticity (Todd 2008), considerable intraspecific morphological variation (Flot et al. 2008), and convergent evolution of morphological characters (Waheed et al. 2015) makes identifying coral species particularly challenging. Further, the use of molecular data in coral systematics has been hampered by a dearth of informative markers for both systematics and species delimitation, as anthozoan mitogenomes generally evolve slowly, and other traditional markers are often inadequate for distinguishing closely-related species (Quek & Huang 2021). Given that corals underpin the most biodiverse marine ecosystems, the inability to establish species boundaries limits our ability to understand the individual ecological functions and essential ecosystem services that each species provides to communities around the globe (Roberts et al. 2002).

Understanding and mitigating the impacts of climate change and other anthropogenic stressors also requires accurate taxonomic assignments. Coral reefs are declining globally (Carpenter et al. 2008, Hughes et al. 2017a). However, not all corals are equally affected: some taxa are bleaching more frequently and suffer higher mortality than others (Edmunds et al. 2014; Hughes et al. 2018). Correctly documenting the shift of coral communities and understanding the differential response of different taxa is contingent on accurately identifying species. For example, during the 2016-2017 Great Barrier Reef bleaching assessment, all bleaching response data from corals within the family Agariciidae were lumped together in a single group, rather than split apart at the generic level as for other Scleractinia (Hughes et al. 2017a). This simplification likely masks variation in interspecific sensitivity, such as within the genus *Pavona*, which includes species with a broad spectrum of bleaching susceptibility responses (Marcelino et al. 2013, Swain et al. 2017). These and other taxonomic challenges across all coral taxa (Fukami et al. 2008; Budd et al. 2010; Kitahara et al. 2010; Benzoni et al. 2012; Huang et al. 2014; Marti-Puig et al. 2014; Arrigoni et al. 2016; Johnston et al. 2017; Forsman et al. 2017) hinders our ability to accurately record and understand the response of these important foundation species to climate change.

In some cases, robust phylogenies and informative morphological characters have led to substantial progress towards understanding coral diversity, evolutionary relationships, and historical biogeography (Benzoni et al. 2012; Budd et al. 2012; Huang et al. 2012; Arrigoni et al.

2014; Huang et al. 2016; Forsman et al. 2017). Molecular phylogenetic studies have revealed that morphologically-based studies both overestimated and underestimated species diversity. For instance, early studies of *Pocillopora* recognized more than thirty morphologically distinct species (see Veron & Pichon 1976) but molecular and micromorphological characters recovered fewer than ten highly morphologically-variable species (Schmidt-Roach et al. 2014, Johnston et al. 2017). By contrast, current taxonomic assessments of *Acropora* likely underestimate diversity because of the synonymization of morphologically- and genetically-distinct forms (Cowman et al. 2020). Other studies have found cryptic species concealed within wide-ranging nominal species, with some restricted to certain depths (Bongaerts et al. 2021). Yet others have found cryptic species with smaller ranges concealed within broadly-distributed nominal species, but at the same time effectively synonymized other nominal species such that overall species richness remained constant (Arrigoni et al. 2020). These diverse resolutions of coral taxonomy, phylogeny, and geographic distributions, i.e., increase and decrease in overall richness and distributions, are likely explained by the aforementioned biology of corals and complex biogeographical landscape of the Indo-Pacific (IP) (Bellwood et al. 2005; Renema et al. 2008; Briggs and Bowen 2012; Obura et al. 2016).

The family Agariciidae (Gray 1847) is notable amongst corals for unusual biogeographic patterns: 1) just one species is geographically restricted to the hotspot of marine biodiversity in the coral triangle (CT), 2) multiple nominal species span several zoogeographic breaks between IP marine provinces, and 3) agaricids are well-represented in the generally depauperate East Pacific. These patterns can be summarized as an over-representation of pandemics, and fewer-than-expected CT endemics (Hughes et al. 2002). The exceptional range size of agariciid species is readily apparent in global databases (Veron 2000): out of 18 coral families analyzed, Agariciidae has the 3rd highest average range size (Fig. S2.1), and 7 of the 15 largest ranged species are agariciids (Fig. S2.2).

The unusual species' distributions among agaricids are likely, to some degree, caused by unrecognized cryptic species (Fukami et al. 2008; Budd et al. 2010; Kitahara et al. 2010; Benzoni et al. 2012; Huang et al. 2014; Marti-Puig et al. 2014; Arrigoni et al. 2016; Johnston et al. 2017; Forsman et al. 2017). A handful of molecular studies have included agaricids, but these

have been geographically focused (Luck et al. 2013, Terraneo et al. 2017, Waheed et al. 2015), and are therefore unable to detect cryptic sister species confined to either side of IP biogeographic breaks. The majority of IP agaricid species are represented by two genera predominantly segregated by depth: mesophotic *Leptoseris* (Milne Edwards & Haim 1849) and shallow-water *Pavona* (Lamarck 1801). Depending on the taxonomic authority, these two genera consist of 13 to 17 and 15 to 19 species, respectively, in the IP (WoRMS Hoeksema and Cairns 2021; CotW Veron et al. 2016; IUCN Hoeksema et al. 2014). The family includes three additional monotypic genera exclusive to the IP, *Gardineroseris* (Dana 1846), *Coeloseris* (Vaughan 1918), and *Dactylolechus* (Wells 1954), the latter of which is a deep water azooxanthellate coral.

In this study we assessed patterns of nominal species diversity for the wide-ranging, coral family, Agariciidae. Specifically, we tested the monophyly of mtDNA sequences from several widely distributed nominal species, including the wide-ranging (Fig SM2, Veron 2000), abundant (Dietzel et al. 2021) and highly morphologically diverse (Veron and Pichon 1980) *Pavona varians*. We combined new sequence data from 208 corals with 191 previously published sequences from across the IP. We sampled widely geographically, including specimens from 26 sites across five biogeographic provinces, including between 79 % and 100 % (depending on the taxonomic source) of all nominal species of *Pavona* (15/19 WoRMS, 15/15 CotW, 15/16 IUCN), the majority of *Leptoseris* species (11/17 WoRMS, 11/14 CotW, 11/13 IUCN), and the monotypic genus *G. planulata*. This work provides a broad geographical and taxonomic assessment of this unusual but understudied family of corals.

METHODS

Sample Collection

From 2006 to 2019, 208 samples were collected from across the Indo-Pacific (Fig. 1, see Table S2.1 for full details). Where possible, colonies were photographed *in situ* prior to collection using a Canon G6 camera, in underwater housing (Canon WP-DC34). Photographs for available specimens are presented in Figs. S2.5-14. Specimens were collected while snorkeling,

SCUBA, or rebreather diving, using a hammer and chisel. Small pieces of the colony (<1 cm²) were preserved in either DMSO saturated salt (NaCl) buffer or 96-100% ethanol, and stored at 4° C. Ten species were collected from type localities (seven *Pavona*, three *Leptoseris*, see Table S2.2 for details).

Species Identification

Species were identified by CJL where possible based on colony and corallite morphology, using reference guides (Veron 2000; Veron et al. 2016, Fenner 2005) as well as original descriptions. Type material of Agariciidae deposited in the Harvard Museum of Comparative Zoology (MCZ), Boston, USA, the Natural History Museum (NHM), London, UK, and the US National History Museum (USNM), Washington DC, USA were studied in person by CJL to help identification. Reference images were taken to aid identification of collected specimens. Please see Table S2.2 for full details. Individuals that were not identified to species at collection and were unable to be identified later were given the designation. L. /P. sp. with no numeral. We do not make any attempt to designate the valid version of a species, nor to assess or revise the taxonomy.

DNA Extraction and Sequencing

DNA was extracted using Qiagen DNeasy kits according to the manufacturer's recommendations, with the modification of an extended overnight incubation of tissue with proteinase K, an addition for 4ul of 100mg/ml RNase A before the lysing step, and samples were eluted in 70°C H₂O instead of buffer. The cox1-1-rRNA intron was amplified from 172 colonies using primers and protocol described in Luck et al. (2013). PCR products were sequenced with only the forward primer at the University of Hawai'i at Mānoa's Advanced Studies in Genomics, Proteomics and Bioinformatics sequencing facility using an Applied Biosystems 3730XL DNA Analyzer.

An additional 35 individuals' intron sequences were generated from assembling restriction-site associated DNA sequence libraries to a reference sequence. Libraries were generated for a forthcoming study and prepared following the ezRAD protocol (Toonen et al. 2013), using kapa kits for some libraries as well as Illumina. Libraries were sequenced on

Illumina HiSeq paired-end platform at the Hudson Alpha Institute for Biotechnology and the University of California Berkeley QB3 Genomics facility, except for sample 757 which was sequenced on a paired-end MiSeq platform at Hudson Alpha Institute for Biotechnology.

Reads were paired, trimmed of adapters, and cleaned to remove low quality bases to a minimum Q score of 30 in Geneious R10. Reads were then assembled to published *P. clavus* (DQ643836, Medina et al. 2006) or *P. decussata* (NC_026527, Shi et al. 2016) or previously generated mitogenomes in (Geneious see Table S2.3 for full details), and checked for completeness by eye. Introns generated from Sanger sequencing and the mitogenomes were aligned, after which the intron region from the mitogenome was extracted for use in subsequent analyses.

Phylogenetic analyses and geographic distributions

Intron sequences from 208 specimens for this study were manually checked and edited using Geneious R10, and combined with 191 published sequences retrieved from NCBI Genbank or EMBL (Table S2.1; Medina et al. 2006, Luck et al. 2013; Wares 2014; Shi et al. 2016; Waheed et al. 2015; Bongaerts et al. 2015; Terraneo et al. 2017; Chapter 4). Original identifications were retained including any putative new species with “sp. 1” designations.

A total of 399 sequences were aligned under default parameters using the ClustalW plug-in in Geneious R10. A Maximum Likelihood phylogeny was constructed using IQ-Tree (Nguyen et al. 2015) on the CIPRES computing cluster (Miller et al. 2010), under default parameters, and 1000 replicates to determine bootstrap support values. Prior to phylogenetic tree construction the K2P DNA substitution model with a proportion of invariant sites, was selected as the best model determined from ModelFinder and corrected Bayesian Information Criterion (Trifinopoulos et al. 2016; Kalyaanamoorthy et al. 2017) within IQ-Tree.

A second phylogeny was built using the Bayesian inference criterion implemented in MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001) on the CIPRES computing cluster (Miller et al. 2010), under a K2P + I model. The phylogenetic analysis ran four runs of 5,000,000 generations on four Markov chains, sampling every 2,000 generations. The temperature was set to 0.3, with 3

swaps between chains attempted every generation. The first 500,000 generations were discarded as burn-in. The traces of the four runs were assessed for mixing and convergence in Tracer v1.7.2 (Rambaut et al. 2018), and combined which allowed for an Effective Sample Size of over 625 for all estimated parameters, and this combined tree was used for further analysis. For both Maximum Likelihood and Bayesian inference *Siderastrea radians* was used as an outgroup (DQ643838, Medina et al. 2006).

Preliminary analyses revealed that many nominal species were polyphyletic but that many small groups of sequences formed well-supported clades. We labeled each distinct clade with a number for ease of reference within this paper. We delineated putative species under two circumstances. First, if clades were reciprocally monophyletic and morphologically distinct, we considered them putative species. Second, we considered paraphyletic species as taxa that were morphologically distinct from the monophyletic clade nested within. We make the exception of paraphyly for two reasons. First, speciation is a process and paraphyly is an intermediate state on the way to monophyly (deQueiroz 2007, Mallet 2013). Many species are likely paraphyletic, and the recognition of only monophyletic species is likely not an effective tool for describing biodiversity at the species level (Nixon & Wheeler 1990; Rieseberg & Brouillet 1994). Second, the benefits of retaining highly distinct paraphyletic species outweigh those of a strict phylogenetic classification for many end-users in ecology and conservation (Schmidt-Lebuhn 2010). Lumping taxa with radically different morphological forms (and probable ecological function) based on a single marker that has likely not yet sorted into reciprocal monophyletic clades is potentially premature, and potentially counterproductive until more data are gathered.

We assessed the biogeographic distributions of putative species by determining whether an individual within the clade is found in one of the five biogeographic provinces. We recognize these are not true distribution maps but are instead meant to visualize if lineages are restricted to particular provinces. For these maps we assume contiguous distribution of lineages, so if individuals are found in non-adjacent provinces we included the intervening province as part of the distribution (Table S2.4).

RESULTS

Total DNA alignment of the *cox1*-rRNA intron was 878 bp long and contained 399 sequences between 392 bp and 745 bp. Both Maximum Likelihood and Bayesian phylogenies resolved the same overall topology (Figs. 2.2, S2.3, S2.4), and both had similarly high bootstrap and posterior probability clade support. Neither tree included a monophyletic *Pavona* or *Leptoseris*, similar to previous studies.

Overall, the *cox1*-rRNA phylogeny shows that despite numerical similarity there is little correspondence between clades (32) and nominal Indo-West Pacific agaricid species (31): most of the nominal species are not monophyletic (Fig 2.2). Sequences from thirteen of 31 (42%) nominal taxa (*L. explanata*, *L. hawaiiensis*, *L. incrustans*, *L. mycetoseroides*, *L. scabra*, *L. tubulifera*, *P. chiriquienis*, *P. clavus*, *P. decussata*, *P. duerdeni*, *P. explanulata*, *P. varians*, *P. venosa*) were polyphyletic. Sequences from two nominal taxa (6%) were paraphyletic (*P. sp. 1*, *L. sp. 1*), both with a single morphologically-distinct clade of sequences nested within that unambiguously matched the description of a different nominal species of either *Pavona* or *Leptoseris*. Only sequences from seven of 31 (23%) nominal species (*L. foliosa*, *L. papyracea*, *L. yabei*, *P. minuta*, *G. planulata*, *L. fragilis*, and *P. maldivensis*) were monophyletic. The remaining nine of 31 (29%) nominal taxa appear in a single clade in the tree (not polyphyletic), but are indistinguishable at this marker from other nominal species (*L. cf. hawaiiensis*, *L. glabra*, *P. bipartita*, *P. cactus*, *P. danai*, *P. diffluens*, *P. frondifera*, *P. gigantea*, *P. sp. 2*). Bootstrap and PP support for most of the 32 clades was strong: 30 (94%) clades have over 75 bootstrap support and 22 (69%) clades have over 95 posterior probability.

Most of the 32 clades are present in more than one biogeographic province. Two (6%) were found in every province, twelve (38%) were found in three or four adjacent provinces, seven (22%) were found in two provinces, and eleven others (34%) were found in a single province (Fig. 2.3, S2.5 -14). Our phylogeny resolved one instance of cryptic diversity associated with a known phylogeographic break. All samples of the nominal species *P. maldivensis* formed a monophyletic clade, but Indian Ocean/Red Sea and Pacific individuals formed two reciprocally monophyletic clades (Fig. 2.2).

DISCUSSION

We evaluated the phylogenetic relationships of Indo-Pacific (IP) corals in the family Agariciidae and testing the species cohesiveness of *Pavona varians*, the most abundant and morphologically variable member of the family. To achieve these goals, we analyzed 399 sequences of the mitochondrial *cox1*-1-rRNA intron from 31 nominal taxa. The sampling represents the majority (77%) of IP agaricids, generating one of the largest regional phylogenetic studies of any coral family to date.

The analysis yielded two primary results. First, less than one-quarter of nominal IP agaricid species were monophyletic. Although two nominal taxa were paraphyletic and likely represent taxa whose mtDNA genomes may have not yet sorted themselves into monophyletic clades, thirteen of 32 nominal agaricids in this study were polyphyletic, nominal species with representative sequences scattered widely across the agaricid mtDNA tree. A striking example is *P. duerdeni*, which forms semi-massive characteristic “pork chop” lobes (Fig. S2.6), with highly interconnected, tightly packed corallites which gives colonies a smooth surfaced appearance. Individuals unequivocally corresponding to the nominal species *P. duerdeni* were recovered in three clades (6, 7, & 28), two of which (6 & 28) with at least three specimens each. Thus, in contrast to most other cryptic marine invertebrate species that consist of complexes of genetically distinct, but closely related lineages or cryptic species “complexes” (Knowlton 1993), many of the cryptic agaricids uncovered in this study appear distantly related taxa.

Most of the cryptic diversity was associated with morphological forms that unambiguously corresponded to two nominal species, *P. varians* and *L. mycetoseroides*. Indeed, previous studies of agaricids have found cryptic taxa (Luck et al. 2013; Terraneo et al. 2017), but the discovery of potentially six putative species corresponding to the morphological description of *P. varians* was unexpected. The original description of *P. varians* is brief, explicitly mentioning many colony forms, and describing generalized morphological traits (e.g., “short angular or convoluted crests rising from the surface”, Verrill 1864, pp. 55). Our collections were focused on capturing the morphological diversity of *P. varians*, and we observed slight but

consistent differences between several of these polyphyletic lineages: characters observable from photographs including skeletal traits such as ridge shape and patterning, and soft tissue traits such as polyp extension and fluorescence. For example Fig. 2.4, includes images of two colonies that both match the taxonomic description of *P. varians*, but the *cox1-1-rRNA* phylogeny places them in different parts of the tree, clades 26 and 32. Despite matching the description of *P. varians*, there are consistent morphological differences between the two lineages, such as more narrow and acutely angled ridges in individuals from clade 26, thicker septa-costae in individuals from clade 32, and differences in relative corallite size (Fig. 2.4). Not all of the lineages of *P. varians* are morphologically distinguishable, as individuals from clade 21 appear informally indistinguishable from individuals of clade 7, but were considered separate species given their different position in the *cox1-1-rRNA* tree. Future quantitative morphological analyses may identify more consistent synapomorphies that distinguish most putative species.

In contrast to the splitting and spreading of the morphological forms of several nominal taxa across the agaricid tree, our second major finding was that several other morphologically distinct taxa were not phylogenetically distinct at the *cox1-1-rRNA* intron. For example, clade 7 includes nearly identical (<2%) sequences from several highly morphologically distinct species. This clade contains a spectrum of intergrading morphological forms ranging from encrusting with little ridge formation (*P. varians* Fig. 2.4), to semi-massive forms with chunky, often angular fronds (*P. frondifera*), to delicate thin leaf-like morphologies (*P. cactus*)(Fig. S2.7 & S2.8). Similarly, clade 18, includes species with massive globular forms with densely packed interconnected corallites (*P. gigantea*), as well as uni-facial laminar colonies with widely-spaced, large corallites (*L. explanata*) (Fig. S2.11, Terraneo et al. 2017). Although *P. varians* from clade 7 exhibits a high degree of phenotypic plasticity in the development of colony surface ridges in response to light variation (Chapter 4), the gross morphological differences among colonies of these species is unlikely to be explained by intra-specific variation or phenotypic plasticity.

There are several explanations for widespread polyphyly within the agaricids. The scattering of morphologies corresponding to *P. varians* and *L. mycetoseroides* across the agaricid tree may be the result of convergent evolution, where ridged morphologies have evolved independently multiple times. In a whole genome analysis of eighteen *Acropora* species, each of

the four recovered clades was found to have multiple diverse morphologies indicating independent evolution of morphotypes (Shinzato et al. 2021). Alternatively, the folded or crested encrusting to laminar morphologies of *P. varians* and *L. mycetoseroids* may represent a plesiomorphic morphology that has been retained in extant lineages.

Both paraphyly and the lumping of morphologically distinct taxa could also be explained by interspecific gene flow, a process long thought to be important in coral evolution (Veron 1995; van Oppen et al. 2000; Vollmer & Palumbi 2002; Richard & Hobbs 2015), and which is increasingly recognized in other systems (Lamichhaney et al. 2015; Campbell et al. 2018). Our overall results are similar to those from a phylogenetic analysis of an mtDNA intergenic spacer in *Acropora*, in which most nominal species were also polyphyletic, but results were not consistent with a nuclear marker (van Oppen et al. 2001). This extensive disconnect between current taxonomy and recovered lineages in acroporids, as well as mito-nuclear discordance, was observed in several multilocus datasets (Cowman et al. 2020; Ramírez-Portilla et al. 2022). In the present study of agaricids, the sympatric distribution of many of the agaricid lineages we recovered supports the potential for hybridization in this family. Despite a general paucity of spawning information for agaricids, records of sympatric species spawning simultaneously is consistent with the possibility of hybridization (Baird et al. 2020 and references therein). Indeed, in the East Pacific (the location of the majority of studies on spawning of *Pavona*), *P. varians* spawns throughout the year, producing many gametes (Glynn et al. 2017), and multiple opportunities for hybridization.

The lack of phylogenetic resolution between morphologically distinct nominal species and lineages resembling *P. varians* and *L. mycetoseroides* may reflect recent bursts of speciation and the retention of ancestral mtDNA polymorphisms: species whose morphological evolution, presumably driven by natural selection, has outpaced the rate at which mtDNA neutrally sorts into reciprocally-monophyletic clades. This is particularly likely for many corals with demographic traits known to slow the process of sorting, such as large populations, and therefore assumed effective population sizes, due to their wide ranges in the Indo-Pacific (Dietzal et al. 2021, but see Hedgecock & Pudovkin 2011). Further, the slow mitochondrial mutation rates of corals, a feature of anthozoans more broadly (Shearer et al. 2002), may also extend the time for

sufficient mutations to accumulate which enable differentiation of new species. Whether all of the nominal species included in clade 7 and others are recovered, will have to be resolved with multilocus data and species delimitation methods that can together discriminate ancestral polymorphism from hybridization and introgression.

Identifying agaricids, as with many coral families, is challenging, compounded by generalized species descriptions focused on overall colony form and shape (see above), missing type specimens (*P. cactus* and *P. frondifera*), and multiple holotypes with varying morphologies (as for *P. varians*, Table S2.2). For example, *P. duerdeni* and *P. clavus* have a complicated and confusing taxonomic history (Crossland 1952, Wells 1954, Scheer & Pillai 1974, Veron & Pichon 1979; Veron 2000). Despite the type specimens appearing markedly different in septa-costae, gross morphology, and colony surface topology, they were at one time synonymized because of high intraspecific variability (Scheer & Pillai 1974; Veron & Pichon 1979). Unsurprisingly, one sequence in clade 6 from a colony identified as *P. clavus* from a previous study, clusters in a clade group otherwise comprising seven sequences from *P. duerdeni* specimens (Medina et al. 2006). If this individual were considered *P. duerdeni*, then the nominal species *P. clavus* would no longer be polyphyletic in our phylogeny. Therefore, a few instances of polyphyly could be the result of misidentification. However, the majority of polyphyletic nominal taxa are likely to be the result of biological signal because there are multiple specimens and corresponding sequences from the polyphyletic and lumped taxa, and in some instances specimens and sequences from different studies. For example, specimens identified as *L. mycetoseroides* in three different studies were recovered into two different clades: 12 (Terraneo et al. 2017 & this study) and 30 (Luck et al. 2013 & this study). Further, *P. chiriquiensis* was recovered as polyphyletic (clades 31 and 32) despite being collected by one of the describing authors of the species (Glynn et al. 2001).

A third finding from our study was that, despite the recovery of so many closely related and potentially recently diverged species, few sister clades are associated with IP biogeographic boundaries. We expected some of the exceptionally large ranges within IP agaricids to be an artifact of cryptic species formed in allopatry on either side of known biogeographic barriers. Yet we recovered only one instance in which sister clades are associated with any of the four IP

biogeographic boundaries. The two sister lineages of *P. maldivensis*, one including individuals from the Indian Ocean and Red Sea, and the other comprised of samples from the Pacific, are the only example of sister-clades whose origin may be linked to the Sunda Shelf Barrier (Gaither & Rocha 2013; Choat et al. 2012; Williams & Reid 2004; Barber et al. 2006; Oury et al. 2020). The SSB forms as a result of sea-level change associated with the Plio-Pleistocene glacial cycles (< 2.5 mya), when lower sea-level leads to reduced connectivity between the Indian and Pacific Oceans (Gaither & Rocha 2013). This unexpected outcome can be explained in three ways. First, biogeographic evidence of speciation caused by the periodic emergence of land or intensification of oceanographic barriers can be quickly erased by range expansions (Valentine & Jablonski 1983; Marko 1998; Ellingson & Krug 2006; Bowen et al. 2016). A second explanation is that these barriers may not be important drivers of agaricid speciation in the IP. Lastly, this single intron may be evolving too slowly to capture recent divergence between Indian and Pacific ocean agaricid populations.

Lastly, we found that despite being subdivided into six genetically-distinct clades, several clades of *P. varians* still have exceptionally large ranges. Among the six cryptic lineages of *P. varians*, the geographic range of *P. varians* from clades 32 and 7 span the entire Indo-Pacific, from the Indian Ocean to Panama, a distribution found in only 3% of corals (Veron et al. 2015). Further, none of the other lineages resembling *P. varians* (Clades 21, 22, 23, 26) are reduced to a single biogeographic province. And while, this could be interpreted as a positive indicator for these putative species, current estimates of nominal species abundances are likely to be overestimated, such as e.g., *L. mycetoseroides* and *P. varians* (Dietzel et al. 2021). And while some *P. varians* lineages may remain exceptionally abundant (e.g., *P. varians* from Clade 7), others could be wide-ranging but not abundant or locally rare. Clarifying the taxonomy and identification of these putative new species is essential to accurately manage them.

CONCLUSION

Accurately identifying species and determining their evolutionary relationships to each other, are fundamental tasks in biology. They provide the framework from which we can answer complex questions about speciation, community dynamics, and conservation management. These

tasks have proven particularly difficult in corals, due to their extensive phenotypic plasticity, intraspecific morphological variation, and recent speciation among others (Stat et al. 2012).

Corals in the family Agariciidae exemplify a lot of these problems, and add the additional challenges associated with large ranges. Detailed studies of cryptic species typically demonstrate that most are ecologically differentiated (Fišer et al. 2017). Here we extend the findings of polyphyly in Hawaiian coral genera, *Leptoseris* and *Pavona* (Luck et al. 2013) to demonstrate that this is an ocean-wide phenomenon. The discovery of such high cryptic diversity in *Pavona* and *Leptoseris* potentially changes our understanding of agaricid ecological functions and stress response at a time when corals are under mounting anthropogenic pressures. Previous bleaching surveys may have been inaccurately lumping sympatric *P. varians* clades into a single averaged bleaching response, when each lineage may have differing sensitivities which are currently being overlooked. Further, the apparent bleaching resistance of some *Pavona* species has been the focus of mechanistic bleaching research including the effect of symbiont communities and skeletal geometry (Cunning et al. 2015; Marcelino et al. 2013), again including separate lineages as a single evolutionary unit could lead to incomplete or erroneous conclusions. Alternatively, these cryptic species may be ecologically similar and functionally redundant in the ecosystem, thereby increasing the resiliency of the reef as a whole (Elmqvist et al. 2003, Fiser et al. 2017, McWilliam et al. 2018).

Table S2.1. Collection information for Indo-Pacific agariciid coral samples. Date and location only included only for samples not taken from GenBank. Recovered Cox-1-rRNA clade only included for Indo-Pacific species (*Pavona* and *Leptoseris*).

ID	Sample ID	Date (dd/mm/yyyy)	Location	Cox1-1-rRNA Clade	Source
<i>S. radians</i>					Medina et al. 2006
<i>A. humilis</i>					Medina et al. 2006
<i>A. sp</i>	KP178910				Bongaerts et al. 2016
<i>A. sp</i>	KP178911				Bongaerts et al. 2016
<i>A. sp</i>	KP178912				Bongaerts et al. 2016
<i>A. sp</i>	KP128908				Bongaerts et al. 2016
<i>A. sp</i>	KP128909				Bongaerts et al. 2016
<i>A. sp</i>	KP128901				Bongaerts et al. 2016
<i>A. sp</i>	KP128902				Bongaerts et al. 2016
<i>A. sp</i>	KP128903				Bongaerts et al. 2016
<i>A. sp</i>	KP128904				Bongaerts et al. 2016
<i>A. sp</i>	KP128905				Bongaerts et al. 2016
<i>A. sp</i>	KP128906				Bongaerts et al. 2016
<i>A. sp</i>	KP128907				Bongaerts et al. 2016
<i>L. scabra</i>	KF437753			3	Luck et al. 2013
<i>L. scabra</i>	KF437770			3	Luck et al. 2013
<i>L. scabra</i>	KF437748			3	Luck et al. 2013

<i>L. scabra</i>	KF437732			3	Luck et al. 2013
<i>L. scabra</i>	KF437726			3	Luck et al. 2013
<i>L. scabra</i>	KF437725			3	Luck et al. 2013
<i>L. scabra</i>	KF437724			3	Luck et al. 2013
<i>L. scabra</i>	KF437723			3	Luck et al. 2013
<i>L. scabra</i>	KF437729			3	Luck et al. 2013
<i>L. scabra</i>	KF437730			3	Luck et al. 2013
<i>L. scabra</i>	KF437740			3	Luck et al. 2013
<i>L. scabra</i>	KF437731			3	Luck et al. 2013
<i>L. scabra</i>	OAK60	2017	Kewalo Basin, O‘ahu	3	This study
<i>P. cactus</i>	JPN43	12/11/2017	Seragaki, Okinawa, Japan	7	This study
<i>P. cactus</i>	P. cactus 1			7	Terraneo et al. 2017
<i>P. cactus</i>	P. cactus 2			7	Terraneo et al. 2017
<i>P. cactus</i>	P. cactus 3			7	Terraneo et al. 2017
<i>P. cactus</i>	P. cactus 4			7	Terraneo et al. 2017
<i>P. cactus</i>	PAL12	15/12/2015	Ngeruktabel, Palau	7	This study
<i>P. cactus</i>	PAL2	15/12/2015	Ngeruktabel, Palau	7	This study
<i>P. frondifera</i>	AMS17	19/03/2016	Fagasa Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS21	19/03/2016	Faga'alu Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS25	19/03/2016	Faga'alu Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS36	19/03/2016	Faga'alu Bay, American Samoa	7	This study
<i>P. frondifera</i>	GM30	11/12/2015	Power Plant Channel, Guam	7	This study
<i>P. frondifera</i>	GM33B	10/12/2015	Agana Bay, Guam	7	This study
<i>P. frondifera</i>	AMS32	19/03/2016	Faga'alu Bay, American Samoa	7	This study

<i>P. frondifera</i>	AMS37	19/03/2016	Faga'alu Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS5	19/03/2016	Fagasa Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS71	21/03/2016	Faga'alu Bay, American Samoa	7	This study
<i>P. frondifera</i>	AMS8	19/03/2016	Fagasa Bay, American Samoa	7	This study
<i>P. frondifera</i>	GM10	11/12/2015	Power Plant Channel, Guam	7	This study
<i>P. frondifera</i>	GM55	11/12/2015	Power Plant Channel, Guam	7	This study
<i>P. frondifera</i>	<i>P. frondifera</i> 1			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 1*			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 2			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 3			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 4			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 5			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 6			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 7			7	Terraeno et al. 2017
<i>P. frondifera</i>	<i>P. frondifera</i> 8			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 1			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 2			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 3			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 4			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 5			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 6			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 7			7	Terraeno et al. 2017
<i>P. danai</i>	<i>P. danai</i> 8			7	Terraeno et al. 2017
<i>P. varians</i>	757	7/8/2010	Midway Atoll, HI	7	This Study
<i>P. varians</i>	AMS14	19/03/2016	Fagasa Bay, American Samoa	7	This Study

<i>P. varians</i>	AMS48	21/03/2016	Faga'alu Bay, American Samoa	7	This Study
<i>P. varians</i>	AMS53	20/03/2016	Leone Bay, American Samoa	7	This Study
<i>P. varians</i>	BIP3 (2)	15/04/2016	Puako Bay, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIR3	19/04/2016	Richards Beach Park, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIR9 (2)	19/04/2016	Richards Beach Park, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	GM2	11/12/2015	Powerplant Channel, Guam	7	This Study
<i>P. varians</i>	GM24	11/12/2015	Powerplant Channel, Guam	7	This Study
<i>P. varians</i>	GM25	11/12/2015	Family Beach, Guam	7	This Study
<i>P. varians</i>	GM28	11/12/2015	Family Beach, Guam	7	This Study
<i>P. varians</i>	GM60	11/12/2015	Family Beach, Guam	7	This Study
<i>P. varians</i>	OAM5	8/3/2016	Maunalua Bay, O'ahu, HI	7	This Study
<i>P. varians</i>	RMI13	30/05/2015	Arno Dock, Republic of Marshall Islands	7	This Study
<i>P. varians</i>	RMI45	1/6/2015	Arno Dock, Republic of Marshall Islands	7	This Study
<i>P. varians</i>	08-1884	15/06/2008	Kure Atoll, HI	7	This Study
<i>P. varians</i>	AMS13	19/03/2016	Fagasa Bay, American Samoa	7	This Study

<i>P. varians</i>	AMS33	19/03/2016	Faga'alu Bay, American Samoa	7	This Study
<i>P. varians</i>	AMS35	19/03/2016	Faga'alu Bay, American Samoa	7	This Study
<i>P. varians</i>	BIL1	16/04/2016	Limukoko Point, Hawai'i Island, HI	7	PP Paper
<i>P. varians</i>	BIL4	16/04/2016	Limukoko Point, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIL5	16/04/2016	Limukoko Point, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIL6	16/04/2016	Limukoko Point, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIP10	15/04/2016	Puako Bay, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIP4	15/04/2016	Puako Bay, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIP8	15/04/2016	Puako Bay, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIP9	15/04/2016	Puako Bay, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIR1	19/04/2016	Richards Beach Park, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIR5	19/04/2016	Richards Beach Park, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	BIR6	19/04/2016	Richards Beach Park, Hawai'i Island, HI	7	This Study
<i>P. varians</i>	GENO1			7	Chapter 4
<i>P. varians</i>	GENO2			7	Chapter 4
<i>P. varians</i>	GENO3			7	Chapter 4

<i>P. varians</i>	GM29	11/12/2015	Powerplant Channel, Guam	7	This Study
<i>P. varians</i>	GM3	10/12/2015	Agana Bay, Guam	7	This Study
<i>P. varians</i>	GM4	10/12/2015	Agana Bay, Guam	7	This Study
<i>P. varians</i>	GM42	11/12/2015	Family Beach, Guam	7	This Study
<i>P. varians</i>	GM48	12/12/2015	Double Reef, Guam	7	This Study
<i>P. varians</i>	GM49	11/12/2015	Powerplant Channel, Guam	7	This Study
<i>P. varians</i>	GM58	11/12/2015	Powerplant Channel, Guam	7	This Study
<i>P. varians</i>	JON4211	5/6/2006	Johnston Atoll	7	This Study
<i>P. varians</i>	JON4285	6/6/2006	Johnston Atoll	7	This Study
<i>P. varians</i>	JON4332	7/6/2006	Johnston Atoll	7	This Study
<i>P. varians</i>	JPN3	9/11/2017	Hedo, Okinawa, Japan	7	This Study
<i>P. varians</i>	KF437747			7	Luck et al. 2013
<i>P. varians</i>	KF437754			7	Luck et al. 2013
<i>P. varians</i>	KF437755			7	Luck et al. 2013
<i>P. varians</i>	KF437761			7	Luck et al. 2013
<i>P. varians</i>	KF437773			7	Luck et al. 2013
<i>P. varians</i>	KF437786			7	Luck et al. 2013
<i>P. varians</i>	KF437789			7	Luck et al. 2013
<i>P. varians</i>	MLD26	27/11/2019	Magoodhoo Atoll, Maldives	7	This study
<i>P. varians</i>	MLD47	29/11/2019	Magoodhoo Atoll, Maldives	7	This study
<i>P. varians</i>	MLD6	27/11/2018	Magoodhoo Atoll, Maldives	7	This study
<i>P. duerdeni</i>	O50	05/02/2010	Howland Island, USA	7	This study
<i>P. varians</i>	OAKB1	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study

<i>P. varians</i>	OAKB10	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAKB2	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This Study
<i>P. varians</i>	OAKB3	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAKB5	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	Chapter 4
<i>P. varians</i>	OAKB7	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAKB8	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAKB9	25/08/2016	Kāneʻohe Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAM2	3/8/2016	Maunalua Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAM4	1/8/2016	Maunalua Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAM6	3/8/2016	Maunalua Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAM7	3/8/2016	Maunalua Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	OAM8	3/8/2016	Maunalua Bay, Oʻahu, HI	7	This study
<i>P. varians</i>	PAL28	16/12/2015	Nikko Bay, Palau	7	This study
<i>P. varians</i>	PAN20	8/12/2018	Canal de Afuera Island, Gulf of Chiriquí, Panama	7	This study
<i>P. varians</i>	PAN21	8/12/2018	Canal de Afuera Island, Gulf of Chiriquí, Panama	7	This study

<i>P. varians</i>	PAN22	8/12/2018	Canal de Afuera Island, Gulf of Chiriquí, Panama	7	This study
<i>P. varians</i>	PHU039	15/02/2011	Phiphi Don, Thailand	7	This Study*
<i>P. varians</i>	PHU125	15/02/2011	Phiphi Lae, Thailand	7	This Study*
<i>P. varians</i>	PHU311	16/02/2011	Hae, Thailand	7	This Study*
<i>P. varians</i>	PHU386	17/02/2011	Ao Tangken, Thailand	7	This Study*
<i>P. varians</i>	RMI44	1/6/2015	Arno Dock, Republic of Marshall Islands	7	This study
<i>P. varians</i>	RMI46	1/6/2015	Arno Dock, Republic of Marshall Islands	7	This study
<i>P. sp.</i>	RSKA11	9/5/2011	Abu Madafi, Red Sea, Saudi Arabia	7	This study
<i>P. varians</i>	SCS6248		Dongsha Atoll	7	This study
<i>P. varians</i>	SCS6238		Dongsha Atoll	7	This study
<i>P. venosa</i>	PAL18	15/12/2015	Ngeruktabel, Palau	7	This study
<i>P. venosa</i>	GM19	10/12/2015	Agana Bay, Guam	7	This study
<i>P. venosa</i>	GM21	11/12/2015	Powerplant Channel, Guam	7	This study
<i>P. venosa</i>	JPN18	10/11/2017	Seragaki, Okinawa, Japan	7	This study
<i>P. venosa</i>	PAL6	15/12/2015	Ngeruktabel, Palau	7	This study
<i>P. venosa</i>	RMI15	30/05/2015	Arno Dock, Republic of Marshall Islands	7	This study
<i>P. clavus</i>				6	Medina et al. 2016 (clavus)
<i>P. duerdeni</i>				6	Luck et al. 2013

<i>P. duerdeni</i>	393	19/04/2010	Kingman Reef, USA	6	This study
<i>P. duerdeni</i>	GM57 (2)	12/12/2015	Double Reef, Guam	6	This study
<i>P. duerdeni</i>	JPN54	13/11/2017	Seragaki, Okinawa, Japan	6	This study
<i>P. duerdeni</i>	GM65	12/12/2015	Double Reef, Guam	6	This study
<i>P. duerdeni</i>	JAR146	3/4/2010	Jarvis Island, USA	6	This study
<i>P. duerdeni</i>	PAL8	16/12/2015	Nikko Bay, Palau	6	This study
<i>P. sp 1</i>	KF437745			5	Luck et al. 2013
<i>P. sp 1</i>	KF437774			5	Luck et al. 2013
<i>P. sp 1</i>	KF437744			5	Luck et al. 2013
<i>P. sp 1</i>	KF437743			5	Luck et al. 2013
<i>P. sp 1</i>	KF437742			5	Luck et al. 2013
<i>P. minuta</i>	MLD46	28/11/2019	Magoodhoo Atoll, Maldives	4	This study
<i>P. minuta</i>	MLD50	28/11/2019	Magoodhoo Atoll, Maldives	4	This study
<i>P. minuta</i>	MLDX	27/11/2019	Magoodhoo Atoll, Maldives	4	This study
<i>L. yabei</i>	L. yabei 1			2	Terraneo et al. 2017
<i>L. yabei</i>	L. yabei 2			2	Terraneo et al. 2017
<i>L. yabei</i>	L. yabei 3			2	Terraneo et al. 2017
<i>L. yabei</i>	L. yabei 4			2	Terraneo et al. 2017
<i>L. yabei</i>	JPN15	12/11/2017	Seragaki, Okinawa, Japan	2	This study
<i>L. mycetoseroides</i>	KF437768				Luck et al. 2013
<i>P. clavus</i>	P. clavus 1			19	Terraneo et al. 2017
<i>P. clavus</i>	PAL25	16/12/2015	Nikko Bay, Palau	19	This study
<i>P. clavus</i>	MLD18	27/11/2019	Magoodhoo Atoll, Maldives	19	This study

<i>P. bipartita</i>	MLD7	27/11/2019	Magoodhoo Atoll, Maldives	19	This study
<i>L. tubulifera</i>	OAK42	2016	Kewalo Basin, O‘ahu	1	This study
<i>L. tubulifera</i>	OAK35	2016	Kewalo Basin, O‘ahu	1	This study
<i>L. mycetoseroides</i>	KF437775			1	Luck et al. 2013
<i>L. mycetoseroides</i>	KF437777			1	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437784			1	Luck et al. 2013
<i>L. sp.</i>	KF437739			1	Luck et al. 2013
<i>P. sp. 2</i>	KF437760			1	Luck et al. 2013
<i>P. sp. 2</i>	KF437765			1	Luck et al. 2013
<i>P. sp. 2</i>	KF437764			1	Luck et al. 2013
<i>P. sp. 2</i>	KF437785			1	Luck et al. 2013
<i>L. sp.</i>	SA0943			1	Terraneo et al. 2017
<i>L. sp.</i>	SA0967			1	Terraneo et al. 2017
<i>L. papyracea</i>	KF437781			8	Luck et al. 2013
<i>L. papyracea</i>	KF437778			8	Luck et al. 2013
<i>L. foliosa</i>	LK934507			9	Terraneo et al. 2014
<i>L. foliosa</i>	LK934508			9	Terraneo et al. 2014
<i>P. explanulata</i>	TER28			10	Waheed et al. 2015
<i>P. explanulata</i>	<i>P. explanulata</i> 2			10	Terraneo et al. 2017
<i>P. explanulata</i>	<i>P. explanulata</i> 3			10	Terraneo et al. 2017
<i>P. explanulata</i>	<i>P. explanulata</i> 4			10	Terraneo et al. 2017
<i>P. explanulata</i>	<i>P. explanulata</i> 5			10	Terraneo et al. 2017

<i>L. hawaiiensis</i>	KF437720			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437721			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437722			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437736			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437737			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437738			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437749			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437750			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437751			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437752			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437782			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437783			11	Luck et al. 2013
<i>L. hawaiiensis</i>	KF437787			11	Luck et al. 2013
<i>L. mycetoseroides</i>	JPN47	11/11/2017	Hedo, Okinawa, Japan	12	This study
<i>L. mycetoseroides</i>	JPN49	12/11/2017	Seragaki, Okinawa, Japan	12	This study
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 7			12	Terraneo et al. 2017

<i>L. mycetoseroides</i>	L. mycetoseroides 8			12	Terraneo et al. 2017
<i>L. mycetoseroides</i>	L. mycetoseroides 9			12	Terraneo et al. 2017
<i>L. mycetoseroides</i>	L. mycetoseroides 10			12	Terraneo et al. 2017
<i>L. mycetoseroides</i>	L. mycetoseroides 11			12	Terraneo et al. 2017
<i>L. mycetoseroides</i>	L. mycetoseroides 12			12	Terraneo et al. 2017
<i>L. incrustans</i>	OAK10	2016	Kewalo Basin, O‘ahu	13	This study
<i>L. incrustans</i>	OAK13	2016	Kewalo Basin, O‘ahu	13	This study
<i>L. incrustans</i>	OAK15	2016	Kewalo Basin, O‘ahu	13	This study
<i>L. incrustans</i>	KF437766			13	Luck et al. 2013
<i>L. incrustans</i>	KF437767			13	Luck et al. 2013
<i>L. incrustans</i>	KF437757			13	Luck et al. 2013
<i>L. incrustans</i>	KF437758			13	Luck et al. 2013
<i>L. incrustans</i>	KF437759			13	Luck et al. 2013
<i>L. sp1</i>	KF437771			15	Luck et al. 2013
<i>L. sp1</i>	KF437756			15	Luck et al. 2013
<i>L. sp1</i>	KF437728			15	Luck et al. 2013
<i>L. sp1</i>	KF437733			15	Luck et al. 2013
<i>L. sp1</i>	KF437734			15	Luck et al. 2013
<i>L. sp1</i>	KF437746			15	Luck et al. 2013
<i>L. sp1</i>	KF437727			15	Luck et al. 2013
<i>L. sp1</i>	KF437741			15	Luck et al. 2013

<i>L. sp</i>	JPN8	10/11/2017	Seragaki, Okinawa, Japan	14	This study
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 1			14	Terraneo et al. 2017
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 2			14	Terraneo et al. 2017
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 3			14	Terraneo et al. 2017
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 4			14	Terraneo et al. 2017
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 5			14	Terraneo et al. 2017
<i>L. mycetoseroides</i>	<i>L. mycetoseroides</i> 6			14	Terraneo et al. 2017
<i>L. explanata</i>	<i>L. explanata</i> 3			16	Terraneo et al. 2017
<i>P. explanulata</i>	<i>P. explanulata</i> 1			16	Terraneo et al. 2017
<i>L. tubulifera</i>	KF437763			17	Luck et al. 2013
<i>L. tubulifera</i>	KF437772			17	Luck et al. 2013
<i>L. tubulifera</i>	KF437769			17	Luck et al. 2013
<i>P. explanulata</i>	AMS78	23/03/2016	Leone Bay, American Samoa	18	This study
<i>P. explanulata</i>	O63		Howland	18	This study
<i>P. explanulata</i>	JPN64	13/11/2017	Seragaki, Okinawa, Japan	18	This study
<i>P. explanulata</i>	RED05			18	Waheed et al. 2015
<i>P. gigantea</i>	PAR4	3/6/2017	Sea of Cortez, Mexico	18	This study

<i>P. gigantea</i>	PAR6	3/6/2017	Sea of Cortez, Mexico	18	This study
<i>L. scabra</i>	L. scabra 1			18	Terraneo et al. 2017
<i>L. scabra</i>	L. scabra 2			18	Terraneo et al. 2017
<i>L. scabra</i>	L. scabra 3			18	Terraneo et al. 2017
<i>L. scabra</i>	L. scabra 4			18	Terraneo et al. 2017
<i>P. diffluens</i>	P. diffluens 1			18	Terraneo et al. 2017
<i>P. diffluens</i>	P. diffluens 2			18	Terraneo et al. 2017
<i>P. diffluens</i>	P. diffluens 3			18	Terraneo et al. 2017
<i>P. diffluens</i>	P. diffluens 4			18	Terraneo et al. 2017
<i>P. diffluens</i>	P. diffluens 5			18	Terraneo et al. 2017
<i>L. explanata</i>	L. explanata 1			18	Terraneo et al. 2017
<i>L. explanata</i>	L. explanata 2			18	Terraneo et al. 2017
<i>L. glabra</i>	L. glabra 1			18	Terraneo et al. 2017
<i>L. glabra</i>	L. glabra 2			18	Terraneo et al. 2017
<i>L. glabra</i>	L. glabra 3			18	Terraneo et al. 2017
<i>L. glabra</i>	L. glabra 4			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 1			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 2			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 3			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 4			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 5			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 6			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 7			18	Terraneo et al. 2017
<i>L. incrustans</i>	L. incrustans 8			18	Terraneo et al. 2017
<i>L. cf. hawaiiensis</i>	SA0884			18	Terraneo et al. 2017
<i>G. planulata</i>	TGAR1	04/1999	Tahiti, French Polynesia	20	This study
<i>G. planulata</i>	TGAR7	04/1999	Tahiti, French Polynesia	20	This study
<i>G. planulata</i>	MLD29	27/11/2019	Magoodhoo Atoll, Maldives	20	This study

<i>G. planulata</i>	G. planulata 1			20	Terraneo et al. 2017
<i>G. planulata</i>	G. planulata 2			20	Terraneo et al. 2017
<i>G. planulata</i>	G. planulata 3			20	Terraneo et al. 2017
<i>G. planulata</i>	G. planulata 4			20	Terraneo et al. 2017
<i>P. varians</i>	AMS55	21/03/2016	Faga'alu Bay, American Samoa	23	This study
<i>P. varians</i>	AMS85	24/03/2016	Masefau Bay, American Samoa	23	This study
<i>P. varians</i>	BIL3	16/04/2016	Limukoko Point, Hawai'i Island, HI	23	This study
<i>P. varians</i>	OAKB4	25/08/2016	Kāne'ōhe Bay, O'ahu, HI	23	This study
<i>P. varians</i>	OAKB6	25/08/2016	Kāne'ōhe Bay, O'ahu, HI	23	This study
<i>P. varians</i>	FFS3285	25/05/2006	French Frigate Shoals, HI	23	This study
<i>P. varians</i>	FFS3286	25/05/2006	French Frigate Shoals, HI	23	This study
<i>P. varians</i>	AMS63			23	This study
<i>P. varians</i>	OAM10	3/8/2016	Maunalua Bay, O'ahu, HI	22	This study
<i>P. varians</i>	RSKA151	9/5/2011	Abu Madafi, Red Sea, Saudi Arabia	22	This study*
<i>P. varians</i>	ZAN077		Changuu, Zanzibar, Tanzania	22	This study*
<i>P. varians</i>	ZAN044		Changuu, Zanzibar, Tanzania	22	This study*
<i>P. varians</i>	OAM9	3/8/2016	Maunalua Bay, O'ahu, HI	21	This study
<i>P. varians</i>	BIR8	19/04/2016	Richards Beach Park, Hawai'i Island, HI	21	This study
<i>P. varians</i>	GENO4 (2)		O'ahu, HI	21	This study

<i>P. varians</i>	BIP5	15/04/2016	Puako Bay, Hawai‘i Island, HI	21	This study
<i>P. varians</i>	JON3996	4/6/2006	Johnston Atoll, USA	21	This study
<i>P. varians</i>	OAM3	3/8/2016	Maunalua Bay, O‘ahu HI	21	This study
<i>P. varians</i>	JPN2	10/11/2017	Seragaki, Okinawa, Japan	21	This study
<i>P. decussata</i>	AMS30	19/03/2016	Faga'alu Bay, American Samoa	24	This study
<i>P. decussata</i>	GM23	10/12/2015	Agana Bay, Guam	24	This study
<i>P. decussata</i>	GM13	10/12/2015	Agana Bay, Guam	24	This study
<i>P. decussata</i>	GM5	10/12/2015	Agana Bay, Guam	24	This study
<i>P. decussata</i>	GM59	11/12/2015	Family Beach, Guam	24	This study
<i>P. decussata</i>	GM18	10/12/2015	Agana Bay, Guam	24	This study
<i>P. decussata</i>	PHU108	15/02/2011	Phiphi Lae, Thailand	24	This study*
<i>P. decussata</i>	NC_026527			24	Shi et al. 2016
<i>P. decussata</i>	AGJA89		Subri Reef, Persian Gulf	25	This study
<i>P. decussata</i>	AGJA108		Subri Reef, Persian Gulf	25	This study
<i>P. decussata</i>	<i>P. decussata</i> 1			25	Terraneo et al. 2017
<i>P. decussata</i>	<i>P. decussata</i> 2			25	Terraneo et al. 2017
<i>P. decussata</i>	<i>P. decussata</i> 3			25	Terraneo et al. 2017
<i>P. varians</i>	RMI19	30/05/2015	Arno Dock, Republic of Marshall Islands	26	This study
<i>P. varians</i>	BIR10	19/04/2016	Richardsons Beach Park, Hawai‘i Island, HI	26	This study

<i>P. varians</i>	FFS3292	25/05/2006	French Frigate Shoals, HI	26	This study
<i>P. varians</i>	RMI07	30/05/2015	Arno Dock, Republic of Marshall Islands	26	This study
<i>P. varians</i>	RMI4	30/05/2015	Arno Dock, Republic of Marshall Islands	26	This study
<i>P. varians</i>	JPN37	19/11/2017	Hedo, Okinawa, Japan	26	This study
<i>P. varians</i>	JPN68	13/11/2017	Seragaki, Okinawa, Japan	26	This study
<i>P. varians</i>	MLD49	29/11/2019	Magoodhoo Atoll, Maldives	26	This study
<i>P. varians</i>	MLD44	28/11/2019	Magoodhoo Atoll, Maldives	26	This study
<i>P. varians</i>	MLD34	28/11/2019	Magoodhoo Atoll, Maldives	26	This study
<i>P. varians</i>	MLD4	26/11/2019	Magoodhoo Atoll, Maldives	26	This study
<i>P. maldivensis (p)</i>	TAEK	29/01/2010	Johnston Atoll, USA	29	This study
<i>P. maldivensis (p)</i>	TLEK	28/01/2010	Johnston Atoll, USA	29	This study
<i>P. maldivensis (p)</i>	O73	2/5/2010	Howland Island, USA	29	This study
<i>P. maldivensis (p)</i>	AMS77	23/03/2016	Leone Bay, American Samoa	29	This study
<i>P. maldivensis (p)</i>	AMS68	23/03/2016	Leone Bay, American Samoa	29	This study
<i>P. maldivensis (p)</i>	KF437780			29	Luck et al. 2013
<i>P. maldivensis (p)</i>	LAC07	2017		29	Waheed et al. 2015
<i>P. maldivensis (p)</i>	LOY12	2018		29	Waheed et al. 2015

<i>P. maldivensis</i> (p)	LAC23	2017		29	Waheed et al. 2015
<i>P. maldivensis</i> (i)	MLD2	27/11/2019	Magoodhoo Atoll, Maldives	29	This study
<i>P. sp.</i>	RSKA20	11/5/2011	Site 23? Red Sea, Saudi Arabia	29	This study
<i>P. maldivensis</i> (i)	MAL18	2018		29	Waheed et al. 2015
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 1			29	Terraneo et al. 2017
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 2			29	Terraneo et al. 2017
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 3			29	Terraneo et al. 2017
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 4			29	Terraneo et al. 2017
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 5			29	Terraneo et al. 2017
<i>P. maldivensis</i> (i)	<i>P. maldivensis</i> 6			29	Terraneo et al. 2017
<i>P. chiriquiensis</i>	PAN14	11/8/2018	Uva Island, Gulf of Chiriquí, Panama	31	This study
<i>P. chiriquiensis</i>	384	19/04/2010	Kingman Reef, USA	31	This study
<i>P. chiriquiensis</i>	C03	14/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C42	13/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C22	16/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C39	16/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C41	16/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C44	16/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C20	14/05/2017	Kiritimati	31	This study
<i>P. chiriquiensis</i>	C38	16/05/2017	Kiritimati	31	This study
<i>L. mycetoseroides</i>	C29	14/05/2017	Kiritimati	30	This study
<i>L. mycetoseroides</i>	OAK30	2016	Kewalo Basin, O‘ahu	30	This study
<i>L. mycetoseroides</i>	KF437776			30	Luck et al. 2013
<i>L. mycetoseroides</i>	KF437788			30	Luck et al. 2013
<i>P. duerdeni</i>	705		Midway Atoll, HI	28	This study
<i>P. duerdeni</i>	RM18	31/05/2015	Arno Dock, Republic of Marshall Islands	28	This study

<i>P. duerdeni</i>	AMS73	23/03/2016	Leone Bay, American Samoa	28	This study
<i>L. fragilis</i>	L. fragilis 1			27	Terraneo et al. 2017
<i>L. fragilis</i>	L. fragilis 2			27	Terraneo et al. 2017
<i>P. varians</i>	AMS15	19/03/2016	Fagasa Bay, American Samoa	32	This study
<i>P. varians</i>	JPN5	11/11/2017	Hedo, Okinawa, Japan	32	This study
<i>P. chiriquiensis</i>	PAN18	12/8/2018	Canal de Afuera Island, Gulf of Chiriquí, Panama	32	This study
<i>P. varians</i>	PH1922	19/06/2008	Pearl & Hermes	32	This study
<i>P. varians</i>	BIL7		Limukoko Point, Hawai'i Island, HI	32	This study
<i>P. varians</i>	BIP1		Puako Bay, Hawai'i Island, HI	32	This study
<i>P. varians</i>	BIL2		Limukoko Point, Hawai'i Island, HI	32	This study
<i>P. varians</i>	PH1914	6/19/2008	Pearl & Hermes	32	This study
<i>P. varians</i>	PH0537	6/19/2009	Pearl & Hermes	32	This study
<i>P. varians</i>	PH0542	6/20/2009	Pearl & Hermes	32	This study
<i>P. varians</i>	JON4020	4/6/2006	Johnston Atoll	32	This study
<i>P. varians</i>	JON3985	4/6/2006	Johnston Atoll	32	This study
<i>P. varians</i>	PH1915	19/06/2008	Pearl & Hermes	32	This study
<i>P. varians</i>	PH1916	19/06/2008	Pearl & Hermes	32	This study
<i>P. varians</i>	AMS51	21/03/2016	Faga'alu Bay, American Samoa	32	This study
<i>P. varians</i>	AMS84	24/03/2016	Masefau Bay, American Samoa	32	This study
<i>P. varians</i>	GM44	12/12/2015	Double Reef, Guam	32	This study
<i>P. varians</i>	JPN46	9/11/2017	Hedo, Okinawa, Japan	32	This study

<i>P. varians</i>	MLD20	27/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	MLDZ	27/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	PHU140	15/02/2011	Phi Phi Lae, Thailand	32	This study*
<i>P. varians</i>	MLD32	27/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	MLD43	28/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	MLD48	28/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	MLD40	28/11/2019	Magoodhoo Atoll, Maldives	32	This study
<i>P. varians</i>	ZAN346		Banda Kuu, Zanzibar, Tanzania	32	This study*
<i>P. varians</i>	RSKA25	9/5/2011	Abu Madafi, Red Sea, Saudi Arabia	32	This study
<i>P. sp.</i>	KF437762			32	Luck et al. 2013
<i>P. venosa</i>	<i>P. venosa</i> 1			32	Terraneo et al. 2017
<i>P. varians</i>	<i>P. varians</i> 2			32	Terraneo et al. 2017
<i>P. varians</i>	<i>P. varians</i> 3			32	Terraneo et al. 2017
<i>P. varians</i>	<i>P. varians</i> 4			32	Terraneo et al. 2017
<i>P. varians</i>	<i>P. varians</i> 5			32	Terraneo et al. 2017
<i>P. varians</i>	<i>P. varians</i> 6			32	Terraneo et al. 2017

* Indicates sample previously published in LaJeunesse et al. (2010) but not at this marker.

Table S2.1. (Continued). **Collection information for Indo-Pacific agaricid coral samples**

Table S2.2. Type specimen information for Indo-Pacific agaricids. Including original description source (authority). Recognition of each species for three different authorities. X indicates inclusion. Bold represents the type species of the genus. WoRMS = World Register of Marine Species, CotW = Corals of the World (Veron 2000), IUCN = International Union for the Conservation of Nature. USNM = Smithsonian National Museum of Natural History, USA, MCZ = Harvard Museum of Comparative Zoology, USA, NHM = Natural History Museum, UK,

Genus	species	Authority	WoRMS	CotW	IUCN	Sequenced	From Type Locality	Type locality	Type Specimen Location	Studied Type
<i>Pavona</i>	<i>bipartita</i>	Nemenzo 1980 // 1979	X	X	X	X		Philippines	Silliman University, Philippines	
<i>Pavona</i>	<i>cactus</i>	(Forskål 1775)	X	X	X	X	X	Red Sea*		
<i>Pavona</i>	<i>chiriquiensis</i>	Glynn Mate & Stemmann 2001	X	X	X	X	X	Panama	Smithsonian	X (USNM 100871, USNM 100872 Paratype)
<i>Pavona</i>	<i>clavus</i>	Dana 1846	X	X	X	X		Fiji	Smithsonian	X (USNM 221 syntype)
<i>Pavona</i>	<i>danai</i>	(Milne Edwards 1860)	X	X	X	X		Sulu Sea, Philippines	Smithsonian & Harvard MCZ	X (USNM 136 as <i>Lophoseris danai</i> , & MCZ 5441)
<i>Pavona</i>	<i>decussata</i>	(Dana 1846)	X	X	X	X		Fiji	Smithsonian & Harvard MCZ	X (USNM 176, 200-1; & MCZ 5431)
<i>Pavona</i>	<i>diffluens</i>	(Lamarck 1816)	X	X	X	X	X	Red Sea*		
<i>Pavona</i>	<i>diminuta</i>	Veron 1990	X					Phuket Island, Thailand	Queensland Museum	
<i>Pavona</i>	<i>divaricata</i>	Lamarck 1816	X					Indian Ocean		
<i>Pavona</i>	<i>duerdeni</i>	Vaughan 1907	X	X	X	X	X	Hawai'i	Smithsonian	X (USNM 21630-21631)
<i>Pavona</i>	<i>explanulata</i>	(Lamarck 1816)	X	X	X	X	X	Indian Ocean*		
<i>Pavona</i>	<i>frondifera</i>	(Lamarck 1816)	X	X	X	X		Australian Sea		
<i>Pavona</i>	<i>gigantea</i>	(Verrill 1869)	X	X	X	X		Panama	Smithsonian	X (USNM 62702)

<i>Pavona</i>	<i>maldivensis</i>	(Gardiner 1905)	X	X	X	X	X	Maldives, Bikini Atoll	NHM, Smithsonian	X (USNM 44792 as <i>Pseudocolumnastrea pollicata</i>)
<i>Pavona</i>	<i>minor</i>	(Brüggemann 1879)	X					Federated States of Micronesia		
<i>Pavona</i>	<i>minuta</i>	Wells 1954	X	X	X	X		Bikini Atoll, Republic of Marshall Islands	Smithsonian	X (USNM 44786)
<i>Pavona</i>	<i>varians</i>	(Verrill 1864)	X	X	X	X	X	Hawai‘i	Harvard	X (MCZ 1061-63)
<i>Pavona</i>	<i>venosa</i>	(Ehrenberg 1834)	X	X	X	X		Red Sea	Berlin	
<i>Pavona</i>	<i>xarifae</i>	Scheer & Pillai 1974	X		X			Nicobar Islands, Panama	Hessian State Museum, Darmstadt	
<i>Gardineroseris</i>	<i>planulata</i>	Scheer & Pillai 1974 // Dana 1846	X	X	X	X				
<i>Dactylotrachus</i>	<i>cervicornis</i>	(Moseley 1880)	X							
<i>Coeloseries</i>	<i>mayeri</i>	Vaughan 1918	X	X	X			Australia		
<i>Leptoseris</i>	<i>amitoriensis</i>	Veron 1990	X	X	X			Japan		
<i>Leptoseris</i>	<i>explanata</i>	Yabe & Sugiyama 1941	X	X	X	X		Palau		
<i>Leptoseris</i>	<i>foliosa</i>	Dinesen 1980	X	X	X	X		Lizard Island, Australia	NHM & Smithsonian	

<i>Leptoseris</i>	<i>fragilis</i>	Milne Edwards & Haime 1849	X			X			
<i>Leptoseris</i>	<i>gardineri</i>	van der Horst 1922	X	X	X			Indonesia	
<i>Leptoseris</i>	<i>glabra</i>	Dinesen 1980	X			X		Palm Islands, Australia	NHM
<i>Leptoseris</i>	<i>hawaiiensis</i>	Vaughan 1907	X	X	X	X	X	Hawai'i	Smithsonian
<i>Leptoseris</i>	<i>incrustans</i>	Quelch 1886	X	X	X	X		Tahiti	
<i>Leptoseris</i>	<i>kalayaanensis</i>	Licuanan & Alino 2009	X	X				Philippines	
<i>Leptoseris</i>	<i>mycetoseroides</i>	Wells 1954	X	X	X	X		Republic of Marshall Islands	Smithsonian
<i>Leptoseris</i>	<i>papyracea</i>	Dana 1846	X	X	X	X		Sulu Sea	USNM 44805
<i>Leptoseris</i>	<i>scabra</i>	Vaughan 1907	X	X	X	X	X	Hawai'i	NHM & Smithsonian
<i>Leptoseris</i>	<i>solida</i>	Quelch 1886	X	X	X				
<i>Leptoseris</i>	<i>striata</i>	Fenner & Veron 2000	X	X	X				
<i>Leptoseris</i>	<i>trogloodyta</i>	Hoeksema 2012	X					Palau	
<i>Leptoseris</i>	<i>tubulifera</i>	Vaughan 1907	X	X	X	X	X	Hawai'i	Smithsonian
<i>Leptoseris</i>	<i>yabei</i>	Pillai & Scheer 1976	X	X	X	X		Maldives	

* Most likely.

Table S2.2. (Continued). **Type specimen information for Indo-Pacific agaricids.**

Table S2.3. Mitogenome assembly information for *Pavona* and *Leptoseris* species in Chapter 2. Reference, denotes which mitogenome was used as the guide, *P clavus* refers to the reference from Medina et al. (2006), and *P decussata* (Shi et al. 2016). Other names refer to other samples from this study being used as references after they were assembled. Custom settings for mitogenome assembly performed in Geneious: Allow structural variants, and insertions and deletions upto 1000, Allowing 30 gaps per read, Word length of 10. And include structural variants up to a max gap size of 10=5, and index word length of 10. And maximum ambiguity of 20. Custom settings for trimming settings of 757 library in Geneious: trim adapters, Q30 between and at least 51bp. Don't allow mismatches, but allow one sequence if the other is poor.

Species ID	Sample ID	Reference	Reads assembled	HQ %	Length (bp)	Ambiguities
<i>P. frondifera</i>	AMS17	757	20,210	100	18,265	1
<i>P. frondifera</i>	AMS21	757	26,779	100	18,264	0
<i>P. frondifera</i>	AMS25	757	30,365	100	18,264	2
<i>P. frondifera</i>	AMS36	757	7,147	100	18,266	7
<i>P. frondifera</i>	GM30	757	4,894	100	18,268	410
<i>P. frondifera</i>	AMS71	757	55,517	100	18,264	0
<i>P. varians</i>	757	<i>P clavus</i>	9,804	100	18,264	0
<i>P. varians</i>	AMS14	757	18,839	100	18,276bp	0
<i>P. varians</i>	AMS48	757	33,698	100	18,264	1
<i>P. varians</i>	AMS53	757	10,174	100	18,264	3
<i>P. varians</i>	BIR3	<i>P clavus</i>	5,784	100	18,265	923
<i>P. varians</i>	GM2	757	22,198	100	18,268	8
<i>P. varians</i>	GM24	757	24,233	100	18,264	1
<i>P. varians</i>	GM25	757	18,650	100	18,264	0
<i>P. varians</i>	GM28	757	13,331	100	18,264	7
<i>P. varians</i>	GM60	757	85,504	100	18,264	0
<i>P. varians</i>	OAM5	757	44,441	100	18,264	3
<i>P. varians</i>	RMI13	757	25,236	100	18,266	25
<i>P. varians</i>	BIR1	757	21,066	100	18,264	0
<i>P. varians</i>	PAL28	757	13,509	100	18,264	0
<i>P. venosa</i>	PAL18	757	9,470	99.6	18,274	42
<i>P. duerdeni</i>	393	<i>P clavus</i>	5,899	100	18,315	5

<i>L. incrustans</i>	OAK10	<i>P. decussata</i>	11,428	100	18,402	4
<i>L. incrustans</i>	OAK13	OAK10	13,830	91.6	18,405	839
<i>P. explanulata</i>	AMS78	<i>P. decussata</i>	12,005	99.5	18,371	102
<i>P. gigantea</i>	PAR4	PAR6	6,103	97.4	18,421	353
<i>P. gigantea</i>	PAR6	OAK10	17,665	99.6	18,411	58
<i>P. varians</i>	AMS55	<i>P. decussata</i>	18,725	100	18,374	2
<i>P. varians</i>	AMS85	<i>P. decussata</i>	21,465	100	18,379	15
<i>P. varians</i>	BIL3	AMS85	15,821	99.1	18,391	162
<i>P. varians</i>	OAM9	TAEK	11,530	99.9	18,388	8
<i>P. varians</i>	RMI19	<i>P. decussata</i>	9,512	99.8	18,389	14
<i>P. maldivensis</i>	TAEK	<i>P. decussata</i>	8,687	100	18,385	0
<i>L. mycetoseroides</i>	C29	<i>P. decussata</i>	11,724	100	18,384	10
<i>P. varians</i>	AMS15	<i>P. decussata</i>	16,812	100	18,416	33

Table S2.3. (Continued). **Mitogenome assembly information for *Pavona* and *Leptoseris* species in Chapter 2.**

Table S2.4. Biogeographic regions associated with recovered clades of Indo-Pacific agaricids. Details of which biogeographic provinces each clade is recovered within, both raw instances, and assuming a contiguous distribution. RS = Red Sea, IO = Indian Ocean, P = Pacific, HI = Hawai‘i, EP = East Pacific.

Raw			Contiguous		
Clade	Biogeographic regions	Combo	Clade	Biogeographic Regions	Combo
1	3	RS + P + HI	1	4	RS + IO + P + HI
2	2	P + RS	2	3	RS + IO + P
3	1	HI	3	1	HI
4	1	IO	4	1	IO
5	1	HI	5	1	HI
6	3	P + HI + EP	6	3	P + HI + EP
7	5	RS + IO + P + HI + EP	7	5	RS + IO + P + HI + EP
8	1	HI	8	1	HI
9	1	P	9	1	P
10	2	P + RS	10	3	RS + IO + P
11	1	HI	11	1	HI
12	2	P + RS	12	3	RS + IO + P
13	1	HI	13	1	HI
14	2	P + RS	14	3	RS + IO + P
15	1	HI	15	1	HI
16	1	RS	16	1	RS
17	1	HI	17	1	HI
18	3	RS + P + EP	18	4	RS + IO + P + EP
19	3	RS + IO + P	19	3	RS + IO + P
20	3	RS + IO + P	20	3	RS + IO + P
21	2	P + HI	21	2	P + HI
22	3	RS + IO + P	22	3	RS + IO + P
23	2	P + HI	23	2	P + HI
24	2	IO + P	24	2	IO + P

25	2	RS + IO	25	2	RS + IO
26	3	IO + P + HI	26	3	IO + P + HI
27	1	RS	27	1	RS
28	2	P + HI	28	2	P + HI
29	3	RS + IO + P	29	3	RS + IO + P
30	2	P + HI	30	2	P + HI
31	2	P + EP	31	2	P + EP
32	5	RS + IO + P + HI + EP	32	5	RS + IO + P + HI + EP

Table S2.4. (Continued). **Biogeographic regions associated with recovered clades of Indo-Pacific agaricids.**

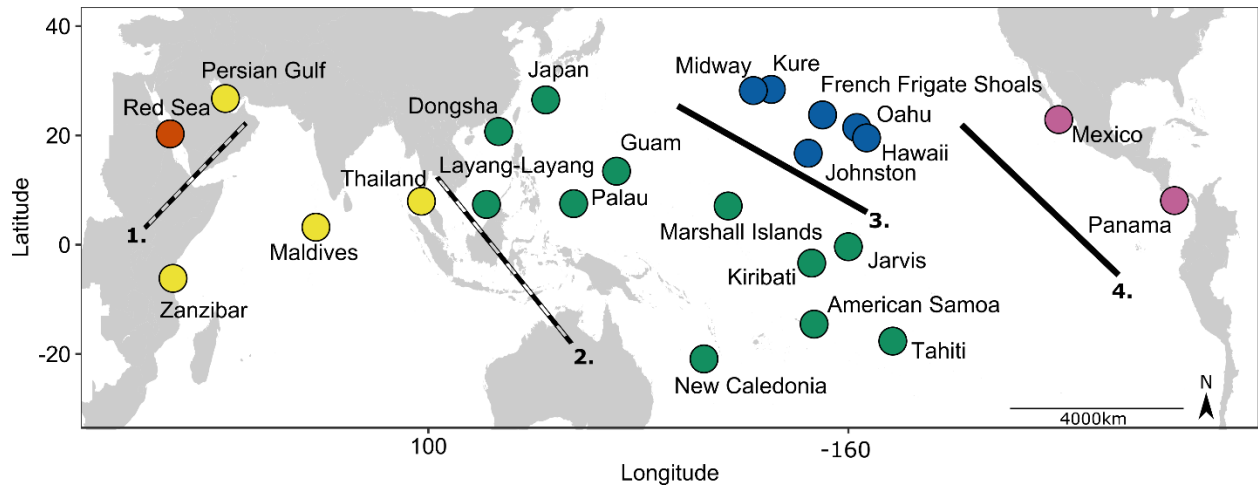


Figure 2.1. Map of sampling sites for corals from the family Agariciidae and biogeographic barriers across the Indo-Pacific; 1. Red Sea Barrier, 2. Sunda Shelf Barrier, 3. Hawai‘i Pacific Barrier, 4. East Pacific Barrier. Dashed lines indicate an ephemeral barrier, associated with sea-level changes, and solid lines indicate a permanent, oceanographic barrier.

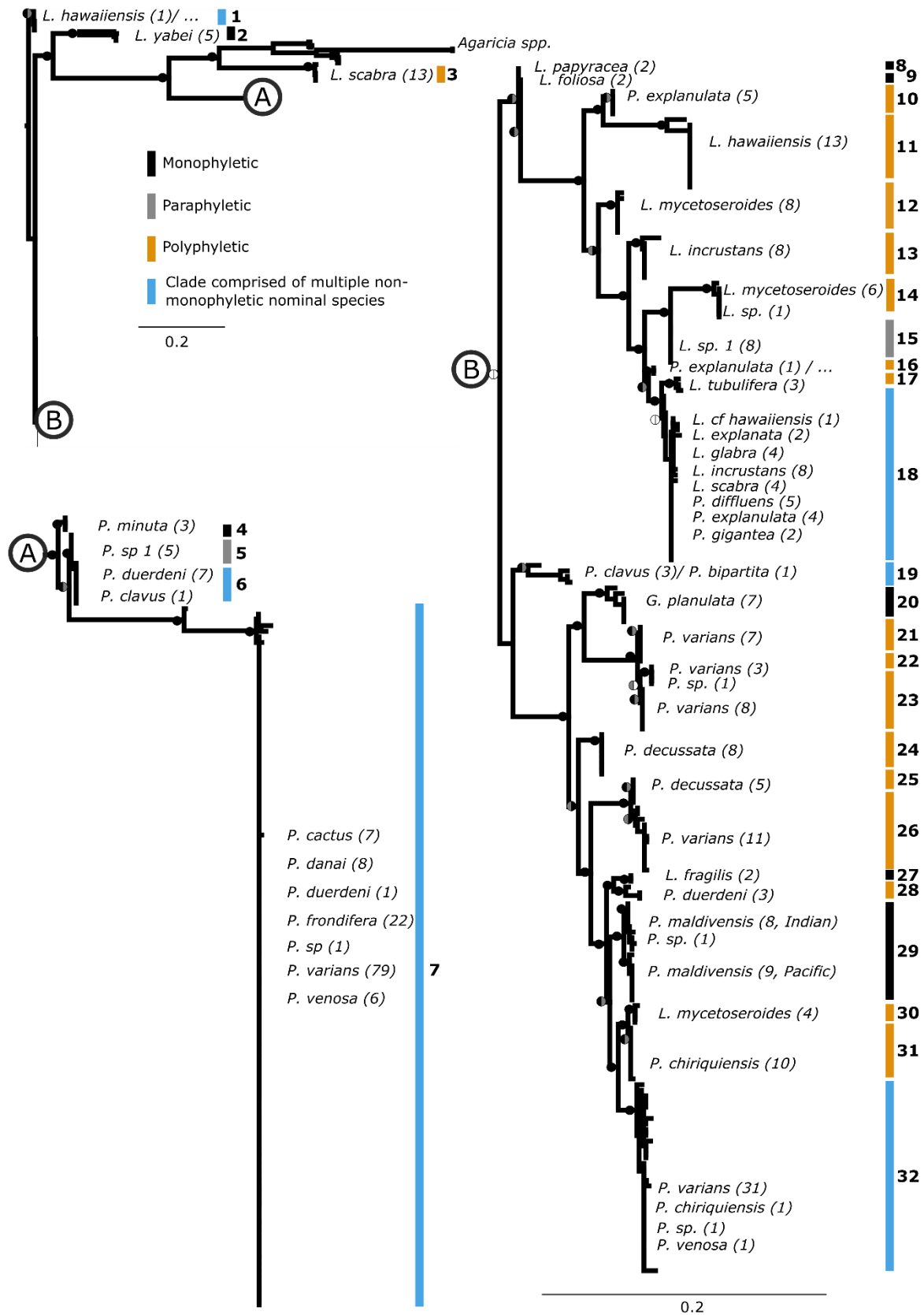


Figure 2.2. Maximum Likelihood phylogeny of *cox1-1*-rRNA intron of corals from the family Agariciidae. Colored circles at nodes indicate support, left side represents bootstrap support for Maximum Likelihood tree (white <50, grey 51-74, black >75), and right posterior probabilities from Bayesian Tree (white <75, grey 76-94, black >95). Numbers of samples of nominal taxon in parentheses. Black/colored bars indicate a clade, and number corresponds to numbered clades as referenced in the main text and supporting materials.

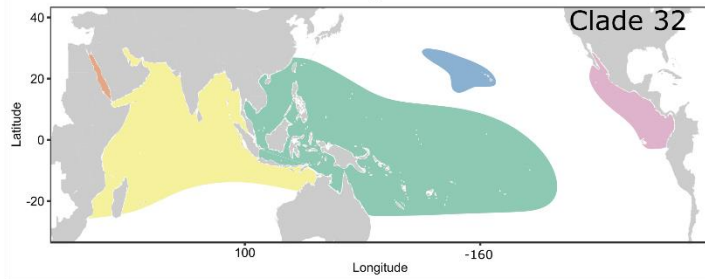
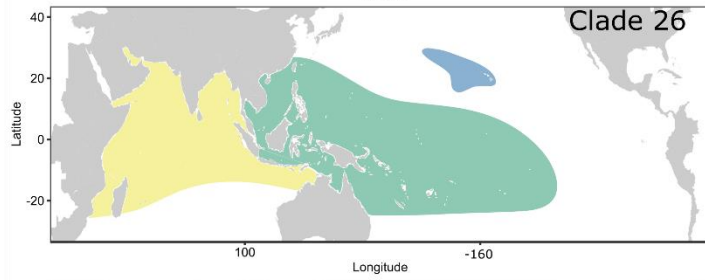
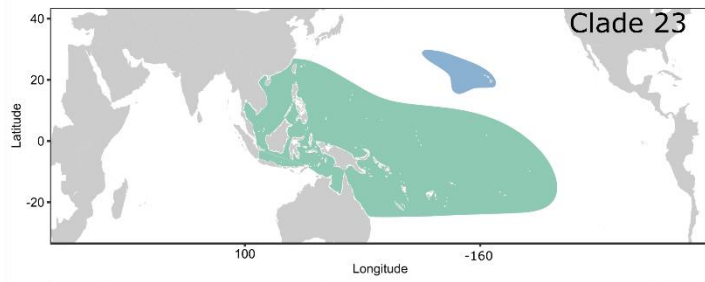
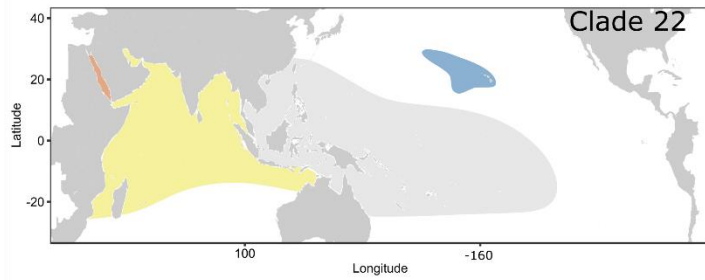
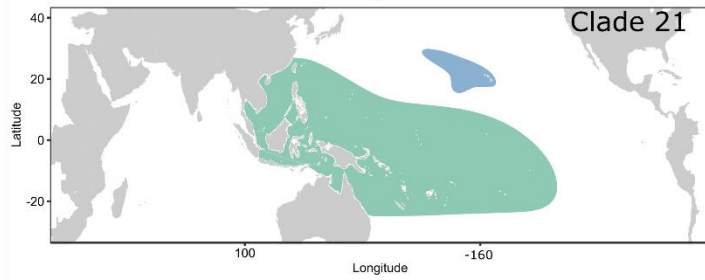
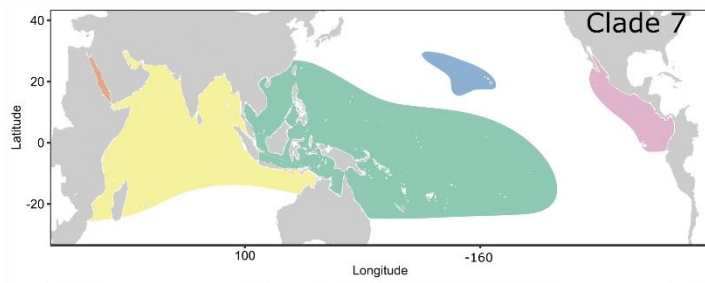


Figure 2.3. Maps representing presence in the five biogeographic provinces of the Indo-Pacific, for six clades which contain individuals of *Pavona varians*. Photographs indicate representative samples of each of the clades, and the color corresponds to the collection province. Sample numbers: clade 7 MLD26; clade 21 OAM9; clade 23 OAKB4; clade 26 RMI7; clade 32 JPN5. All PC: CJL.



Figure 2.4. Two individuals identified as *Pavona varians* growing adjacent on a Maldivian reef. The top colony is recovered in clade 32, and the bottom in clade 26. Note the differences in morphology although they both fit the *P. varians* description.

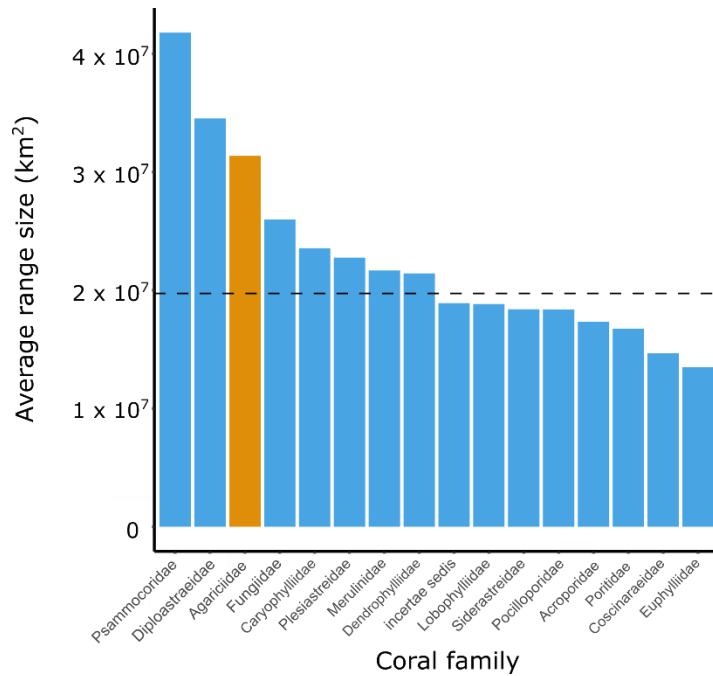


Figure S2.1. Average of species range sizes within each major Indo-Pacific coral family, Agariciidae highlighted in orange. Data from Veron (2000).

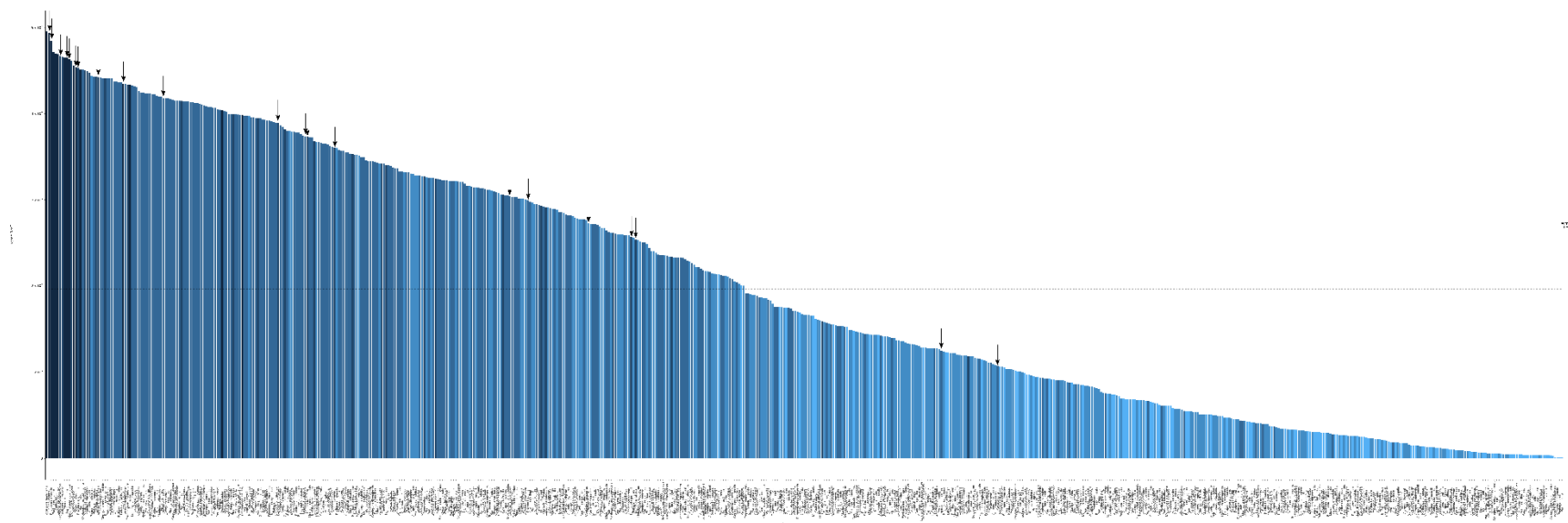


Figure S2.2. Ranked range size from largest to smallest of 675 Indo-Pacific corals. Agaricid species are marked with arrows. Dotted lines represents the average range size of all corals. And color corresponds to number of biogeographic provinces that species is found in darkest (5) to lightest (1). Data from Veron (2000).



Figure S2.3. Maximum Likelihood phylogeny of *cox1*-1-rRNA intron for Indo-Pacific agaricids, made in IQTree, numbers at node denote bootstrap support values. Sample names correspond to those in Table S2.1.

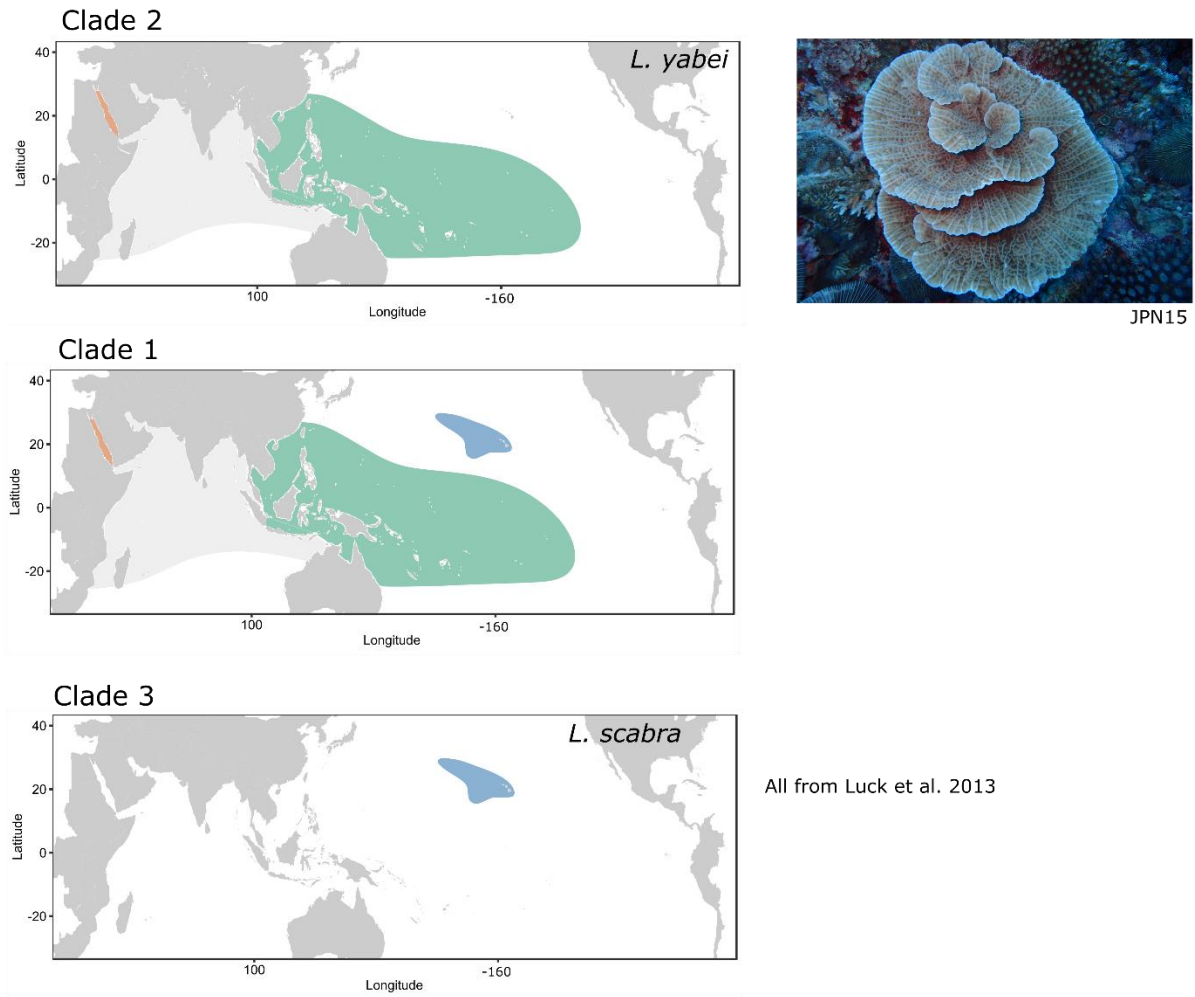


Figure S2.5. Representation of presence in biogeographic provinces and available photographs for clades 1-3. PC: CJL.

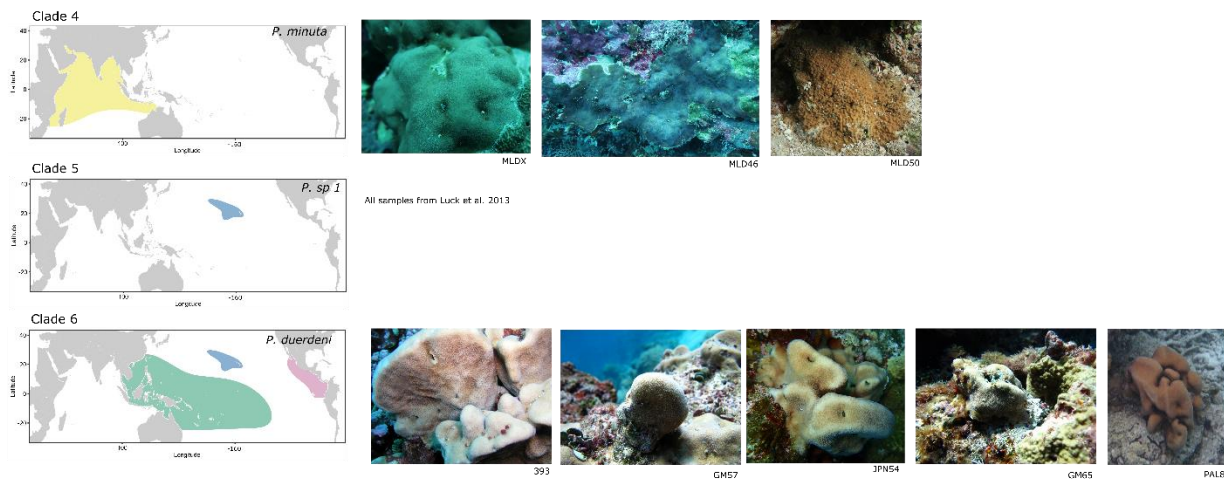


Figure S2.6. Representation of presence in biogeographic provinces and available photographs for clades 4-6. PC: CJL, except 393 J Maragos.

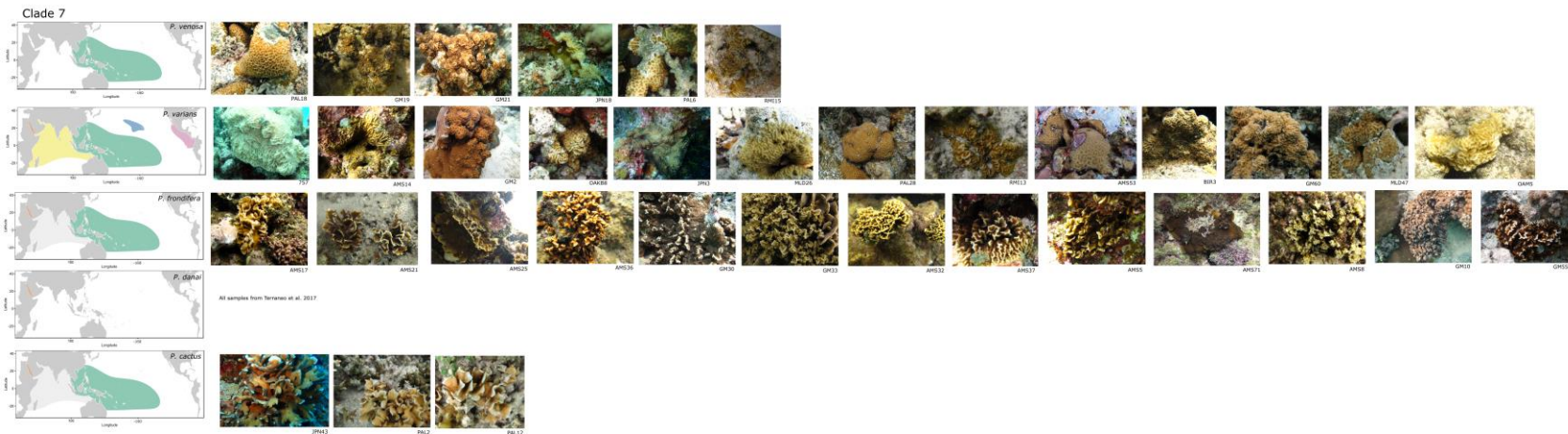


Figure S2.7. Representation of presence in biogeographic provinces and available photographs for taxa in clade 7. PC: CJL, except 757 JMaragos.

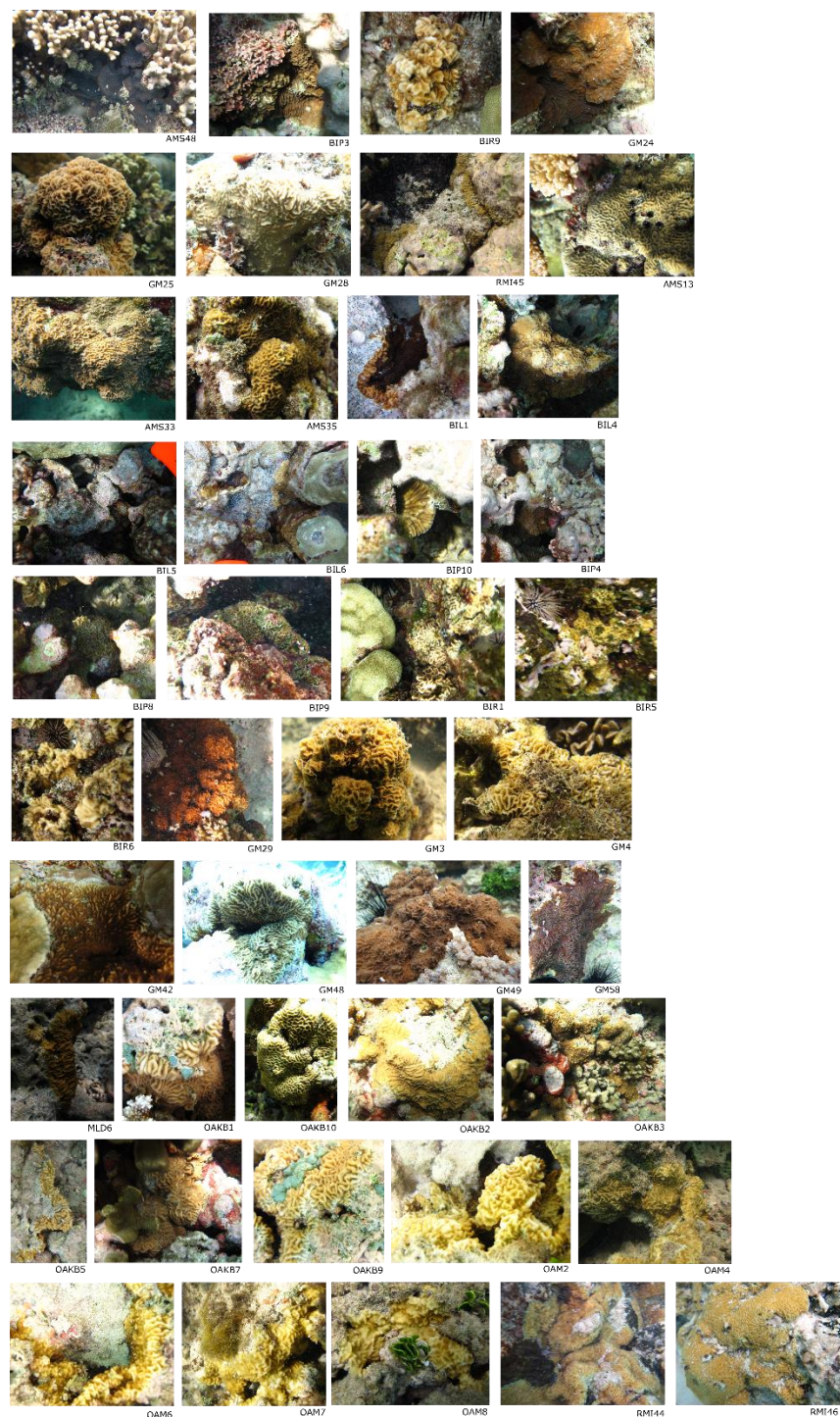


Figure S2.8. Photographs of *Pavona varians* in clade 7 continued. PC: CJL.

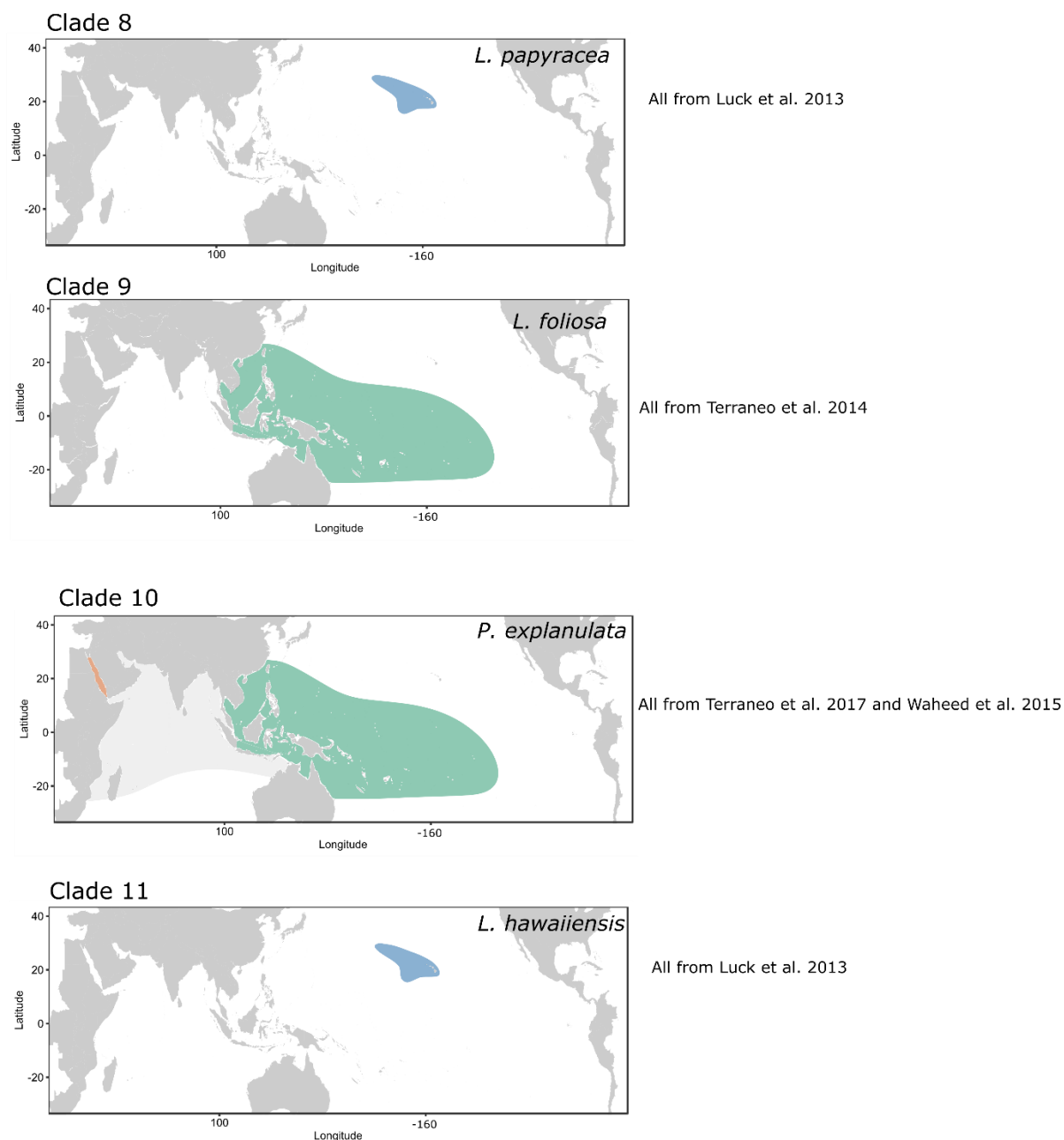


Figure S2.9. Representation of presence in biogeographic provinces and available photographs for clades 8-11.

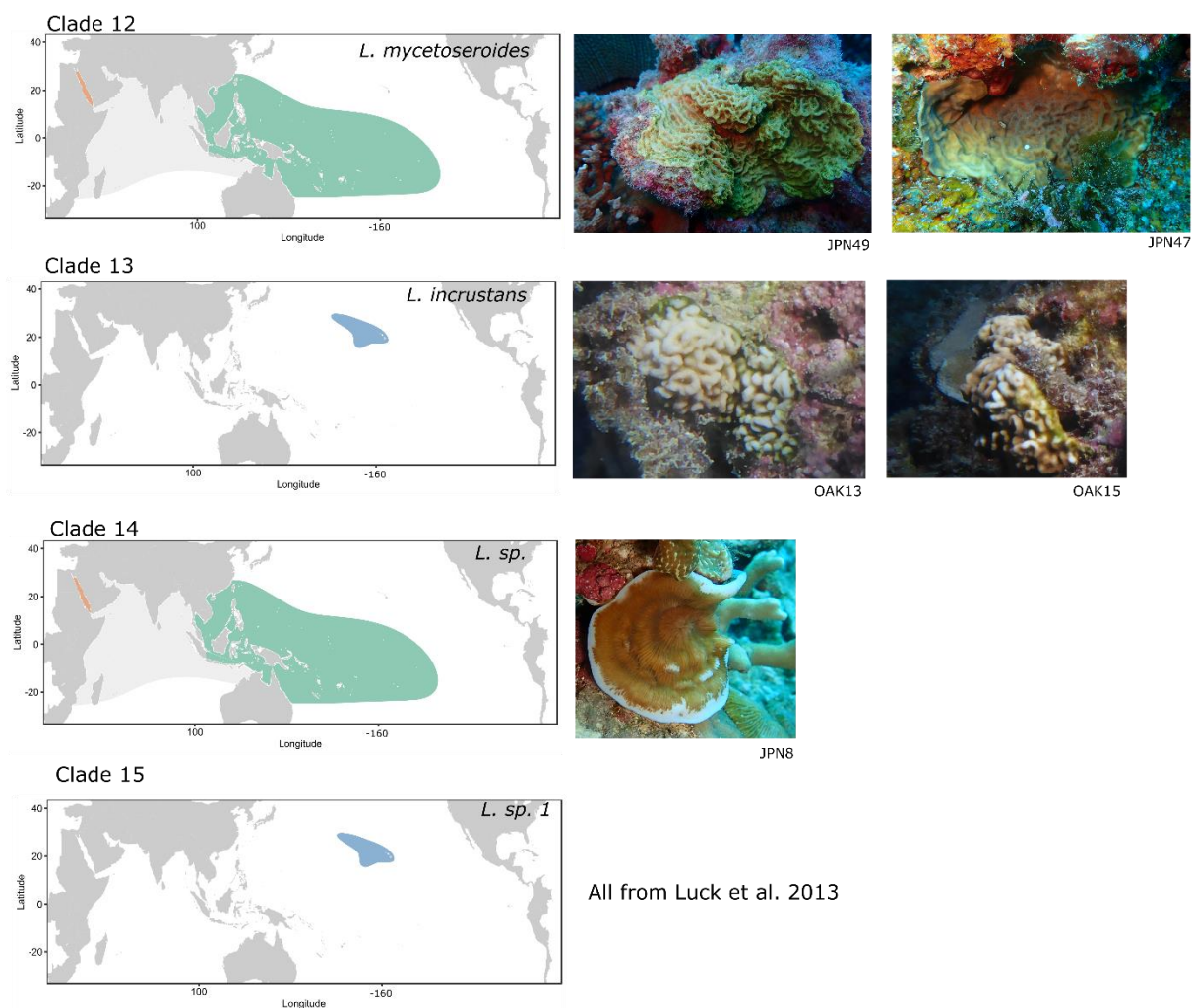


Figure S2.10. Representation of presence in biogeographic provinces and available photographs for clades 12-15. PC: CJL, except OAK13,35 D Pence.

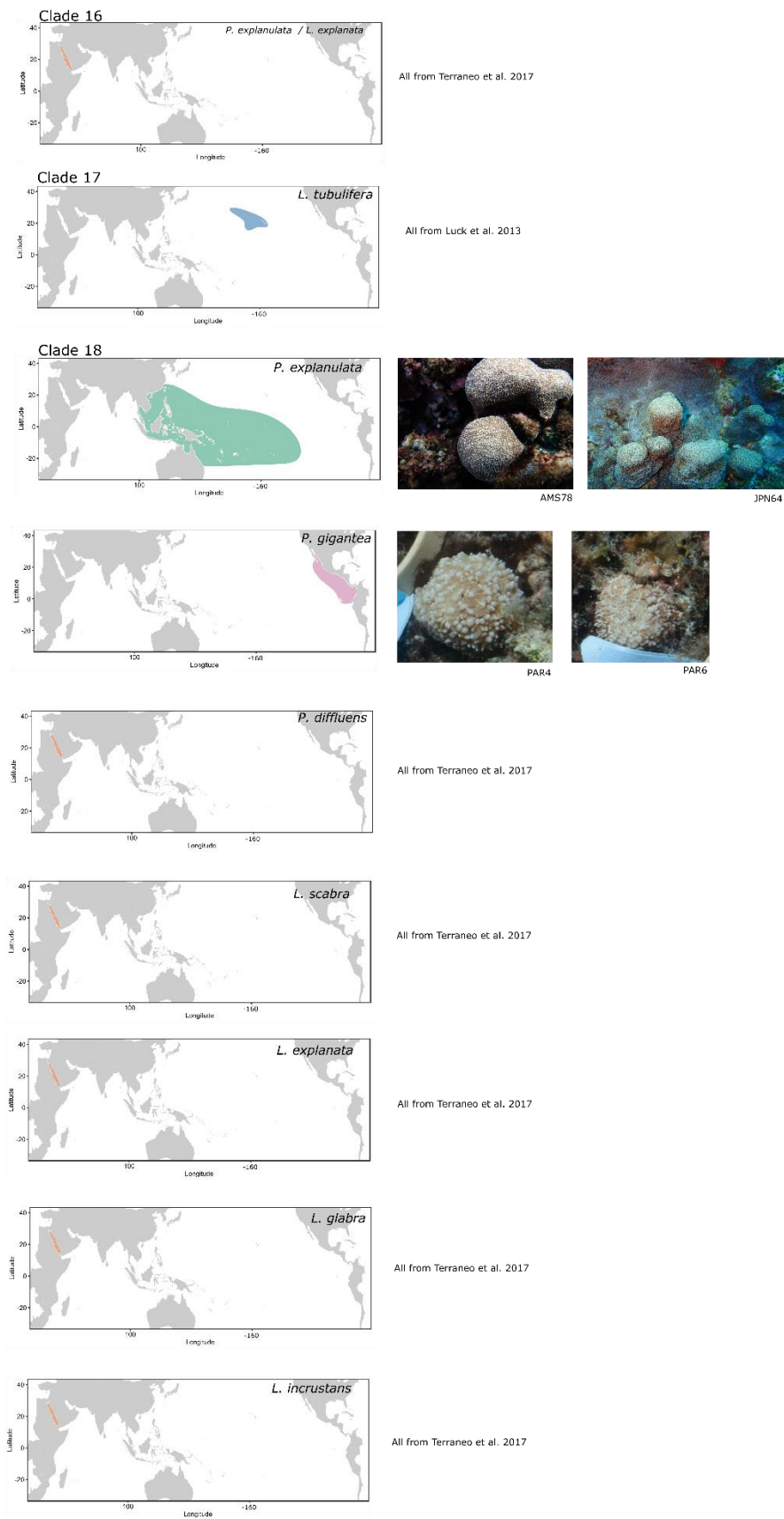


Figure S2.11. Representation of presence in biogeographic provinces and available photographs for clades 16-18. PC: CJL, except PAR4,6 M Iacchei.

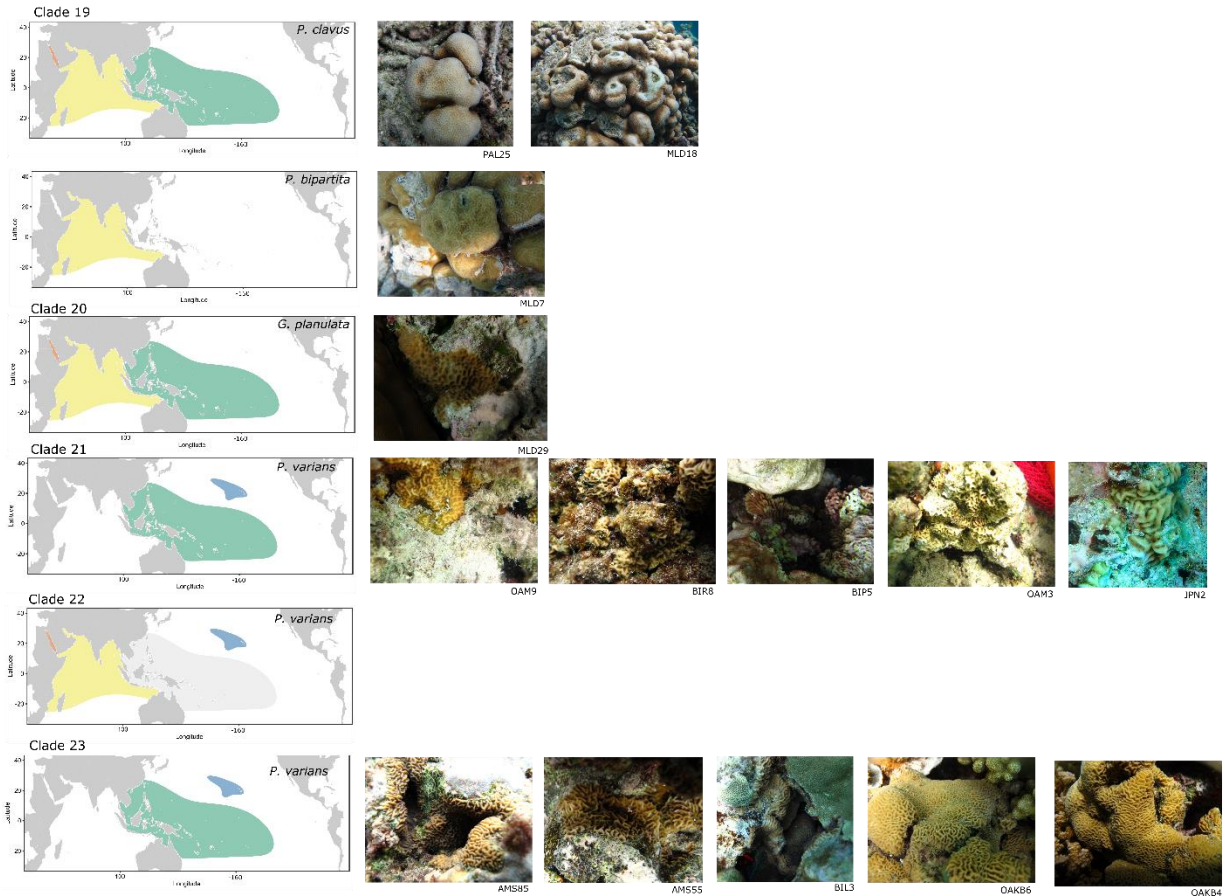


Figure S2.12. Representation of presence in biogeographic provinces and available photographs for clades 19-23. PC: CJL.

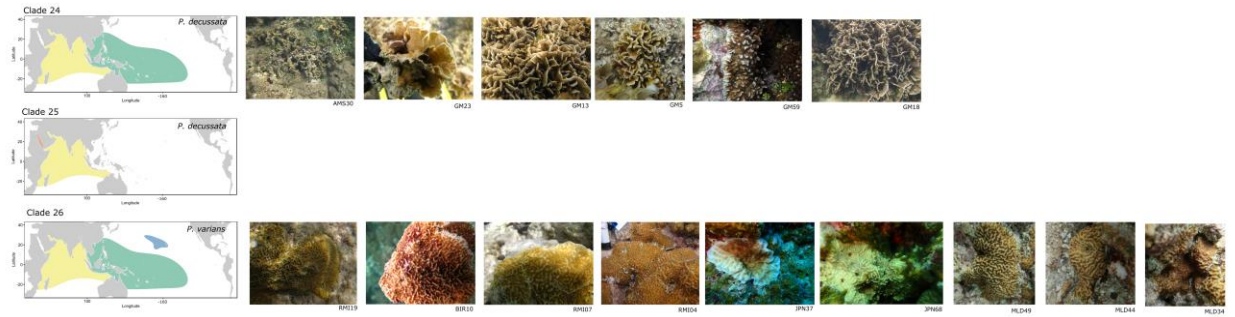


Figure S2.13. Map of presence in biogeographic province for each nominal taxon in each clade. And images of colonies in that clade. PC: CJL.

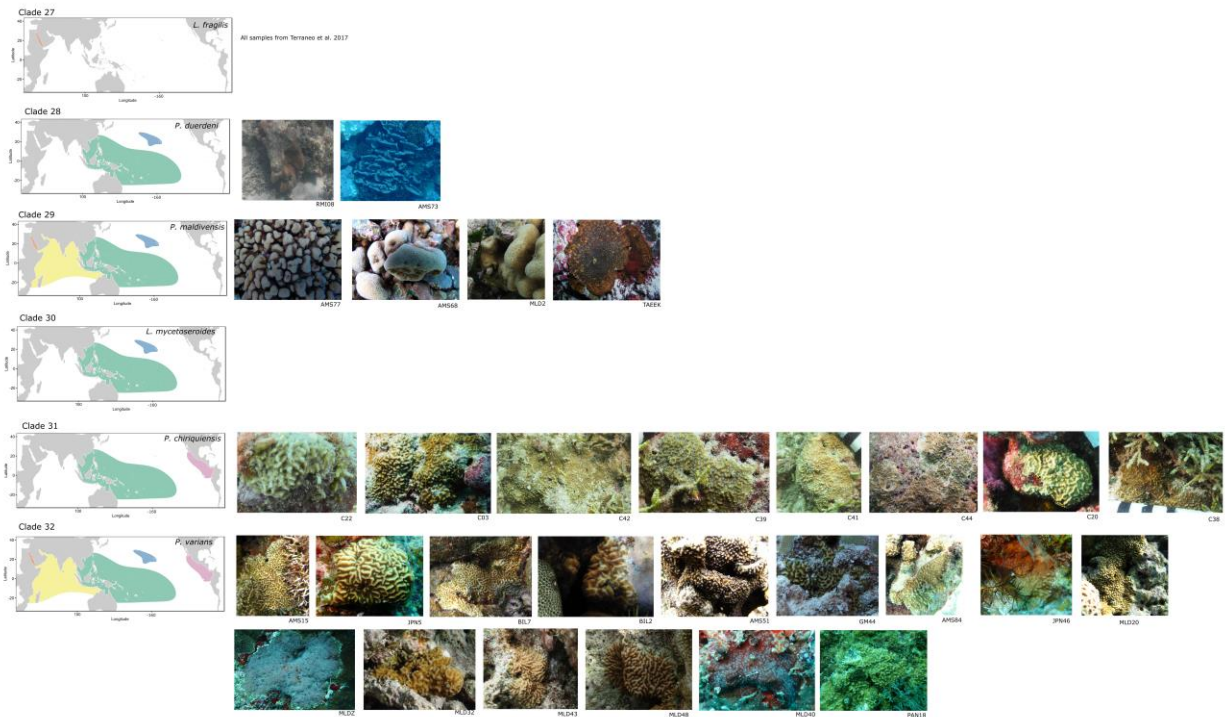


Figure S2.14. Map of presence in biogeographic province for each nominal taxon in each clade. And images of colonies in that clade. PC: CJL, except C* M Hoban, PAN23 J Maté.

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CHAPTER 3. PHYLOGENOMICS OF THE STONY CORAL FAMILY AGARICIIDAE

ABSTRACT

Coral phylogenetics is notoriously challenging, but genomic data are recovering well-supported topologies across the scleractinian tree. These data are also uncovering cytonuclear and gene tree discordance, as well as identifying evidence of introgression within taxonomic families. Previous studies of the coral family Agariciidae revealed discordance between the current taxonomy and the clades as recovered from a mitochondrial intron. We generated RAD-seq libraries for 120 corals from twenty nominal Indo-Pacific agaricid taxa, the most comprehensive phylogenetic assessment of the agaricids to date. From these libraries, we assembled complete mitochondrial genomes for twenty species and generated SNP (Single Nucleotide Polymorphism) data sets from a combination of de novo and reference-guided assemblies. Phylogenetic analysis of SNPs consistently recovered three well-supported clades, but neither *Pavona* or *Leptoseris* were monophyletic, indicating *Pavona* and *Leptoseris* need to be reorganized into at least three genera. Mitogenome clade structure was also strongly supported by the data, but was discordant with the SNP trees. D-statistics applied to the SNP data provided no evidence of introgression. Polyphyly of nominal species suggests numerous putative cryptic species resembling the nominal taxa *P. varians* and *L. mycetoseroides*. This genomic data provides a new platform to sort out the complicated taxonomy and evolutionary history of family Agariciidae.

INTRODUCTION

Molecular data have added monumentally to our phylogenetic knowledge, but for the most part they have substantiated earlier work based on morphological data. Scleractinian corals are one group for which the insights gleaned from molecular data have conflicted deeply with morphologically-based systematics, requiring substantial reorganization of the taxonomy and systematics of corals in a profound and extensive way (Romano & Palumbi 1996; Kerr et al. 2005; Fukami et al. 2008; Kitahara et al. 2010; Budd et al. 2012; Huang et al. 2012; 2016;

Arrigoni et al. 2014; 2016; Terraneo et al. 2016). Discordance between molecules and taxonomy in corals has been attributed to the notoriously challenging morphology of corals, which is homoplasious, plastic, and highly variable within species (Todd 2008; Budd et al. 2010; Schmidt-Roach et al. 2014). This combined with the exceptionally slow mitochondrial evolution of corals confounded species delimitation during initial attempts to assess diversity (Shearer et al. 2002; Hellberg 2006; Chen et al. 2009).

The advent of the next generation molecular era has enhanced the recovery of well-defined species and phylogenies in some of the most challenging coral groups (Quek & Huang 2021). Reduced representation studies, notably restriction-site associated DNA (RAD-seq) efforts have revealed well-supported phylogenies via RAD loci and SNP datasets in genera such as *Pocillopora* (Combosch & Vollmer 2015; Johnston et al. 2017), *Leptastrea* (Arrigoni et al. 2020), *Pachyseris* (Bongaerts et al. 2021), *Porites* (Forsman et al. 2017; Forsman et al. 2020), *Montipora* (Cunha et al. 2019), and others (Rosser et al. 2017; Wepfer et al. 2020). Recent efforts to develop bait-sets for ultra-conserved elements (UCEs) within corals have resolved relationships within the notoriously thorny and species-rich genus *Acropora* (Cowman et al. 2020; Ramírez-Portilla et al. 2022). And while the above studies are generally limited to the most well-studied genera, complete mitogenomes are being generated rapidly for species across the scleractinian tree (Liu et al. 2015; Niu et al. 2018; Tong et al. 2019; Seiblitiz et al. 2020). And as more scleractinian genomes become available, whole genome studies are recovering not only phylogenetic relationships but the relative impact of Incomplete Lineage Sorting (ILS) and introgression, two processes which are likely to be prevalent in corals.

Phylogenomic methods allow for more data from across the genome, inherently increasing the opportunity for gene tree - species tree discordance. Although there is a singular species tree representing the evolutionary history of a group, different genes or areas of the genome can have different topologies and branch lengths (Takahata & Nei 1985). Discordance between the nuclear and mitogenomes is particularly likely to occur because the mitogenome is physically unlinked from the nuclear genome and inherited as a single locus (Neigel & Avise 1986; Shaw 2002; Bonnet et al. 2017; Sarver et al. 2021). Discordance can also be generated by differences in the direction and strength of selection (Lamichanney et al. 2015), hybridization or

introgression of the nuclear genome (Edelman et al. 2019), or, most commonly, due to incomplete lineage sorting (Hudson & Coyne 2002); distinguishing between these different underlying causes has been historically challenging (Funk & Omland 2003; Toews & Brelsford 2012). Large population sizes, overlapping geographic distributions (Dietzel et al. 2021), external fertilization, and both experimental (e.g., Willis et al. 1997) and molecular phylogenetic evidence compatible with horizontal gene transfer (e.g., Odorico and Miller 1997) has prompted some researchers to suggest that exceptionally frequent hybridization, introgression, and reticulate evolution occurs within corals (Willis et al. 2006; Veron et al. 2016a). However, large range sizes, long generation times, and rapid speciation, also traits associated with corals, are likely to prolong incomplete lineage sorting (Hudson & Coyne 2002; Rosenberg 2003). With the increase in genomic data, attempts to distinguish between these possibilities are recovering some evidence of introgression in corals, although it is not extensive (Mao et al. 2018; Cunha et al. 2019).

The coral family Agariciidae (Gray 1847) is composed of three prominent genera, two of which are found in the Indo-Pacific. These genera, *Leptoseris* and *Pavona*, are predominantly associated with mesophotic and shallow reefs respectively (Luck et al. 2013; Veron 2000). Within the Indo-Pacific the agaricids species are notable for exceptionally large ranges, and very few species are confined to a singular biogeographic province or the Coral Triangle (Hughes et al. 2002; Chapter 2). While our understanding of coral systematics has improved considerably over the past decade, the agaricids have yet to be the focus of a phylogenomic study. Thus far all molecular work in this family has been limited to a handful of markers, most notably a highly variable mitochondrial intron which has some concordance with morphological characters (Luck et al. 2013; Waheed et al. 2015; Bongaerts et al. 2015; Terraneo et al. 2017; Chapter 2). However, this marker may not evolve quickly enough to delimit recent species, as it failed to distinguish between morphologically disparate nominal taxa (Terraneo et al. 2017; Chapter 2). These previous studies recovered multiple putative cryptic species, and highlight the need for a phylogenomic assessment of this family.

The nominal taxon *P. varians* (Verrill 1864) is of particular interest, because of the potential for undescribed cryptic diversity. This species is extremely widely distributed across

the Indo-Pacific, from the Red Sea to Panama, and from shallow to mesophotic depths (Luck et al. 2013; Roberts et al. 2019). This species is exceptionally common and abundant across the Indo-Pacific (DeVantier & Turak 2017; Dietzel et al. 2021). Therefore it is not surprising that *P. varians* was one of only four species described as common depth generalists in an assessment of mesophotic and shallow reefs in American Samoa (Montgomery et al. 2021). This taxon is also highly morphologically variable, hence the name, and has long been recognized as something of a “dustbin” species, i.e., a group of cryptic species with similar morphology (Wells 1954; Veron & Pichon 1980). Some of this intraspecific variation can be attributed to light-associated plasticity (Chapter. 4); however; this is unlikely to explain all of the morphological variation within this species. Indeed, previous work recovered numerous putative cryptic species associated with this nominal taxon (Chapter 2).

In this study we investigated the phylogenomics of Indo-Pacific species from the stony coral family Agariciidae. We generated ezRAD libraries for 120 corals from twenty nominal taxa across both *Leptoseris*, *Pavona*, and the monotypic genus *Gardineroseris planulata*. This allowed us to produce complete mitochondrial genomes for all twenty taxa, and generate SNP datasets from two different reference guided assemblies, as well as a de novo assembly. We present an unrivaled assessment of the systematics of this diverse, understudied, and enigmatic family.

METHODS

Sample Collection & Identification

From 2006 to 2019, 122 samples were collected from across the Indo-Pacific, 112 of these were previously analyzed in Chapter 2 (see Table S3.1 for details). Where possible colonies were photographed *in situ* prior to collection using a camera (Canon G6), in underwater housing (Canon WP-DC34). Small (<2 cm²) fragments of the coral colony were collected while snorkeling, SCUBA, or rebreather diving, using a hammer and chisel. These fragments were then preserved in either DMSO or 96-100% ethanol for molecular analysis, and stored at 4° C.

Species were identified using the same protocols as described in Chapter 2. Photographs of the overall colony and corallite morphology and skeletal fragments were compared to the taxonomic guides of Veron & Stafford Smith (2000), and Fenner (2005); as well as original descriptions. Type material of Agariciidae deposited in the Harvard Museum of Comparative Zoology (MCZ), Boston, USA, and the US National History Museum (USNM), Washington DC, USA were photographed and examined by CJL to help identification.

DNA Extraction and Sequencing

DNA was extracted using Qiagen DNeasy kits according to the manufacturer's recommendations, with the exception of an extended overnight incubation of tissue with proteinase K, adding 4ul of 100mg/ml RNase A before the lysing step, and DNA was eluted in 70°C H₂O.

RAD libraries were prepared following the ezRAD protocol (Toonen et al. 2013), with the exception of using either Kapa HyperPrep or Illumina TruSeq DNA library preparation kits. Libraries were sequenced on Illumina HiSeq paired-end platforms at the Hudson Alpha Institute for Biotechnology, the University of California Berkeley QB3 Genomics facility and the Texas A&M University Corpus Christi Genomics Core Lab.

Reads were paired, trimmed of adapters, and cleaned using Trimmomatic (Bolger et al. 2014) in dDocent (Puritz et al. 2014a, b) under default settings: bases at the beginning and end of reads cleaned to a minimum Q score of 20, and additional bases trimmed in a 5 bp sliding window if Q score dropped below an average of 10, and minimum length of 15 bp.

Mitochondrial genome assembly

Trimmed and cleaned reads were reference assembled to two published mitochondrial genomes, *P. clavus* (DQ643836, Medina et al. 2006) or *P. decussata* (NC_026527, Shi et al. 2015) in Geneious Prime using default parameters for assembly and consensus generation with the exception of trimming the consensus to the reference (see Table S3.2 for details).

Two mitogenome data sets were generated: protein-coding DNA plus rDNA (hereafter referred to as functional genes) and non-coding DNA (i.e., non-functional) (Table S3.3).

Functional regions of the newly generated mitogenomes were annotated from *P. clavus* (DQ643836, Medina et al. 2006). A total of 15 annotated regions were then extracted from each mitogenome, aligned separately using default settings in the Clustal Omega (Sievers et al. 2011) plugin for Geneious Prime, and then concatenated. For individuals missing certain genes dummy sequences (of Ns) of equal length were included to create a complete matrix. These two datasets, functional only, non-functional only, were analyzed separately and combined, the latter hereafter referred to as the full mitogenome.

Mitogenome phylogeny construction

Maximum likelihood phylogenies for all three datasets were constructed using IQ-Tree (Nguyen et al. 2015) on the CIPRES computing cluster (Miller et al. 2010). Prior to phylogenetic tree construction the best model was determined using ModelFinder (Kalyaanamoorthy et al. 2017) and corrected Bayesian Information Criterion within IQ-Tree, see Table S3.4 for best-fitting models. The functional and full mitogenome phylogenies were assessed for partitioning schemes using partition finder within IQ-Tree (Chernomor et al. 2016), allowing for each gene or rRNA region, and genic regions to be further partitioned based on codon position. See Table S3.4 for best partitions. Trees were constructed using the best supported model in IQ-Tree with ultrafast bootstrap replicates (Minh et al. 2013). Individuals which failed to meet the chi1 threshold were removed prior to analysis.

A phylogeny of the combined mitogenome dataset was generated in Mr Bayes v2.7.a (Huelsenbeck & Ronquist 2001) on the CIPRES computing cluster. The same best-partitioning scheme and model selection from IQ-Tree was implemented. The phylogenetic analysis was repeated three times, each using 3,500,000 generations for each of two Markov chains, sampling every 3,000 generations. The temperature was set to 0.2 with 1 swap between chains attempted every generation. The first 25% of generations were discarded as burn-in. The combined log file was then examined in Tracer v1.7.2 (Rambaut et al. 2018), and assessed for convergence and mixing, and posterior ESS score over 625.

Mitogenome trees and all other rooted trees using other reconstruction methods (below) were rooted with *Gardineroseris planulata*. Clades were assigned based on monophyletic groups which had a distinct morphology from their sister group.

SNP dataset assembly and filtering

Trimmed and cleaned reads were then assembled in dDocent (Purtiz et al. 2014a; Puritz et al. 2014b) on the University of Hawai‘i at Mānoa Mana high performance computing cluster under default settings using three different assembly approaches. Three data sets were assembled, the first a reference-guided assembly to a concatenated sequence of Ultra Conserved Elements from *Leptoseris cf. scabra* (Cowman et al. 2020, coral 69) a total of 1,347,580 bp. Next, reads were reference-assembled to a transcriptome from *P. decussata* (Zhang et al. 2019), concatenated with 200 bp of Ns inserted between each contig. Lastly, a de novo assembly was created under default settings in dDocent (clustering similarity 86%, K1 2, K2 2, Mapping match 1, Mapping mismatch 3, open gap penalty 5). This final assembly makes no attempt to remove potential bacterial, or dinoflagellate symbionts and will hereafter be referred to as the coral holobiont. Briefly, dDocent is a pipeline which aligns reads de novo using the program Rainbow (Zhao et al. 2013), and maps sequences (to a reference if provided) using BWA (Li & Durbin 2009). Once aligned SNPs are then called using FreeBayes (Garrison & Marth 2012) and assembled into a vcf file using vcftools (Danecek et al. 2011).

For each assembly SNPs were initially filtered using vcftools (Danecek et al. 2011) to make the data set more manageable by removing sites with more than 50% missing data, a minor allele count of <4, and a minimum Q score of 35. Individuals with more than 75% missing data were removed and sites were further filtered based on a minimum depth of 5. Sites with indels were removed and any sites remaining with more than 50% missing data were removed. Only biallelic SNPs were retained for all analyses and for the transcriptome and de novo datasets SNPs were thinned to a minimum of one every 300 bp. Lastly, VCF files were converted to Phylip format (Ortiz 2019), and invariant sites were removed (https://github.com/btmartin721/raxml_ascbias).

Phylogenomic reconstructions

IQ-Tree and SplitsTree. 1000 bootstrapped replicates of a maximum likelihood phylogeny were constructed in IQ-Tree, allowing for missing data and with an ascertainment bias correction for SNP data. The IQ-Tree analysis was repeated with a reduced dataset in which individuals with more than 50% missing data were removed. The reduced datasets were then

used to create unrooted networks in SplitsTree v4.18.1 using the neighbor-net algorithm (Huson & Bryant 2006).

Clades were delineated using the topologies from IQ-Tree, a minimum bootstrap threshold of 50, and having consistent morphology (i.e., were nominal species or very similar morphology) distinct from their sister clade, or individuals were from the same biogeographic region, or all those individuals were in a clade from the mitochondrial analysis. There was one clade from the transcriptome tree which has a bootstrap value lower than 50 but was included to prevent merging with two other well defined clades.

SVD Quartets. For the transcriptome and de novo assemblies the reduced datasets were analyzed using svd quartets (Chifman & Kubatko 2014; 2015) implemented in PAUP* v4.a168 on the CIPRES computing cluster. A priori species designations were determined using clades as recovered from the IQ-tree phylogenies, with single individuals which did not fall within clades excluded (see Table S3.5 for details). Every quartet was evaluated in a species tree with 100 bootstraps. A 50% majority-rule consensus tree with bootstrap support was exported from PAUP*.

SNAPP & D_{FOIL}. The reduced transcriptome and de novo assemblies, i.e., those containing individuals with less than 50% missing data, were filtered further for SNAPP v1.5.2 analysis (Bryant et al. 2012). First, only individuals with a maximum of 30% missing data were considered, then only sites with data from 100% of these individuals were retained, to create a dataset with no missing data. For computational feasibility this dataset was then reduced to prioritize particular areas of the phylogeny and nominal species of interest. For the transcriptome dataset three runs of 3 million generations were performed on BEAST v.2.6.6 (Bouckaert et al. 2019) on the CIPRES supercomputer. The combined log files were examined in Tracer v1.7.2 (Rambaut et al. 2018), and assessed for convergence, under a 10% burn in. The .tre files were then combined in LogCombiner v2.6.6, and converted into a maximum clade credibility tree with mean node heights in TreeAnnotator v2.6.6 (Suchard et al. 2018) under a 10% burn-in, and visualized in Fig Tree v1.4.4 (Rambaut 2010). The combined .trees file was visualized in DensiTree v2.2.7 (Bouckaert 2010), shuffled to highlight the most frequent trees in the default

triangle configuration with the consensus tree in black. For the de novo dataset one run of 4 million generations was performed on BEAST. The log file was examined in Tracer v1.7.2 with a 10% burn in, trace files were assessed for convergence and mixing, and posterior ESS score over 625. The tree files were visualized in DensiTree v2.2.7, shuffled to highlight the most frequent trees in the default triangle configuration with the consensus tree in black.

To test for introgression, D-statistics were estimated in D_{FOIL} (Pease & Hahn 2015). This approach is similar to ABBA-BABA tests where discordant topologies of biallelic SNPs are assessed in different combinations. If the topologies are more numerous in one configuration than another, introgression can be inferred. Combinations of five individual libraries were extracted from the complete filtered dataset, then further filtered to create a 100% complete matrix. Combinations were chosen that fit the overall topology required for the model and that allowed testing for introgression both within and between clades. Individuals from the SNAPP tree were chosen to maximize the number of SNPs. These were then analyzed in nine different combinations shown in sets of five following a symmetrical topology of ((P1,P2)(P3,P4)O), where *G. planulata* was always the outgroup and P1 and P2 diverge more recently than P3 and P4 (Table S3.7).

RESULTS

Mitogenomes

Full mitochondrial assemblies were generated for 122 individuals from 20 nominal species ranging in size from 18,257 bp to 18,462 bp, with an average completeness of 98.25% (Table S3.2). Gene and rRNA annotations from 116 individuals representing 20 nominal taxa were aligned for a total length of 15,755 bp. Non-coding regions from 108 individuals representing 20 nominal taxa were aligned for a total length of 2,838 bp. These two alignments were combined from 115 individuals from 20 nominal taxa creating an alignment of total length 18,593 bp.

Both the maximum likelihood and Bayesian phylogenies based on the full mitogenome set recovered 24 well-supported clades, 22 (92%) of which had bootstrap values above 75 percent, and 21 (88%) had posterior probabilities of over 95 (Fig. 3.1 & S3.1). The non-coding

alignment recovered 24 identical clades with 22 (92%) clades with over 75 percent bootstrap support (Fig. S3.2). The functional phylogeny recovered only 20 clades, and 19 (85%) of clades had bootstrap support over 75 percent. The coding data set provided no resolution between clades 11 and 12, 14 and 15, and among three *P. varians* clades 2, 3, 4 (Fig. S3.3).

SNPs

Concatenated sites. SNP datasets varied in the number of individuals included and number of SNPs (Table S3.6). Analyses from the holobiont and transcriptome datasets recovered three main clades (pink, blue, and green)(Fig. 3.2 & 3.3). The IQ-Tree analyses from the *de novo* and transcriptome datasets both recovered these three clades with 100 % bootstrap support, except for the blue clade for the transcriptome data, which was recovered in 94 % of the bootstrap replicates. This tree differed from the mitogenome tree as none of the three colored clades (pink, blue, and green) were recovered as monophyletic in the mitogenome tree. In some cases taxa were placed in different parts of the mitogenome tree such as, *P. maldivensis*, and *P. varians*. In other instances taxa which were polyphyletic in the mitogenome tree, such as *P. duerdeni*, are recovered as monophyletic in the SNP trees (Fig. 3.4).

The SplitsTree networks for both coral holobiont and transcriptome datasets also divided individuals into three clusters corresponding to those recovered from the IQ-Tree analyses. All phylogenies based on the smaller UCE data and constructed with IQ-Tree and SplitsTree recovered clades pink and green with 100% bootstrap support, but failed to recover a monophyletic blue clade (Fig. 3.5).

Species trees. The same three clades were also recovered from the SVD quartets analysis with 100 bootstrap support for each clade from the coral holobiont and transcriptome datasets with the exception of the blue clade for the coral holobiont dataset. SNAPP analyses had fewer individuals and clades included but still recovered these three clades with high posterior support from 0.87 to 1.0 for the pink, blue and green clades from both the transcriptome and *de novo* datasets (Fig. 3.6).

The individuals recovered in these three clades were consistent across datasets and methodologies: the pink clade always contained individuals from the nominal species *P. varians*,

P. cactus, *P. frondifera* and *P. venosa*; the blue clade includes *P. duerdeni*, *P. explanulata*, *P. gigantea*, *P. maldivensis* and several species of *Leptoseris* and the green clade always included individuals from the nominal species *P. varians*, *P. chiriquiensis* and *P. decussata* (Fig. 3.7). The nominal taxon *P. varians* was the only species recovered in more than one of these three main clades.

The holobiont, transcriptome, and UCE datasets recovered 23, 21, and 17 clades respectively. 18 (78%) clades recovered from the holobiont dataset had bootstrap support of over 75, whereas the transcriptome and UCE recovered, 10 (50%) and 9 (53%) clades which had bootstrap support of over 75%.

Introgression and Incomplete Lineage Sorting

D-statistics recovered no evidence of introgression either between or within clades, e.g., pink, blue, and green (Table S3.7).

DISCUSSION

Our phylogenomic analysis of the Agariciidae revealed two primary results. First, phylogenetic analyses of SNPs from each of de novo assemblies of the coral holobiont, reference-guided transcriptomic assemblies, and reference-guided UCE assemblies consistently recovered three well-supported clades across a variety of tree-building approaches. These clades did not correspond to the current systematics of the agaricids: although two clades (green and pink) consisted exclusively of species of *Pavona*, the third clade (blue) is a mixture of *Pavona* and *Leptoseris*. Second, our analysis of complete mtDNA genomes revealed substantial discordance with phylogenies built with SNPs from coral holobiont, transcriptome, and UCE libraries. Together these two outcomes indicate that genome wide data are necessary to understand the relationships within this family and potentially identify and disentangle the relative importance of introgression and incomplete lineage sorting on these relationships. The results suggest that introgression may not a major contributor to gene tree discordance within agaricids, and caution against the exclusive use of mitochondrial data when assessing coral species diversity.

Agaricid phylogenomics

Similar to other phylogenomic analyses of corals, SNPs from de novo coral holobiont metagenomic assemblies and reference-guided assemblies (the latter presumably free of symbiont DNA) produced similar tree topologies in which species are split into three major clades. Despite a strongly-supported tree, neither *Pavona* nor *Leptoseris* are monophyletic, an outcome broadly consistent with previous phylogenetic analyses based on the mtDNA intron (Luck et al. 2013; Terraneo et al. 2016; Chapter 2). The primary clade structure within the family is robust to both resampling of concatenated SNPs via bootstrapping and analysis of data via species tree methods. The holobiont dataset likely includes SNPs from symbiotic algae and other microbes living within and on the surface of the coral. However, concordance with SNPs trees assemble to a coral transcriptome and UCEs indicate that the non-coral DNA is not driving the holobiont topology.

However, there are trends in each clade consistent with some aspects of taxonomy based on gross morphology. Species of *Leptoseris* are restricted to the blue clade, whereas species of *Pavona* are recovered in all three. The blue clade also only includes mounding or massive forms of *Pavona*, (i.e., *P. duerdeni*, *P. maldivensis*, and *P. explanulata*). In contrast, the green clade is composed of *P. decussata*, which forms large, interconnected upright plates, plus two encrusting species, *P. varians* and *P. chiriquiensis*. The pink clade is composed of forms corresponding to the encrusting morphologies of *P. varians* and *P. venosa*, and foliose and frond-forming *P. cactus* and *P. frondifera*. Those patterns aside, there are no obvious shared morphological traits that could be potential synapomorphies defining these three clades or linking the blue and green clades. Similar to trees built with the mitochondrial intron (Chapter 2), colonies whose gross morphology corresponds to that of *P. varians* are represented in both the green and pink clades.

Cytonuclear discordance

Phylogenies recovered from RAD-seq assemblies of the mitogenome had topologies which are well-supported, consistent between functional and non-functional parts of the mitogenome, and nearly identical to those recovered by the intronic data generated with PCR and Sanger sequencing (Chapter 2). However, none of the three clades recovered from the SNP trees are monophyletic in the mitogenome tree. One of the glaring differences is that the mitochondrial phylogeny distributed the nominal species *P. duerdeni* among three well-supported clades,

irrespective of whether the data were introns generated from PCR or mitogenomes generated from reference assemblies of the RAD reads. The morphology of this species is highly distinct, with colonies forming large “pork chop” shaped lobes (resulting in some of the largest colonies of any corals in the world (Veron et al. 2016b). The corallites of *P. duerdeni* are also tightly packed, inter-connected and flush to the surface, unique among Indo-Pacific agaricids. In the SNP phylogenies based on the same individuals, every specimen of *P. duerdeni* was consistently recovered as one well-supported monophyletic clade. Further, three mitogenomic clades of *P. varians* (2, 3, & 4) formed a monophyletic group distantly related to *P. varians* in clade 22 in the mitogenome phylogeny, but these individuals were all recovered in the pink clade along with *P. varians* from clade 22 in the SNP phylogenies. Furthermore, in the mitogenome phylogeny, *L. mycetoseroides* individuals from clade 7 were most closely related to *P. varians* from Clade 9 and *P. chiriquiensis* in clade 8, however in the SNP phylogenies they were more closely related to other *Leptoseris* species, *L. yabei* and *L. scabra*, within the blue clade.

Disagreement between mitochondrial and nuclear data has been recovered in scleractinians but is not the rule (van Oppen et al. 2001). There are few studies involving both mitochondrial and genomic nuclear data within corals. Some of these studies recovered well-supported nuclear and mitogenome phylogenies, but with differing topologies such as within *Porites* and *Pachyseris* (Forsman et al. 2017; Bongaerts et al. 2021). Whereas others recovered consistent signals across the two datasets, albeit with less resolution in the mitochondrial data (Johnston et al. 2017; Cunha et al. 2019; Arrigoni et al. 2020). The taxonomic scale of the cytonuclear discordance we recover here is somewhat unusual within corals generally, and further study is necessary to tease apart different hypotheses that could be driving this trend. For example, whole genome studies could help distinguish between ancient introgression, a large horizontal transfer event, or some systematic bias in the dataset.

Incomplete Lineage Sorting and Introgression

In addition to deep cytonuclear discordance, gene tree discordance is evident in the poorly defined backbone and alternate shallow topologies visible in the SNAPP trees based on SNPs in reads mapping to the coral holobiont metagenome and coral transcriptome. Although discord among gene trees created by incomplete lineage sorting, gene duplications, and homoplasy is expected in any phylogenomic analysis, it is also created by hybridization and

introgression (Tajima 1983; Maddison 1997). Hybridization and reticulate evolution has been thought to be important in the evolutionary history of corals, but only now with genomic data sets can that hypothesis be statistically tested.

Therefore, we estimated D-statistics (Green et al. 2010; Durand et al. 2011; Pease & Hahn 2015) to evaluate the relative importance of hybridization and introgression in agaricids. Overall, we found no evidence for introgression in the SNP data. However, the wide taxonomic coverage in this study limited the D-statistics data set to 100s of SNPs shared among all OTUs, typical of RAD-seq phylogenomics. If agaricid evolutionary history is not marked by frequent introgression, then incomplete mitogenome lineage sorting seems an unlikely explanation for the discordance observed here, especially given that the effective population size of mitochondrial genomes is one-quarter that of the nuclear genome. Therefore, the cytonuclear discordance in our trees requires an alternate explanation, possibly including introgression of the mitochondrial genome alone (Hudson & Coyne 2002). Future studies of complete genomes will have more power to detect introgression (Pease & Hahn 2015; Zheng & Yanke 2018) and will be able to use newer branch-length based techniques to estimate the extent of introgression (Edelman et al. 2019).

Cryptic Diversity

Analysis of the mitochondrial intron recovered numerous monophyletic clades that are likely cryptic species within the agaricids (Chapter 2). In the current study, phylogenies of larger SNP datasets recovered well-supported clades of morphologically similar species, distributed in different parts of the tree, each sister to morphologically distinct species. Some of these taxa were recovered as monophyletic in the SNP phylogenies, e.g., *P. duerdeni*, but others were still polyphyletic. Most of these cryptic lineages were associated with two nominal taxa, *P. varians* and *L. mycetoseroides*, which were polyphyletic in the mtDNA intron tree (Chapter 2) and the mitogenome tree (this study). In our SNP phylogenies, representatives of the nominal species *L. mycetoseroides* were recovered in two well-supported clades, which were more closely related to other morphologically distinct species than to each other. We recovered four clades which contained *L. mycetoseroides* individuals in the intron phylogeny (Chapter 2), but this difference partly reflects the reduced taxon sampling in the SNP data set. The final clade of *L. mycetoseroides* from the mitochondrial intron tree also contained a sample identified as *L. sp.*,

this individual is included in this study and is recovered in a distinct clade most closely related to other nominal taxa, clade H in the holobiont tree. Therefore we found support for all clades of *L. mycetoseroides* from the intron phylogeny for which we included samples.

In contrast to the splitting of some morphologically similar taxa, a striking result from the intronic study (Chapter 2) was the inability to distinguish morphologically distinct taxa, an outcome that we expected to be resolved with genomic data. Despite more data, however, some nominal and morphologically distinct taxa remain non-monophyletic clustered in well-supported clades with other nominal taxa. For example, within the pink clade of the reduced de novo tree, we delineated six further clades, the two most closely related of these include the morphologically distinct nominal species: *P. cactus*, *P. frondifera*, *P. venosa*, and *P. varians*. The remaining four clades are all composed of individuals which are visually identified as *P. varians*. The morphologies of *P. cactus* and *P. varians* are markedly different: the former has delicate bifacial fronds with small sparse corallites, in contrast *P. varians* is a predominantly encrusting species with irregular ridges and tightly packed corallites. The morphology of the four species recovered in this clade runs a spectrum between the two morphologies described above, with considerable intraspecific variation (Veron & Pichon 1980; Ayre & Willis 1988). While ridge extent and colony rugosity is plastic in *P. varians* (Chapter 4), and *P. cactus* also has considerable variation in colony form, these two species can be found within meters of one another. These co-distributions indicate that morphological differences are unlikely to be the result of plasticity alone. Whole genome data may reveal key islands of differentiation between these two species which we are unable to detect with our reduced representation approach (Wolf & Ellegren 2017). Whole genome analyses of eighteen *Acropora* species recovered morphologically distinct taxa as closely related sister species (Shinzato et al. 2021).

In trees generated from all three assemblies, the common species *P. varians* was recovered in two of the three broad clades, green and pink. In the mitochondrial phylogenies we recovered six clades of *P. varians*, three of which were closely related, and another of which contained four other nominal taxa, clade 22. We recovered eight clades of *P. varians* in the holobiont tree. Although broadly concordant, the clades from the mitochondrial data do not exactly match those from the holobiont tree. For example clades 9 and 12 from the mitogenome tree were distantly related to individuals from clade 22. In the SNP tree these individuals are recovered in the green clade, whereas those from 22 are recovered in the pink clade. However,

within the green clade of the holobiont tree we recover three further divisions (clades N,O,P) which do not correspond to the mitochondrial clades 9 and 12. Alternatively, although clades 2,3,4 are distantly related to individuals from clade 22 in the mitochondrial tree, all of these individuals are recovered in the pink clade of the SNP trees. However, within the pink clade of the holobiont tree, clade T contains only individuals from mitogenome clade 2, and clade W only contains only individuals from mitogenome clades 3 and 4. We recognize that these *P. varians* are all within a single monophyletic clade and may therefore not represent species level differences. However, they are more divergent than some highly morphologically distinct sisters in the same clade. Cryptic species are not uncommon in other coral families, sister species which are nearly indistinguishable morphologically have been recovered as separate species which are reproductively isolated (Ramírez-Portilla et al. 2022), or occupy distinct ecological niches (Bongaerts et al. 2021). Detailed morphometric analysis and species delimitation methods are necessary to determine if synapomorphies are able to distinguish the putative species recovered in our phylogeny.

CONCLUSION

We generated RAD libraries for 120 colonies of corals from the family Agariciidae, representing twenty nominal taxa. SNPs from de novo, transcriptomic, and UCE assemblies consistently recovered three well-supported clades, none of which correspond to *Pavona* or *Leptoseris*. We recommend that *Pavona* and *Leptoseris* be revised into three genera, as the two clades of *Pavona* are not sister. We did not find evidence of rampant nuclear introgression, suggesting that hybridization may not be an important force shaping the evolution of this family. In this context, strong cytonuclear discordance indicates that mitochondrial introgression likely occurred several times in this family. Our results caution against the exclusive use of mitochondrial data for identifying species in the agaricids as it is liable to both split and lump taxa inappropriately.

Table S3.1. Sequencing information for Indo-Pacific agaricid species libraries.

Species	Collection Location	Sample ID	Sequencing Run	Sequencing Facility	Reads	Reads Post-trim
<i>P. duerdeni</i>	Kingman Reef	393	September 2015	Hudson Alpha	6,791,734	6,572,606
<i>P. duerdeni</i>	Hawai'i	A705	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4000	12,656,392	12,325,480
<i>P. decussata</i>	Persian Gulf	AGJA108	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	10,353,584	9,982,552
<i>P. varians</i>	American Samoa	AMS14	July 2016	University of California Berkeley QB3 Genomics	17,973,608	17,586,972
<i>P. varians</i>	American Samoa	AMS15	July 2016	University of California Berkeley QB3 Genomics	17,078,676	16,843,880
<i>P. frondifera</i>	American Samoa	AMS17	June 2017	University of California Berkeley QB3 Genomics	13,295,872	13,151,394
<i>P. frondifera</i>	American Samoa	AMS21	June 2017	University of California Berkeley QB3 Genomics	19,049,720	18,873,332
<i>P. frondifera</i>	American Samoa	AMS25	December 2017	University of California Berkeley QB3 Genomics	21,387,808	10,335,350
<i>P. decussata</i>	American Samoa	AMS30	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	13,170,878	12,769,954
<i>P. frondifera</i>	American Samoa	AMS36	December 2017	University of California Berkeley QB3 Genomics	10,538,156	10,220,222
<i>P. varians</i>	American Samoa	AMS48	July 2016	University of California Berkeley QB3 Genomics	29,877,110	29,309,982
<i>P. varians</i>	American Samoa	AMS51	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	6,539,796	6,055,386
<i>P. varians</i>	American Samoa	AMS53	December 2017	University of California Berkeley QB3 Genomics	8,674,376	8,267,494
<i>P. varians</i>	American Samoa	AMS55	June 2017	University of California Berkeley QB3 Genomics	18,919,182	18,749,086
<i>P. frondifera</i>	American Samoa	AMS71	June 2017	University of California Berkeley QB3 Genomics	21,881,852	21,692,260

<i>P. duerdeni</i>	American Samoa	AMS73	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	7,807,868	7,197,140
<i>P. maldivensis</i>	American Samoa	AMS77	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	8,954,154	8,582,092
<i>P. explanulata</i>	American Samoa	AMS78	June 2017	University of California Berkeley QB3 Genomics	7,909,278	7,848,796
<i>P. varians</i>	American Samoa	AMS85	July 2016	University of California Berkeley QB3 Genomics	12,418,680	12,222,326
<i>P. varians</i>	Hawai'i	BIL3	December 2017	University of California Berkeley QB3 Genomics	15,056,556	14,647,292
<i>P. varians</i>	Hawai'i	BIL4	July 2016	University of California Berkeley QB3 Genomics	18,996,146	18,722,120
<i>P. varians</i>	Hawai'i	BIP1	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	5,075,200	3,660,384
<i>P. varians</i>	Hawai'i	BIP3	July 2016	University of California Berkeley QB3 Genomics	17,869,294	17,474,284
<i>P. varians</i>	Hawai'i	BIR1	December 2017	University of California Berkeley QB3 Genomics	16,206,030	15,795,754
<i>P. varians</i>	Hawai'i	BIR10	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	9,638,000	8,919,218
<i>P. varians</i>	Hawai'i	BIR3	December 2017	University of California Berkeley QB3 Genomics	5,084,234	4,931,308
<i>P. varians</i>	Hawai'i	BIR8	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	8,680,352	1,868,936
<i>P. varians</i>	Hawai'i	BIR9	July 2016	University of California Berkeley QB3 Genomics	18,990,708	18,666,110
<i>L. mycetoseroides</i>	Kiribati	C29	December 2017	University of California Berkeley QB3 Genomics	10,278,862	10,204,080
<i>P. chiriquiensis</i>	Kiribati	C39	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	9,362,102	9,065,024
<i>P. chiriquiensis</i>	Kiribati	C42	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	9,406,050	8,122,632

<i>P. frondifera</i>	Guam	GM10	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4003	11,331,834	10,906,908
<i>P. decussata</i>	Guam	GM18	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4004	10,503,278	10,162,250
<i>P. varians</i>	Guam	GM2	July 2016	University of California Berkeley QB3 Genomics	15,090,826	14,932,312
<i>P. venosa</i>	Guam	GM21	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	11,416,972	10,816,724
<i>P. decussata</i>	Guam	GM23	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	12,998,598	12,701,768
<i>P. varians</i>	Guam	GM25B*	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	12,205,330	11,977,372
<i>P. varians</i>	Guam	GM25*	July 2016	University of California Berkeley QB3 Genomics	17,294,756	17,065,996
<i>P. varians</i>	Guam	GM28	July 2016	University of California Berkeley QB3 Genomics	14,345,278	14,151,366
<i>P. frondifera</i>	Guam	GM30	December 2017	University of California Berkeley QB3 Genomics	1,904,894	1,841,012
<i>P. frondifera</i>	Guam	GM33	December 2017	University of California Berkeley QB3 Genomics	1,623,974	1,570,390
<i>P. frondifera</i>	Guam	GM55	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	5,823,066	4,455,680
<i>P. duerdeni</i>	Guam	GM57	December 2017	University of California Berkeley QB3 Genomics	12,456,388	12,312,852
<i>P. decussata</i>	Guam	GM59	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	3,841,468	3,620,748
<i>P. varians</i>	Guam	GM60	December 2017	University of California Berkeley QB3 Genomics	52,208,246	50,556,770
<i>L. papyracea</i>	Japan	JPN13	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	7,189,570	4,546,808
<i>L. yabei</i>	Japan	JPN15	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	5,776,786	5,007,774

<i>P. venosa</i>	Japan	JPN18	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4003	13,670,162	13,346,776
<i>P. varians</i>	Japan	JPN2	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4004	10,531,216	10,063,062
<i>P. varians</i>	Japan	JPN37	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4005	6,768,872	4,514,302
<i>P. cactus</i>	Japan	JPN43	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4006	2,884,556	1,168,048
<i>L. papyracea</i>	Japan	JPN45	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4007	2,109,230	1,258,276
<i>P. varians</i>	Japan	JPN46	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4008	8,839,708	8,348,250
<i>L. mycetoseroides</i>	Japan	JPN47	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4009	8,397,376	5,921,950
<i>L. mycetoseroides</i>	Japan	JPN49	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4010	11,359,692	10,959,008
<i>P. varians</i>	Japan	JPN5	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4011	8,330,892	7,920,074
<i>P. duerdeni</i>	Japan	JPN54	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4012	11,494,258	11,271,246
<i>P. explanulata</i>	Japan	JPN64	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4013	11,435,942	11,039,266
<i>L. sp</i>	Japan	JPN8	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4014	10,961,240	10,625,984
<i>P. duerdeni</i>	Maldives	MLD12	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4015	8,412,902	5,440,884
<i>P. clavus</i>	Maldives	MLD18	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4016	5,561,710	699,254
<i>P. maldivensis</i>	Maldives	MLD2	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4017	13,896,728	13,579,726
<i>P. varians</i>	Maldives	MLD20	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4018	9,222,860	8,519,708

<i>P. varians</i>	Maldives	MLD26	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4019	9,337,482	8,211,646
<i>P. duerdeni</i>	Maldives	MLD27	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4020	7,053,006	6,148,632
<i>G. planulata</i>	Maldives	MLD29	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4021	13,797,826	13,395,648
<i>P. varians</i>	Maldives	MLD32	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4022	8,983,688	8,678,192
<i>P. varians</i>	Maldives	MLD34	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4023	9,393,426	9,086,464
<i>P. varians</i>	Maldives	MLD4	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4024	12,610,034	12,065,574
<i>P. varians</i>	Maldives	MLD40	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4025	11,263,754	10,971,818
<i>P. varians</i>	Maldives	MLD43	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4026	9,006,372	8,552,982
<i>P. varians</i>	Maldives	MLD44	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4027	8,990,976	7,926,990
<i>P. minuta</i>	Maldives	MLD46	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4028	7,769,960	6,917,080
<i>P. varians</i>	Maldives	MLD47	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4029	9,682,506	9,178,240
<i>P. varians</i>	Maldives	MLD48	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4030	10,157,954	9,879,884
<i>P. varians</i>	Maldives	MLD49	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4031	9,406,506	8,516,464
<i>P. varians</i>	Maldives	MLD6	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4032	7,593,014	6,939,766
<i>P. bipartita</i>	Maldives	MLD7	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4033	12,247,796	11,701,364
<i>P. minuta</i>	Maldives	MLDX	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4034	6,023,456	3,024,494

<i>L. incrustans</i>	Hawai‘i	OAK10	December 2017	University of California Berkeley QB3 Genomics	11,378,744	11,178,272
<i>L. incrustans</i>	Hawai‘i	OAK13	December 2017	University of California Berkeley QB3 Genomics	12,232,600	11,870,094
<i>L. mycetoseroides</i>	Hawai‘i	OAK30	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	8,031,496	7,254,432
<i>L. tubulifera</i>	Hawai‘i	OAK35	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	9,247,296	8,943,382
<i>L. tubulifera</i>	Hawai‘i	OAK42	December 2017	University of California Berkeley QB3 Genomics	4,482,070	4,347,348
<i>L. scabra</i>	Hawai‘i	OAK60	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	12,462,018	12,049,360
<i>P. varians</i>	Hawai‘i	OAKB4	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	13,103,186	12,906,590
<i>P. varians</i>	Hawai‘i	OAKB6	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4003	9,294,940	8,260,562
<i>P. varians</i>	Hawai‘i	OAM10	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4004	8,503,228	8,189,580
<i>P. varians</i>	Hawai‘i	OAM3	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4005	7,835,910	6,973,244
<i>P. varians</i>	Hawai‘i	OAM5	December 2017	University of California Berkeley QB3 Genomics	31,871,624	30,976,188
<i>P. varians</i>	Hawai‘i	OAM6	December 2017	University of California Berkeley QB3 Genomics	2,233,860	2,156,224
<i>P. varians</i>	Hawai‘i	OAM9	December 2017	University of California Berkeley QB3 Genomics	9,808,456	9,386,704
<i>P. cactus</i>	Palau	PAL12	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	10,548,256	10,226,378
<i>P. venosa</i>	Palau	PAL18	June 2017	University of California Berkeley QB3 Genomics	6,859,516	6,782,446
<i>P. cactus</i>	Palau	PAL2	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	8,192,310	7,697,516

<i>P. clavus</i>	Palau	PAL25	June 2017	University of California Berkeley QB3 Genomics	2,197,254	2,154,890
<i>P. clavus</i>	Palau	PAL26	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	6,859,480	2,390,656
<i>P. varians</i>	Palau	PAL28	June 2017	University of California Berkeley QB3 Genomics	11,100,428	11,006,806
<i>P. chiriquiensis</i>	Panama	PAN14	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	10,639,154	10,191,728
<i>P. chiriquiensis</i>	Panama	PAN15	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	15,811,926	15,568,656
<i>P. chiriquiensis</i>	Panama	PAN16	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4003	8,364,098	8,165,110
<i>P. chiriquiensis</i>	Panama	PAN18	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4004	12,279,876	11,876,782
<i>P. varians</i>	Panama	PAN20	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4005	13,447,252	13,301,314
<i>P. varians</i>	Panama	PAN21	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4006	10,648,712	10,101,918
<i>P. varians</i>	Panama	PAN22	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4007	12,621,280	12,359,770
<i>P. varians</i>	Panama	PAN23	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4008	13,532,822	13,451,504
<i>P. varians</i>	Panama	PAN24	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4009	9,488,514	8,660,690
<i>P. gigantea</i>	Mexico	PAR4	December 2017	University of California Berkeley QB3 Genomics	4,792,088	4,678,236
<i>P. gigantea</i>	Mexico	PAR6	December 2017	University of California Berkeley QB3 Genomics	9,763,646	9,601,534
<i>P. varians</i>	Thailand	PHU140	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	8,232,924	6,974,978
<i>P. duerdeni</i>	Marshall Islands	RMI08	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	11,087,492	10,456,468

<i>P. varians</i>	Marshall Islands	RMI13	July 2016	University of California Berkeley QB3 Genomics	19,584,618	19,305,232
<i>P. varians</i>	Marshall Islands	RMI19	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	9,651,192	9,392,010
<i>P. varians</i>	Marshall Islands	RMI45	July 2016	University of California Berkeley QB3 Genomics	3,265,190	3,170,466
<i>P. maldivensis</i>	Johnson Atoll	TAEK	September 2015	Hudson Alpha	8,808,286	7,698,082
<i>G. planulata</i>	French Polynesia	TGAR1	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4001	11,228,506	10,578,054
<i>G. planulata</i>	French Polynesia	TGAR7	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4002	13,748,484	13,332,308
<i>P. maldivensis</i>	Johnson Atoll	TLEK	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4003	14,056,794	13,690,136
<i>P. varians</i>	French Polynesia	TPV2	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4004	6,891,986	6,047,478
<i>P. varians</i>	Tanzania	ZAN044	December 2020	Texas A&M University Corpus Christi Genomics Core Lab, HiSeq4005	9,395,324	9,035,028

* Represents a technical replicate.

Table S3.1. (Continued). **Sequencing information for Indo-Pacific agaricid species libraries.**

Table S3.2. Mitogenome assembly details for Indo-Pacific agaricid species. Reference assembly, denotes which mitogenome was used as the guide. *P clavus* refers to the reference from Medina et al. (2006), and *P decussata* (Shi et al. 2016). HQ% indicates percentage of the assembly considered high quality.

Species	Sample ID	Reads Assembled	Reference Assembly	HQ (%)	Length (bp)	Ambiguities	Completeness (%)
<i>P. duerdeni</i>	393	7,727	<i>P clavus</i>	100	18,314	20	99.89079393
<i>P. duerdeni</i>	A705	24,684	<i>P decussata</i>	100	18,344	0	100
<i>P. decussata</i>	AGJA108	27,087	<i>P decussata</i>	100	18,387	0	100
<i>P. varians</i>	AMS14	24,100	<i>P clavus</i>	100	18,315	14	99.92355992
<i>P. varians</i>	AMS15	20,380	<i>P decussata</i>	100	18,384	16	99.9129678
<i>P. frondifera</i>	AMS17	25,184	<i>P clavus</i>	100	18,316	14	99.9235641
<i>P. frondifera</i>	AMS21	34,009	<i>P clavus</i>	100	18,317	2	99.98908118
<i>P. frondifera</i>	AMS25	42,087	<i>P clavus</i>	100	18,301	8	99.95628654
<i>P. decussata</i>	AMS30	23,849	<i>P decussata</i>	100	18,377	0	100
<i>P. frondifera</i>	AMS36	10,776	<i>P clavus</i>	100	18,315	5	99.97269997
<i>P. varians</i>	AMS48	41,118	<i>P clavus</i>	100	18,283	1	99.99453044
<i>P. varians</i>	AMS51	8,793	<i>P decussata</i>	98.5	18,383	237	98.71076538
<i>P. varians</i>	AMS53	16,835	<i>P clavus</i>	100	18,315	14	99.92355992
<i>P. varians</i>	AMS55	22,447	<i>P decussata</i>	100	18,347	0	100
<i>P. frondifera</i>	AMS71	66,087	<i>P clavus</i>	100	18,303	1	99.99453641
<i>P. duerdeni</i>	AMS73	12,026	<i>P decussata</i>	94.3	18,385	712	96.12727767
<i>P. maldivensis</i>	AMS77	10,293	<i>P decussata</i>	98.6	18,385	186	98.98830568
<i>P. explanulata</i>	AMS78	16,587	<i>P decussata</i>	100	18,383	8	99.95648153
<i>P. varians</i>	AMS85	26,825	<i>P decussata</i>	100	18,347	0	100
<i>P. varians</i>	BIL3	20,275	<i>P decussata</i>	100	18,347	16	99.91279228
<i>P. varians</i>	BIL4	19,375	<i>P clavus</i>	100	18,291	0	100
<i>P. varians</i>	BIP1	4,253	<i>P decussata</i>	87	18,375	2,101	88.56598639
<i>P. varians</i>	BIP3	19,026	<i>P clavus</i>	100	18,315	7	99.96177996

<i>P. varians</i>	BIR1	27,993	<i>P clavus</i>	100	18,315	3	99.98361998
<i>P. varians</i>	BIR10	4,335	<i>P decussata</i>	97.6	18,387	260	98.58595747
<i>P. varians</i>	BIR3	7,579	<i>P clavus</i>	96.8	18,311	267	98.54186008
<i>P. varians</i>	BIR8	8,822	<i>P decussata</i>	96.7	18,347	419	97.71624789
<i>P. varians</i>	BIR9	33,703	<i>P clavus</i>	100	18,295	0	100
<i>L. mycetoseroides</i>	C29						
		14,634	<i>P decussata</i>	100	18,384	3	99.98368146
<i>P. chiriquiensis</i>	C39	6,291	<i>P decussata</i>	95.3	18,375	664	96.38639456
<i>P. chiriquiensis</i>	C42	6,850	<i>P decussata</i>	95.7	18,382	570	96.89914046
<i>P. frondifera</i>	GM10	13,609	<i>P clavus</i>	99.8	18,268	27	99.85220057
<i>P. decussata</i>	GM18	20,997	<i>P decussata</i>	100	18,377	0	100
<i>P. varians</i>	GM2	26,475	<i>P clavus</i>	100	18,315	1	99.99453999
<i>P. venosa</i>	GM21	14,325	PAL18	90.9	18,274	1,355	92.58509358
<i>P. decussata</i>	GM23	20,452	<i>P decussata</i>	97.6	18,378	292	98.41114376
<i>P. varians</i>	GM25B	10,216	<i>P clavus</i>	99.2	18,264	165	99.09658344
<i>P. varians</i>	GM25	22,267	<i>P clavus</i>	100	18,294	0	100
<i>P. varians</i>	GM28	16,940	<i>P clavus</i>	99.9	18,300	66	99.63934426
<i>P. frondifera</i>	GM30	6,782	<i>P clavus</i>	99.2	18,315	85	99.53589954
<i>P. frondifera</i>	GM33	3,834	<i>P clavus</i>	100	18,315	7	99.96177996
<i>P. frondifera</i>	GM55	5,561	<i>P clavus</i>	79.9	18,269	3,237	82.2814604
<i>P. duerdeni</i>	GM57	18,896	<i>P clavus</i>	99.2	18,312	97	99.4702927
<i>P. decussata</i>	GM59	3,707	<i>P decussata</i>	99.3	18,377	42	99.77145345
<i>P. varians</i>	GM60	115,659	<i>P clavus</i>	100	18,316	4	99.97816117
<i>L. papyracea</i>	JPN13	7,585	<i>P decussata</i>	100	18,338	0	100
<i>L. yabei</i>	JPN15	9,142	<i>P decussata</i>	99.8	18,368	37	99.79856272
<i>P. venosa</i>	JPN18	15,692	<i>P clavus</i>	99.7	18,298	27	99.85244289
<i>P. varians</i>	JPN2	9,632	<i>P decussata</i>	100	18,347	0	100
<i>P. varians</i>	JPN37	3,887	<i>P decussata</i>	81.7	18,387	2,999	83.68956328
<i>P. cactus</i>	JPN43	6,702	<i>P clavus</i>	100	18,288	4	99.97812773

<i>L. papyracea</i>	JPN45	4,167	<i>P decussata</i>	99.9	18,338	22	99.88003054
<i>P. varians</i>	JPN46	6,224	<i>P decussata</i>	94.7	18,385	786	95.72477563
<i>L. mycetoseroides</i>	JPN47	19,222	<i>P decussata</i>	74	18,336	4,315	76.46705934
<i>L. mycetoseroides</i>	JPN49	6,993	<i>P decussata</i>	73.6	18,369	4,844	73.62948446
<i>P. varians</i>	JPN5	11,067	<i>P decussata</i>	99.2	18,384	46	99.74978242
<i>P. duerdeni</i>	JPN54	13,564	<i>P clavus</i>	99.6	18,315	101	99.44853945
<i>P. explanulata</i>	JPN64	20,286	<i>P decussata</i>	100	18,415	18	99.9022536
<i>L. sp</i>	JPN8	5,373	<i>P decussata</i>	100	18,362	5	99.97276985
<i>P. duerdeni</i>	MLD12	7,052	<i>P decussata</i>	100	18,389	11	99.94018163
<i>P. clavus</i>	MLD18	3,246	<i>P decussata</i>	100	18,390	17	99.90755846
<i>P. maldivensis</i>	MLD2	15,053	<i>P decussata</i>	95.3	18,385	643	96.50258363
<i>P. varians</i>	MLD20	8,875	<i>P decussata</i>	99.5	18,384	71	99.6137946
<i>P. varians</i>	MLD26	17,673	<i>P clavus</i>	100	18,314	29	99.8416512
<i>P. duerdeni</i>	MLD27	12,400	<i>P decussata</i>	100	18,389	32	99.82598292
<i>G. planulata</i>	MLD29	24,778	<i>P decussata</i>	100	18,379	0	100
<i>P. varians</i>	MLD32	11,752	<i>P decussata</i>	95.7	18,384	405	97.79699739
<i>P. varians</i>	MLD34	10,041	<i>P decussata</i>	100	18,387	0	100
<i>P. varians</i>	MLD4	18,263	<i>P decussata</i>	100	18,387	2	99.98912275
<i>P. varians</i>	MLD40	10,014	<i>P decussata</i>	99.3	18,384	162	99.11879896
<i>P. varians</i>	MLD43	9,505	<i>P decussata</i>	97.5	18,384	210	98.85770235
<i>P. varians</i>	MLD44	6,908	<i>P decussata</i>	91.2	18,388	1,194	93.50663476
<i>P. minuta</i>	MLD46	5,021	<i>P clavus</i>	98.7	18,338	155	99.15476061
<i>P. varians</i>	MLD47	8,617	<i>P clavus</i>	99.9	18,287	14	99.92344288
<i>P. varians</i>	MLD48	12,599	<i>P decussata</i>	99.1	18,462	34	99.81583794
<i>P. varians</i>	MLD49	7,546	<i>P decussata</i>	98.7	18,387	189	98.97209985
<i>P. varians</i>	MLD6	9,144	<i>P clavus</i>	99.9	18,315	6	99.96723997
<i>P. bipartita</i>	MLD7	23,726	<i>P clavus</i>	99.9	18,420	8	99.95656895
<i>P. minuta</i>	MLDX	94,118	<i>P clavus</i>	99.7	18,313	153	99.16452793

<i>L. incrustans</i>	OAK10	15,026	<i>P decussata</i>	100	18,379	5	99.97279504
<i>L. incrustans</i>	OAK13	30,573	<i>P decussata</i>	91.8	18,457	866	95.30801322
<i>L. mycetoseroides</i>	OAK30	4,356	<i>P decussata</i>	96.1	18,384	456	97.51958225
<i>L. tubulifera</i>	OAK35	10,150	<i>P decussata</i>	100	18,346	0	100
<i>L. tubulifera</i>	OAK42	2,729	<i>P decussata</i>	98	18,362	183	99.00337654
<i>L. scabra</i>	OAK60	17,530	<i>P decussata</i>	100	18,404	14	99.92392958
<i>P. varians</i>	OAKB4	13,976	<i>P decussata</i>	99.9	18,347	1	99.99454952
<i>P. varians</i>	OAKB6	15,651	<i>P decussata</i>	99.9	18,347	22	99.88008939
<i>P. varians</i>	OAM10	10,263	<i>P decussata</i>	98	18,347	232	98.73548809
<i>P. varians</i>	OAM3	10,038	<i>P decussata</i>	85.6	18,347	2,191	88.05799313
<i>P. varians</i>	OAM5	60,575	<i>P clavus</i>	100	18,315	4	99.97815998
<i>P. varians</i>	OAM6	2,264	<i>P clavus</i>	74.2	18,257	3,173	82.62036479
<i>P. varians</i>	OAM9	16,035	<i>P decussata</i>	100	18,347	0	100
<i>P. cactus</i>	PAL12	20,130	<i>P clavus</i>	98.2	18,287	218	98.80789632
<i>P. venosa</i>	PAL18	12,387	<i>P clavus</i>	99.9	18,274	10	99.94527744
<i>P. cactus</i>	PAL2	14,964	<i>P clavus</i>	96.8	18,286	348	98.09690474
<i>P. clavus</i>	PAL25	4,640	<i>P decussata</i>	100	18,388	3	99.98368501
<i>P. clavus</i>	PAL26	2,638	<i>P decussata</i>	100	18,389	4	99.97824787
<i>P. varians</i>	PAL28	17,718	<i>P clavus</i>	100	18,315	5	99.97269997
<i>P. chiriquiensis</i>	PAN14	14,073	<i>P decussata</i>	100	18,384	0	100
<i>P. chiriquiensis</i>	PAN15	8,041	<i>P decussata</i>	99.9	18,384	19	99.89664926
<i>P. chiriquiensis</i>	PAN16	7,053	<i>P decussata</i>	100	18,384	0	100
<i>P. chiriquiensis</i>	PAN18	5,092	<i>P decussata</i>	99.4	18,384	113	99.38533507
<i>P. varians</i>	PAN20	3,691	<i>P clavus</i>	100	18,306	10	99.9453731
<i>P. varians</i>	PAN21	3,219	<i>P clavus</i>	99.6	18,315	41	99.77613978
<i>P. varians</i>	PAN22	3,099	<i>P clavus</i>	99.5	18,265	467	97.44319737
<i>P. varians</i>	PAN23	872	<i>P clavus</i>	93.7	18,315	908	95.04231504
<i>P. varians</i>	PAN24	1,438	<i>P clavus</i>	89.4	18,312	1,501	91.80318917

<i>P. gigantea</i>	PAR4	8,294	<i>P. decussata</i>	99.7	18,383	34	99.81504651
<i>P. gigantea</i>	PAR6	8,294	<i>P. decussata</i>	100	18,381	14	99.92383439
<i>P. varians</i>	PHU140	14,761	<i>P. decussata</i>	100	18,416	4	99.97827976
<i>P. duerdeni</i>	RMI08	24,853	<i>P. decussata</i>	100	18,385	9	99.95104705
<i>P. varians</i>	RMI13	30,856	<i>P. clavus</i>	100	18,319	26	99.85807086
<i>P. varians</i>	RMI19	13,914	<i>P. decussata</i>	99	18,387	158	99.14069723
<i>P. varians</i>	RMI45	6,210	<i>P. clavus</i>	100	18,315	7	99.96177996
<i>P. maldivensis</i>	TAEK	11,546	<i>P. decussata</i>	100	18,385	23	99.87489801
<i>G. planulata</i>	TGAR1	17,221	<i>P. decussata</i>	99.7	18,379	0	100
<i>G. planulata</i>	TGAR7	25,097	<i>P. decussata</i>	99.5	18,379	73	99.60280755
<i>P. maldivensis</i>	TLEK	17,799	<i>P. decussata</i>	99.9	18,385	19	99.89665488
<i>P. varians</i>	TPV2	4,353	<i>P. decussata</i>	100	18,347	0	100
<i>P. varians</i>	ZAN044	49,053	<i>P. decussata</i>	100	18,347	5	99.97274759

Table S3.2. (Continued). Mitogenome assembly details for Indo-Pacific agaricid species.

Table S3.3. Partitions of the mitogenome or Indo-Pacific agaricids.

Region	Length (bp)
ATP6	1,044
ATP8	219
COX1	1,614
COX2	744
COX3	789
CYTB	1,152
large rRNA	2,303
ND1	984
ND2	1,098
ND3	357
ND4	1,479
ND4L	330
ND5	1,836
ND6	636
small rRNA	1,170
non-coding	2,838

Table S3.4. Sample, partitions, and model information for mitogenome alignments for Indo-Pacific agaricid species. And clades recovered from the phylogeny generated from each alignment. GTR = General Time Reversible DNA substitution model, HKY = Hasegawa, Kishino, Yano DNA substitution model, F = empirical base frequencies, I = proportion invariant sites, G4 = Gamma model of site heterogeneity with 4 rate categories.

Data Type	Individuals	Nominal Taxa	N char	Parsimony informative	Best Fit Partition	Best Fit Model	Clades
Mitochondrial coding only	116	20	15,755	477	1: COX1 2: Everything else	1: GTR +F + I + G4 2: GTR+ F + I	24
Mitochondrial non-coding only	108	20	2,838	574	N/A		22
Mitochondrial code and non- code	115	20	18,593	1,051	1: ATP6b, large rRNA, ND4L 1 st position, noncoding 2: Everything else	1: HKY + F + I + G4 2: GTR +F + I + G4	24

Table S3.5. Indo-Pacific agaricid sample inclusion in SNP phylogenies. X denoted inclusion in that analysis.

Species	Sample ID	Assembly									
		Coral Holobiont				Transcriptome				UCE	
		Full IQTree	Reduced IQTree & Splits Tree	SVD SNAPP		Full IQTree	Reduced IQTree & Splits Tree	SVD SNAPP		Full IQTree	Reduced IQTree
<i>P. duerdeni</i>	393										
<i>P. duerdeni</i>	A705	X	X	X	X	X	X	X	X	X	X
<i>P. decussata</i>	AGJA108					X					
<i>P. varians</i>	AMS14	X				X	X	X		X	
<i>P. varians</i>	AMS15	X				X	X	X		X	X
<i>P. frondifera</i>	AMS17	X				X				X	
<i>P. frondifera</i>	AMS21	X				X	X	X		X	
<i>P. frondifera</i>	AMS25	X				X	X	X		X	X
<i>P. decussata</i>	AMS30	X	X	X	X	X	X	X	X	X	X
<i>P. frondifera</i>	AMS36	X				X				X	
<i>P. varians</i>	AMS48	X	X	X		X	X	X		X	X
<i>P. varians</i>	AMS51	X	X	X		X	X	X		X	X
<i>P. varians</i>	AMS53	X				X				X	
<i>P. varians</i>	AMS55	X				X	X			X	X
<i>P. frondifera</i>	AMS71	X				X				X	X
<i>P. duerdeni</i>	AMS73	X	X	X		X	X	X		X	X
<i>P. maldivensis</i>	AMS77	X	X	X	X	X	X	X		X	X
<i>P. explanulata</i>	AMS78	X				X				X	
<i>P. varians</i>	AMS85	X				X				X	
<i>P. varians</i>	BIL3										
<i>P. varians</i>	BIL4	X				X	X	X		X	X
<i>P. varians</i>	BIP1	X	X	X		X	X	X		X	X
<i>P. varians</i>	BIP3	X				X	X	X		X	
<i>P. varians</i>	BIR1	X				X	X	X		X	X

<i>P. varians</i>	BIR10	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	BIR3	X				X				X	
<i>P. varians</i>	BIR8	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	BIR9	X	X	X		X	X	X		X	X
<i>L. mycetoseroides</i>	C29	X				X				X	
<i>P. chiriquiensis</i>	C39	X	X	X		X	X	X	X	X	X
<i>P. chiriquiensis</i>	C42	X	X	X	X	X	X	X		X	X
<i>P. frondifera</i>	GM10	X	X		X	X	X	X	X	X	X
<i>P. decussata</i>	GM18	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	GM2	X	X	X		X	X	X		X	X
<i>P. venosa</i>	GM21	X	X	X	X	X	X	X	X	X	X
<i>P. decussata</i>	GM23	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	GM25B	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	GM25	X	X	X		X	X	X		X	X
<i>P. varians</i>	GM28	X				X	X	X		X	
<i>P. frondifera</i>	GM30	X				X				X	
<i>P. frondifera</i>	GM33	X				X				X	
<i>P. frondifera</i>	GM55	X	X	X		X	X	X		X	X
<i>P. duerdeni</i>	GM57	X	X	X		X	X	X		X	X
<i>P. decussata</i>	GM59	X				X				X	
<i>P. varians</i>	GM60	X	X	X	X	X	X	X	X	X	X
<i>L. papyracea</i>	JPN13	X				X				X	
<i>L. yabei</i>	JPN15	X	X	X		X	X	X		X	X
<i>P. venosa</i>	JPN18	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	JPN2	X				X				X	
<i>P. varians</i>	JPN37	X	X	X		X	X	X		X	X
<i>P. cactus</i>	JPN43	X				X					
<i>L. papyracea</i>	JPN45					X					
<i>P. varians</i>	JPN46	X	X	X	X	X	X	X		X	X

<i>L. mycetoseroides</i>	JPN47	X	X	X		X	X	X		X	X
<i>L. mycetoseroides</i>	JPN49	X	X	X		X	X	X		X	X
<i>P. varians</i>	JPN5	X	X	X	X	X	X		X	X	X
<i>P. duerdeni</i>	JPN54	X	X	X		X	X	X		X	X
<i>P. explanulata</i>	JPN64	X	X	X	X	X	X	X		X	X
<i>L. sp</i>	JPN8	X	X	X		X	X	X		X	X
<i>P. duerdeni</i>	MLD12	X	X	X		X				X	X
<i>P. clavus</i>	MLD18										
<i>P. maldivensis</i>	MLD2	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	MLD20	X	X	X		X	X	X		X	X
<i>P. varians</i>	MLD26	X	X	X	X	X	X	X		X	X
<i>P. duerdeni</i>	MLD27	X	X	X		X	X	X		X	X
<i>G. planulata</i>	MLD29	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	MLD32	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	MLD34	X	X	X		X	X	X		X	X
<i>P. varians</i>	MLD4	X	X	X		X	X	X		X	X
<i>P. varians</i>	MLD40	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	MLD43	X	X	X		X	X	X		X	X
<i>P. varians</i>	MLD44	X	X	X	X	X	X	X		X	X
<i>P. minuta</i>	MLD46	X				X				X	
<i>P. varians</i>	MLD47	X	X	X		X	X	X		X	X
<i>P. varians</i>	MLD48	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	MLD49	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	MLD6	X	X	X	X	X	X	X		X	X
<i>P. bipartita</i>	MLD7	X	X	X		X	X	X		X	X
<i>P. minuta</i>	MLDX	X				X				X	
<i>L. incrustans</i>	OAK10	X				X				X	
<i>L. incrustans</i>	OAK13	X	X	X		X	X	X		X	X

<i>L. mycetoseroides</i>	OAK30	X	X	X		X	X	X		X	X
<i>L. tubulifera</i>	OAK35	X	X	X		X	X	X		X	X
<i>L. tubulifera</i>	OAK42	X				X				X	
<i>L. scabra</i>	OAK60	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	OAKB4	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	OAKB6	X	X	X		X	X	X		X	X
<i>P. varians</i>	OAM10	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	OAM3	X	X	X	X	X	X			X	X
<i>P. varians</i>	OAM5	X	X	X		X	X	X		X	X
<i>P. varians</i>	OAM6					X				X	
<i>P. varians</i>	OAM9	X				X				X	
<i>P. cactus</i>	PAL12	X	X	X	X	X	X	X		X	X
<i>P. venosa</i>	PAL18	X				X				X	
<i>P. cactus</i>	PAL2	X	X	X		X	X	X		X	X
<i>P. clavus</i>	PAL25	X								X	
<i>P. clavus</i>	PAL26	X				X				X	
<i>P. varians</i>	PAL28	X				X				X	
<i>P. chiriquiensis</i>	PAN14	X	X	X	X	X	X	X		X	X
<i>P. chiriquiensis</i>	PAN15	X	X	X		X	X	X	X	X	X
<i>P. chiriquiensis</i>	PAN16	X				X				X	
<i>P. chiriquiensis</i>	PAN18	X	X	X		X	X	X		X	X
<i>P. varians</i>	PAN20	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	PAN21	X	X	X	X	X	X	X		X	X
<i>P. varians</i>	PAN22	X	X	X		X	X	X		X	X
<i>P. varians</i>	PAN23	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	PAN24	X	X	X		X	X	X		X	X
<i>P. gigantea</i>	PAR4	X				X				X	
<i>P. gigantea</i>	PAR6	X				X	X	X		X	X
<i>P. varians</i>	PHU140	X				X				X	
<i>P. duerdeni</i>	RMI08	X	X	X		X	X	X	X	X	X

<i>P. varians</i>	RMI13	X				X	X	X		X	
<i>P. varians</i>	RMI19	X	X	X	X	X	X	X	X	X	X
<i>P. varians</i>	RMI45	X				X				X	
<i>P. maldivensis</i>	TAEK										
<i>G. planulata</i>	TGAR1	X	X	X	X	X	X	X	X	X	X
<i>G. planulata</i>	TGAR7	X	X	X		X	X	X	X	X	X
<i>P. maldivensis</i>	TLEK	X	X	X		X	X	X	X	X	X
<i>P. varians</i>	TPV2	X	X			X	X			X	X
<i>P. varians</i>	ZAN044	X	X			X	X			X	X

Table S3.5. (Continued). **Indo-Pacific agaricid sample inclusion in SNP phylogenies.**

Table S3.6. Sample and descriptive statistics for SNP alignments for Indo-Pacific agaricid species. And clades recovered from the phylogeny generated from each alignment. IQT= IQ-Tree, ST= SplitsTree, SVD = SVD Quartets, SNAPP = SNAPP.

Method	Assembly	Missing data %	Individuals	Nominal Taxa	N char (SNPs)	Parsimony informative	Clades
IQT	UCE	<100	113	20	647	360	16
IQT & ST	UCE	<50	82	17	598	329	17
IQT	Transcriptome	<100	115	20	2,960	1,434	22
IQT & ST	Transcriptome	<50	85	17	2,754	1,296	21
IQT	de novo	<100	113	20	18,995	8,856	27
IQT & ST	de novo	<50	75	16	17,183	7,745	23
SVD	Transcriptome	<50	80	16	2,754		21
SVD	de novo	<50	75	16	17,183	7,745	23
SNAPP	Transcriptome	0	22	7	279		11
SNAPP	de novo	0	32	11	411		18*

**P. cactus*, *P. frondifera* and *P. venosa* included as separate clades.

Table S3.7. D statistics for different combinations of five taxa from across the agariciid tree. Codes represent combinations of clades e.g., BP1 = Blue-Pink, PP1 = Pink-Pink. Sample names in Combo correspond to sample IDs from Table S3.1.

Code	Combo ((P1,P2)(P3,P4)Out)	D _{FO} left	D _{FO} right	D _{FO} stat	D _{FO} p- value	D _{IL} left	D _{IL} right	D _{IL} stat	D _{IL} p- value	Introgression?
PP1	((GM10,GM60)(OAKB4,PAN21)MLD29)	88	90	-0.01	0.88	79	99	- 0.11	0.13	No
PP2	((PAL12,GM60)(OAKB4,PAN21)MLD29)	78	92	-0.08	0.28	88	82	0.05	0.64	No
PP3	((PAL12,MLD26)(OAKB4,PAN21)MLD29)	77	91	-0.08	0.28	82	86	- 0.02	0.75	No
GG1	((BIR10,MLD26)(PAN14,MLD44)MLD29)	80	73	0.05	0.57	81	72	0.06	0.47	No
BP1	((GM60,PAN21)(AMS77,AMS73)MLD29)	139	134	0.018	0.76	143	130	0.05	0.43	No
PG1	((GM60,OAKB4)(GM18,PAN14)MLD29)	99	114	-0.07	0.3	100	113	- 0.06	0.37	No
PG2	((GM60,OAKB4)(PAN14,JPN46)MLD29)	56	77	-0.16	0.07	56	77	- 0.16	0.07	No
BG1	((GM18,PAN14)(AMS77,AMS73)MLD29)	184	156	0.08	0.13	185	155	0.09	0.10	No
BG2	((BIR10,MLD26)(AMS77,AMS73)MLD29)	210	179	0.08	0.12	210	179	0.08	0.12	No

Table S3.8. Species codes for Indo-Pacific agariciid species, as reported in phylogenetic trees.

Species	speciescode
<i>G. planulata</i>	Gplan
<i>L. incrustans</i>	Lincs
<i>L. mycetoseroides</i>	Lmyc
<i>L. papyracea</i>	Lpapa
<i>L. scabra</i>	Lscab
<i>L. sp</i>	Lsp
<i>L. tubulifera</i>	Ltub
<i>L. yabei</i>	Lyabi
<i>P. bipartita</i>	Pbipa
<i>P. cactus</i>	Pcact
<i>P. chiriquiensis</i>	Pchqi
<i>P. clavus</i>	Pclav
<i>P. decussata</i>	Pdec
<i>P. duerdeni</i>	Pdud
<i>P. explanulata</i>	Pexp
<i>P. frondifera</i>	Pfron
<i>P. gigantea</i>	Pgiga
<i>P. maldivensis</i>	Pmald
<i>P. minuta</i>	Pmina
<i>P. varians</i>	Pvar
<i>P. venosa</i>	Pveno

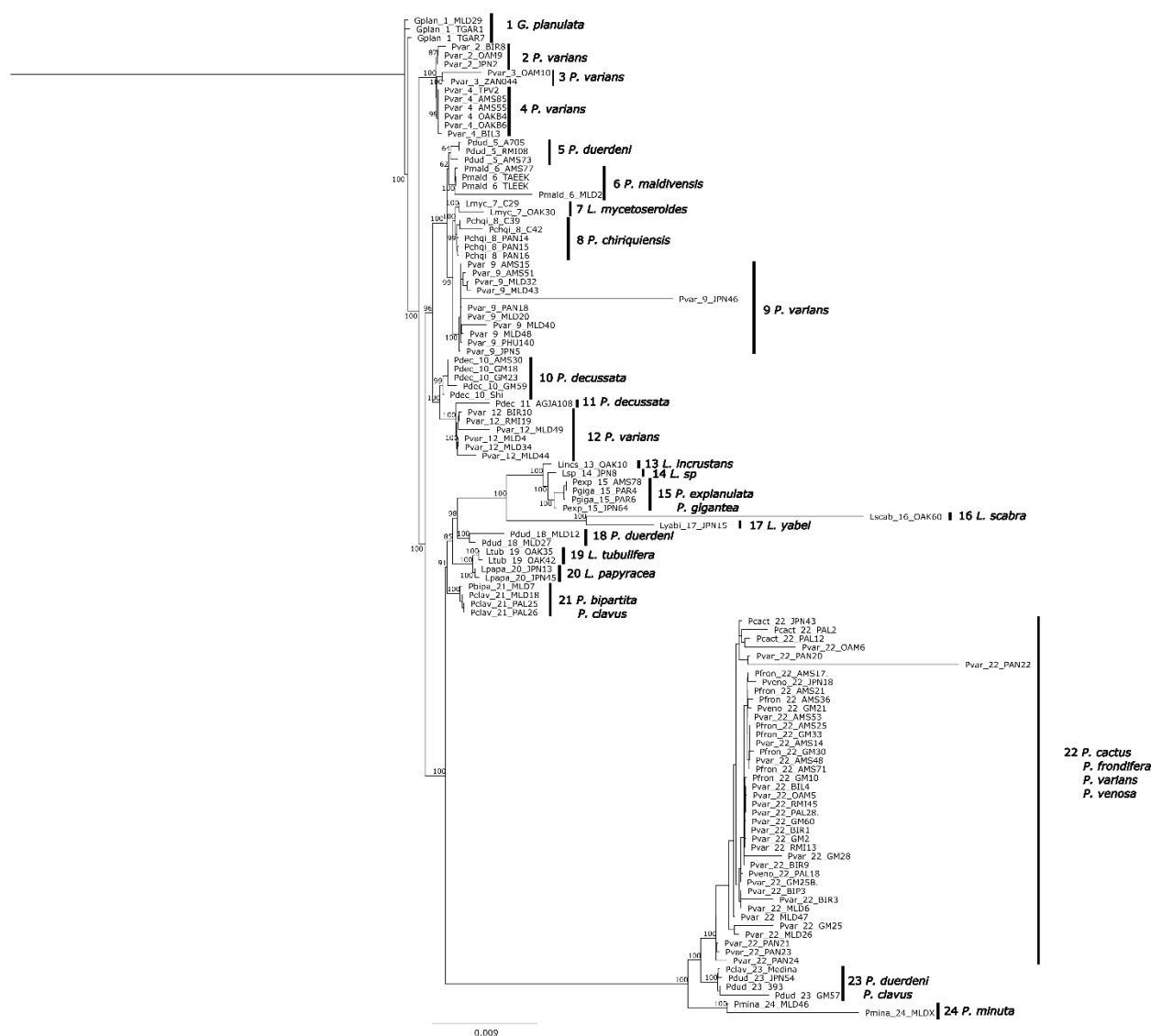


Figure 3.1. Maximum likelihood phylogeny of mitogenomes for Indo-Pacific agaricid species. Tips labels correspond to speciescode_mitogenomeclade_samplecode. Bootstrap support at nodes. Speciescode as described in Table S3.8.

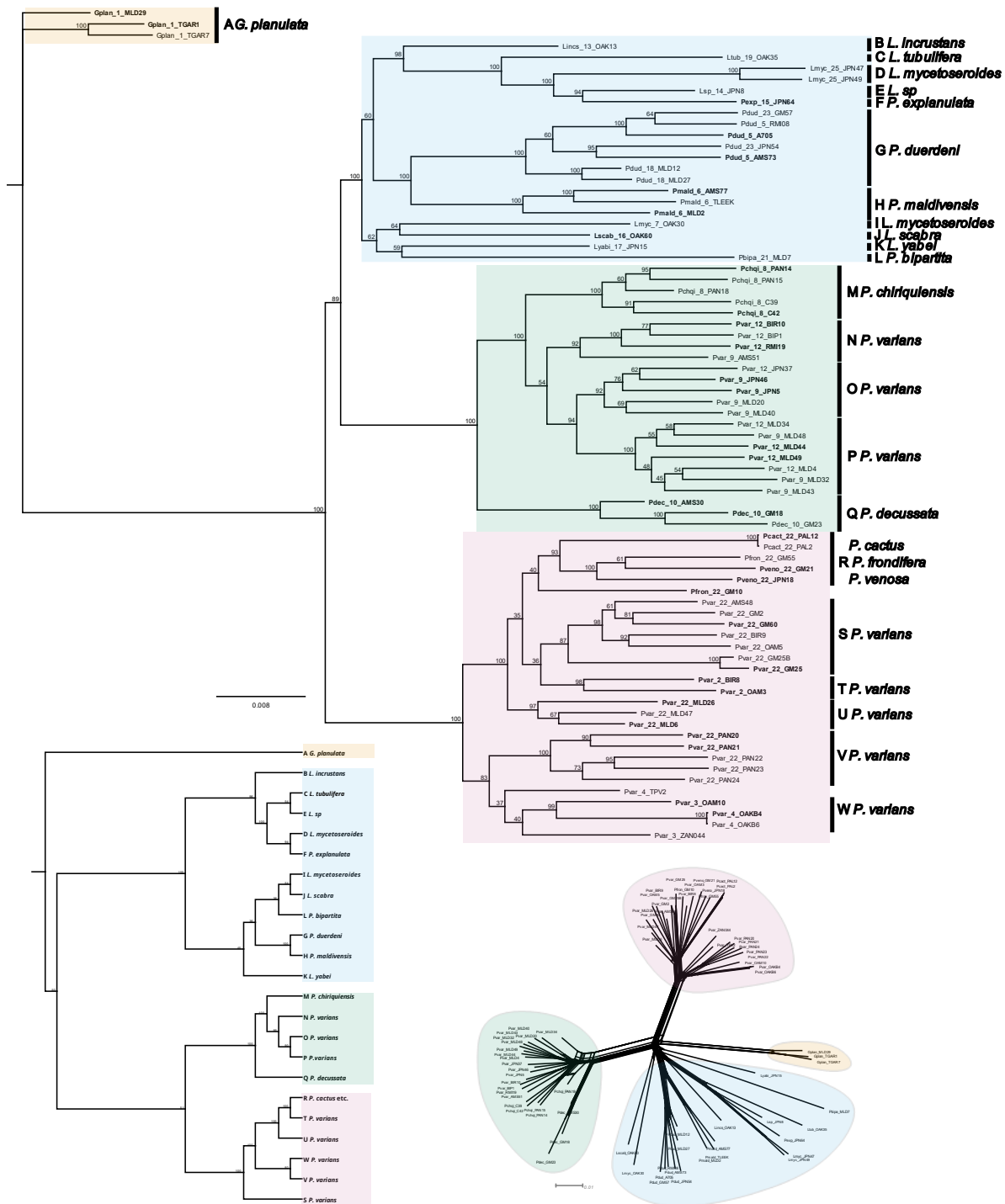
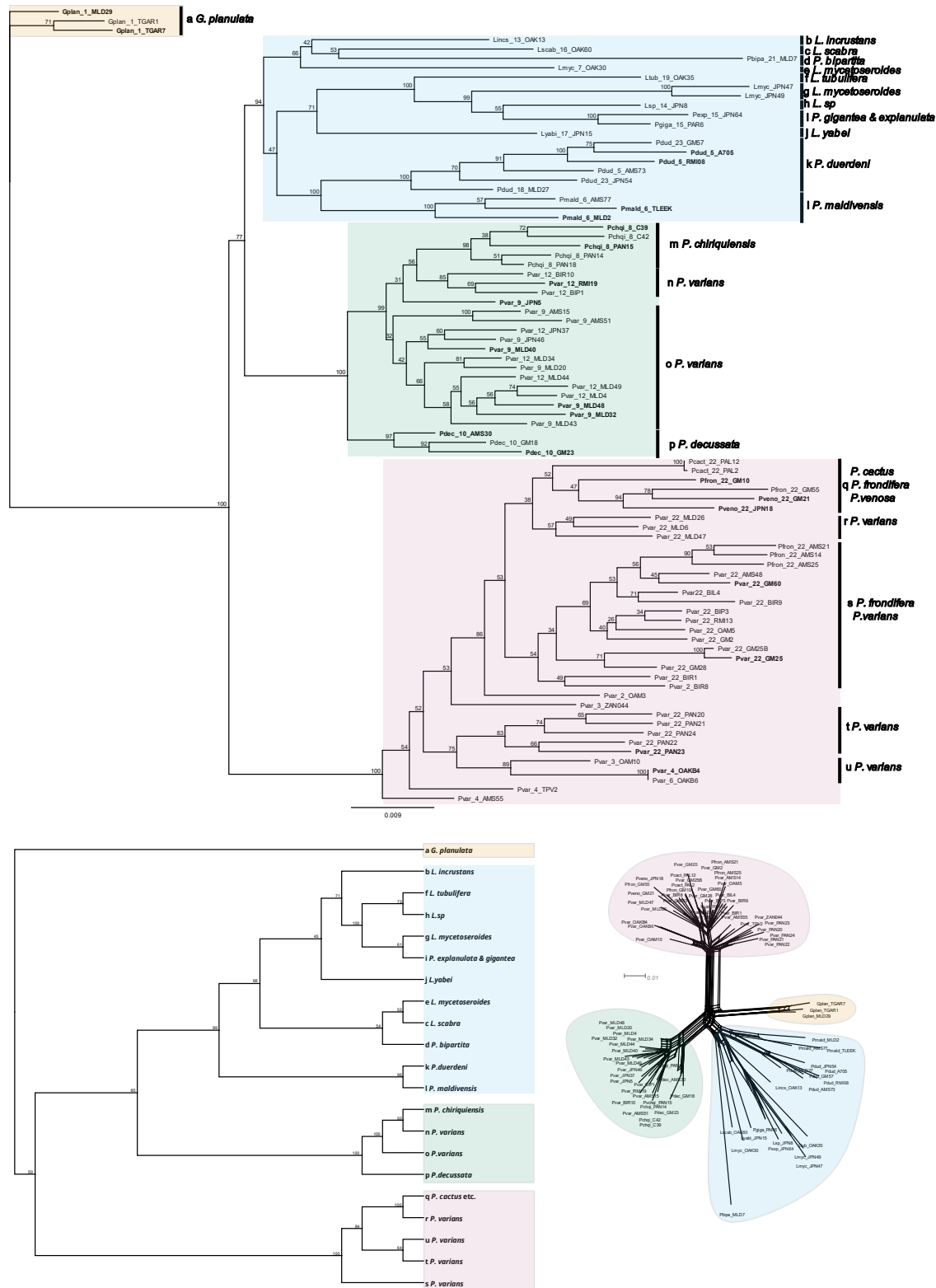


Figure 3.2. Maximum likelihood phylogeny of reduced coral holobiont assembly for Indo-Pacific agaricid species. Main: IQ-Tree, tips names are species_mito_clade_sampleID, bold are samples included in SNAPP trees. bottomleft: SVD Quartets tip labels correspond to those from IQ-Tree clades, bottom right: SplitsTree, tip labels are speciescode_sampleID. Speciescode as described in Table S3.8.



IQ-Tree clades, bottom right: SplitsTree, tip labels are speciescode_sampleID. Note that the letters for each clade do not necessarily match those of the holobiont tree - they are consistent within the figure only. Speciescode as described in Table S3.8.

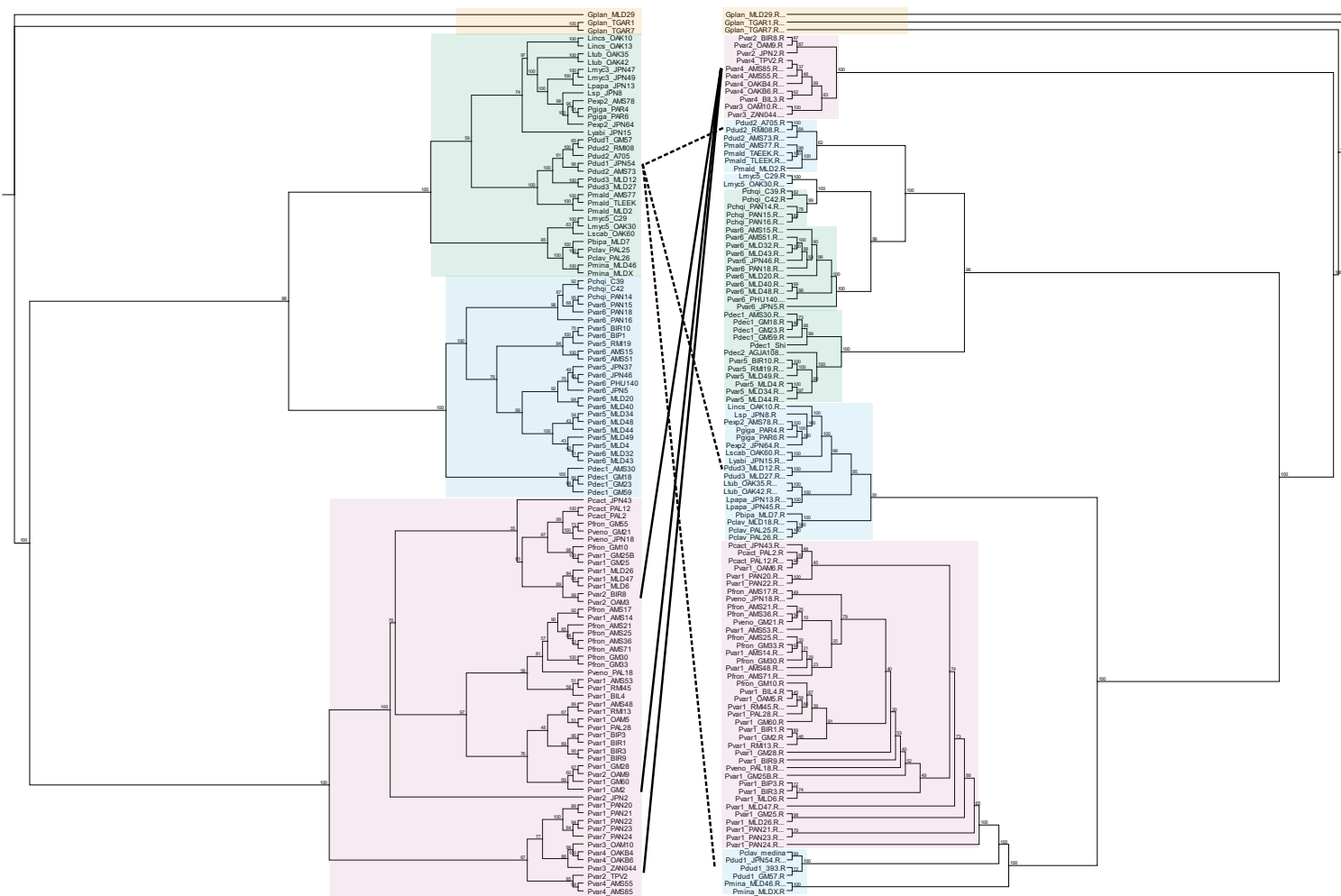


Figure 3.4. Comparison of maximum likelihood phylogenies of full coral holobiont assembly and mitogenomes for Indo-Pacific agaricid species. Dashed lines indicate placement of samples of *P. duerdeni*. Solid lines indicate placement of some samples of *P. varians*.

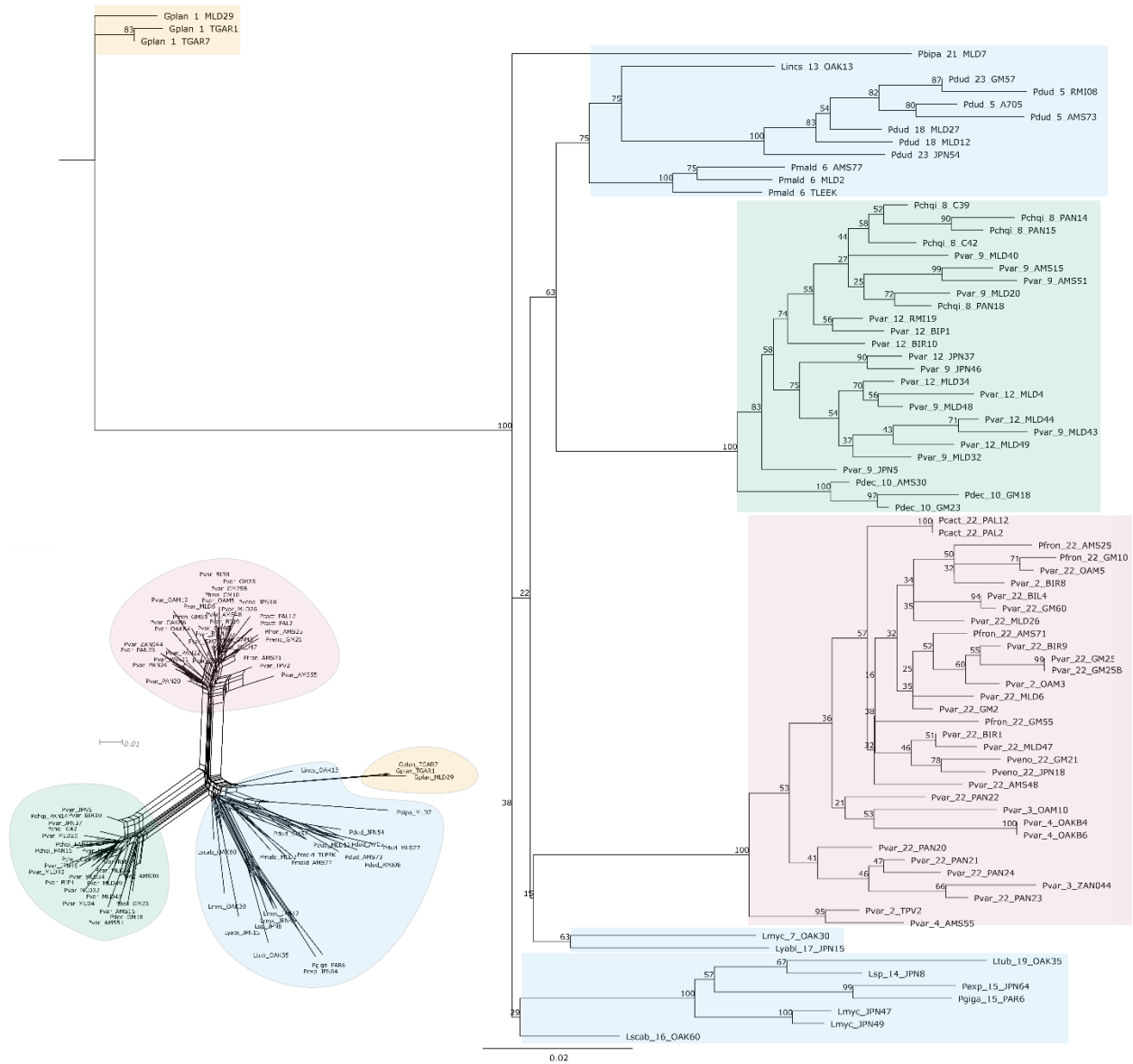


Figure 3.5. Maximum likelihood phylogeny of reduced ultra conserved elements assembly for Indo-Pacific agaricid species. Main: IQ-Tree, tips names are species_mito_clade_sampleID. SplitsTree, tip labels are speciescode_sampleID. Speciescode as described in Table S3.8.

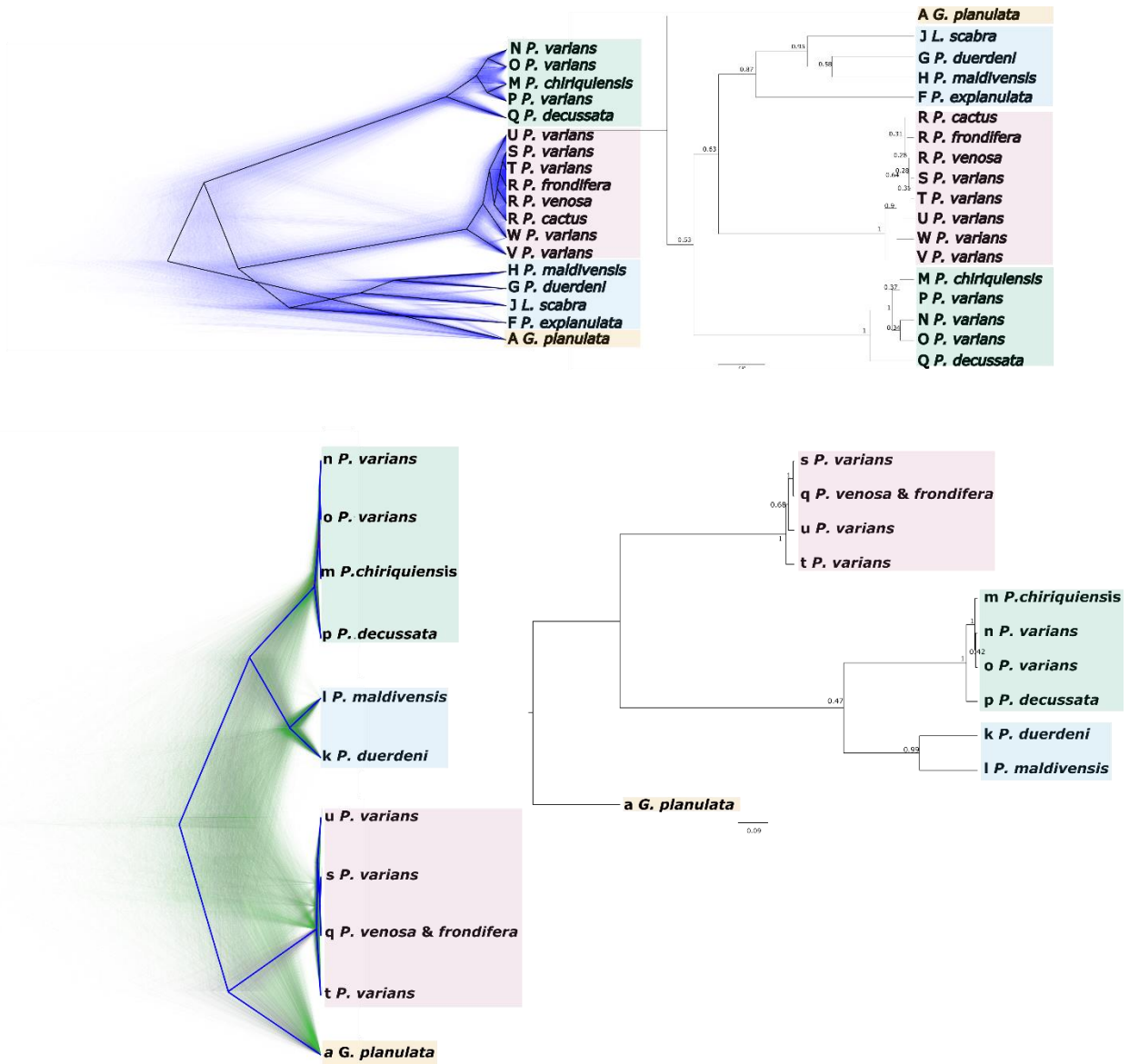


Figure 3.6. Phylogenetic outputs from SNAPP analyses for both coral holobiont and transcriptome SNP assemblies for Indo-Pacific agaricid species. Top: coral holobiont assembly 411 SNPs. Densitree and combined tree. Bottom transcriptome assembly 279 SNPs, Densitree and combined tree. Note that letters before clades are specific to each assembly and do not match across assemblies.

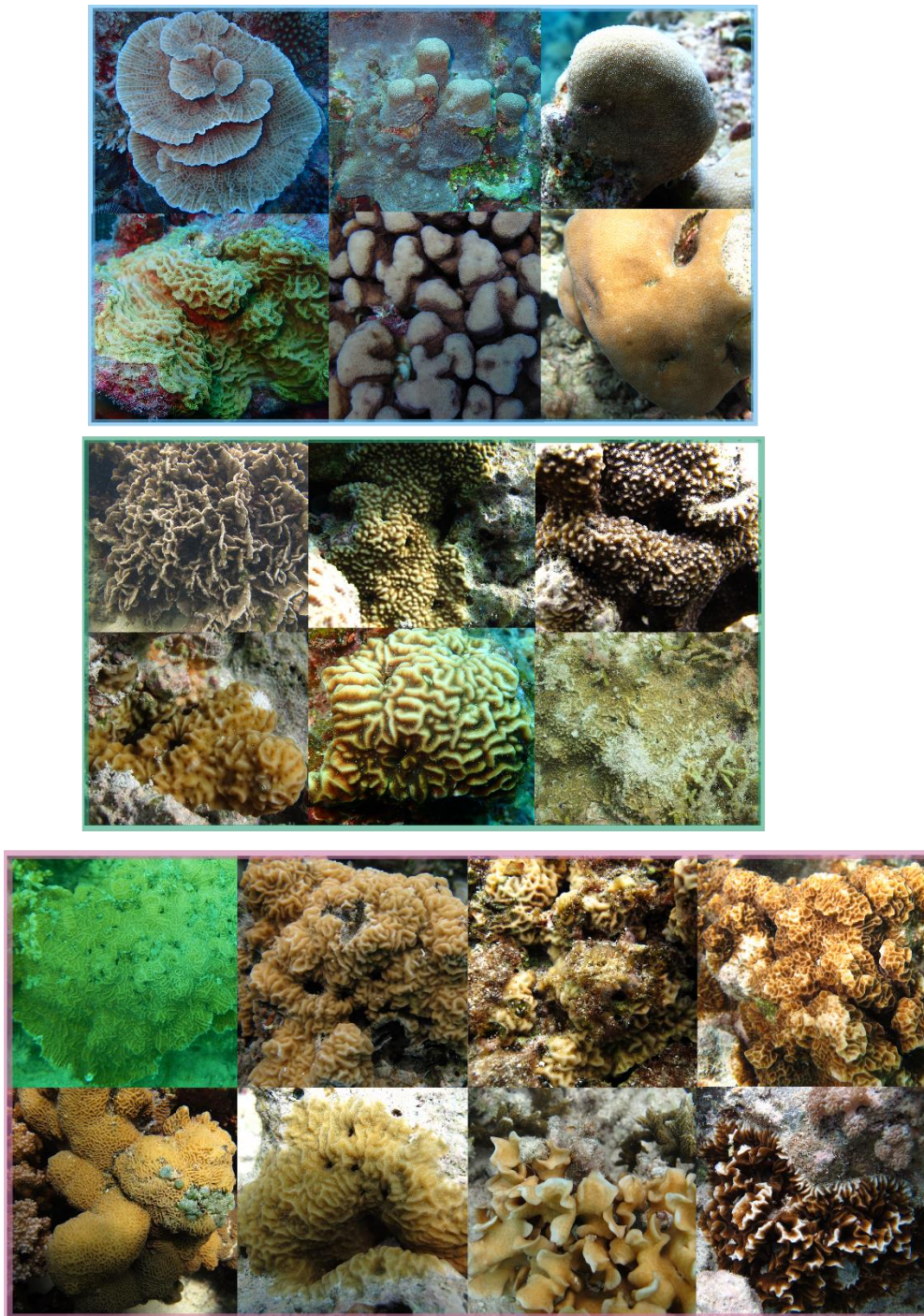


Figure 3.7. Photographs of Indo-Pacific agaricid coral colonies recovered in three clades
 Blue, clockwise from top left: *L. yabei* JPN15; *P. explanulata* JPN64; *P. duerdeni* GM57; *P. duerdeni* MLD27; *P. maldivensis* AMS77; *L. mycetoseroides* JPN49. Green, clockwise from top left: *P. decussata* GM18; *P. varians* MLD20; *P. varians* AMS51; *P. chiriquiensis* C42; *P. varians* JPN5; *P. varians* MLD32. Pink, clockwise from top left: *P. varians* PAN23; *P. varians* GM60; *P. varians* BIR8; *P. venosa* GM21; *P. frondifera* GM55; *P. cactus* PAL2; *P. varians* LD26; *P. varians* OAKB4. Picture credit: PAN23 JM, C42 MH, all others CJL.

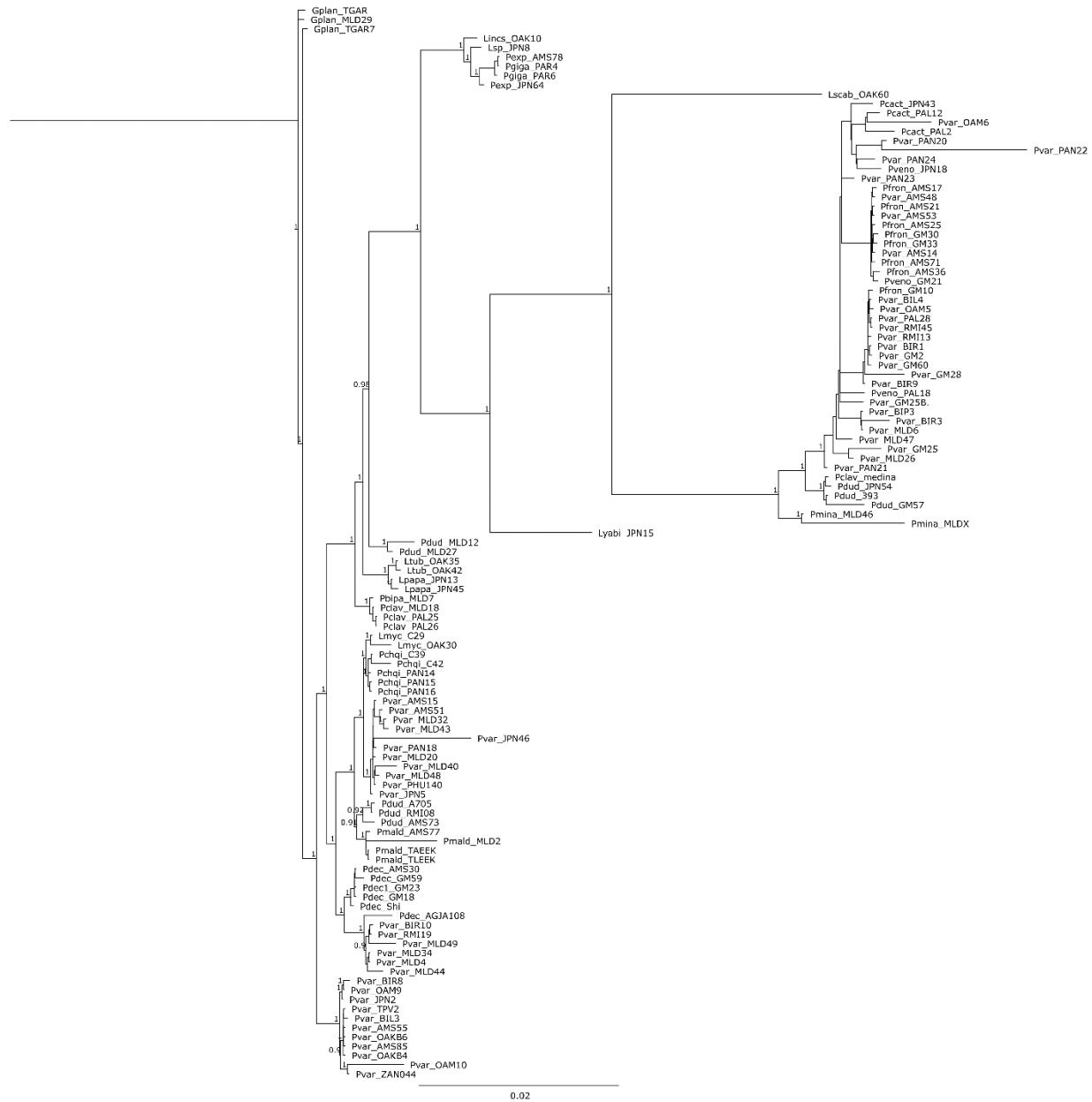


Figure S3.1. Bayesian phylogeny of mitogenomes for Indo-Pacific agaricid species. Partitioned run as explained in Table S3.3. Tips are speciescode_samplecode. Posterior probabilities at nodes.

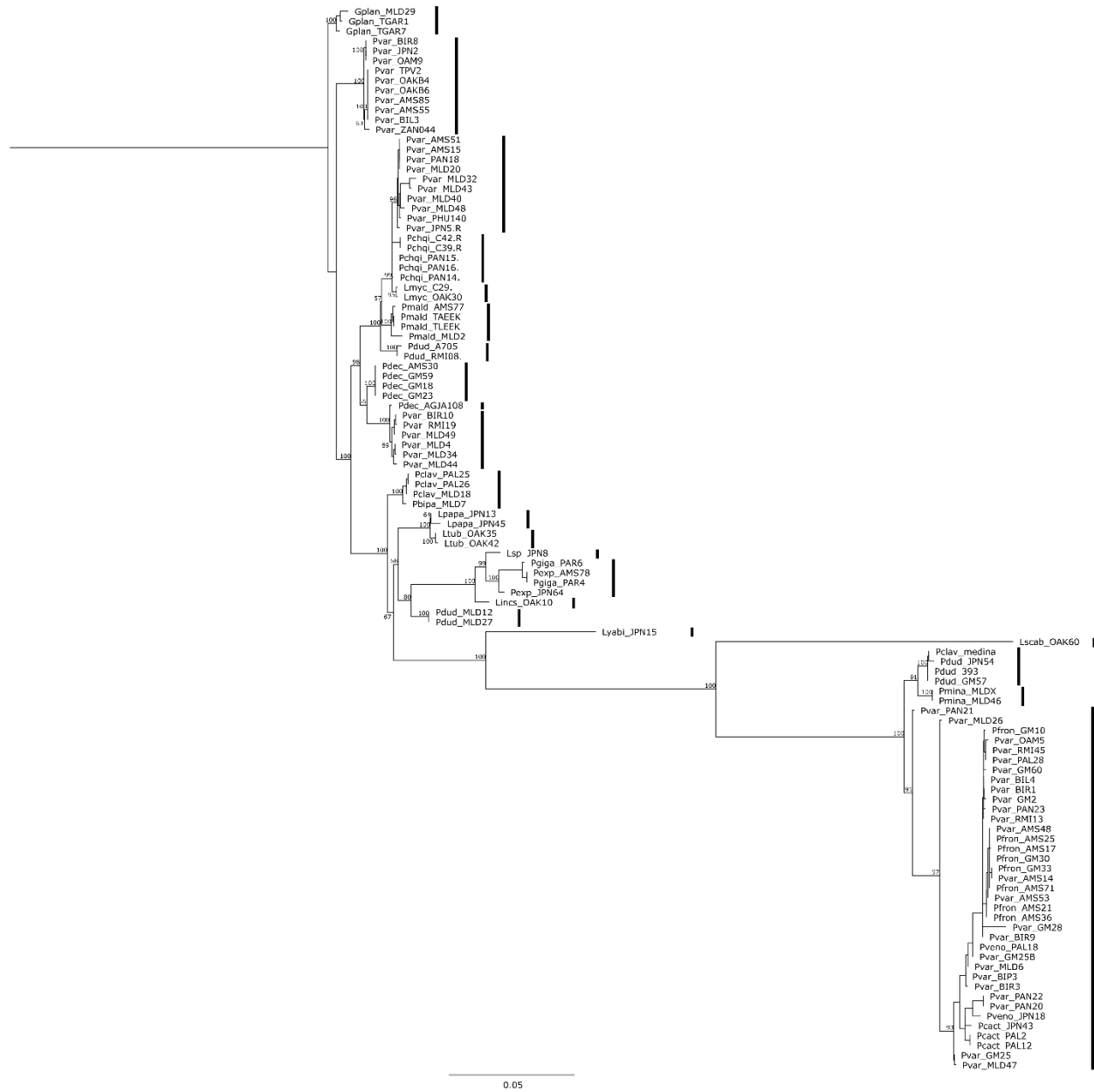


Figure S3.2. Maximum likelihood phylogeny of non-functional regions only from mitogenomes for Indo-Pacific agaricid species. Tips are speciescode_samplecode. Bootstrap support at nodes.



Figure S3.3. Maximum likelihood phylogeny of functional regions only from mitogenomes for Indo-Pacific agaricid species. Tips are speciescode_samplecode. Bootstrap support at nodes.

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CHAPTER 4. LIGHT-DRIVEN PHENOTYPIC PLASTICITY FACILITATES DEPTH GENERALISM IN A COMMON CORAL

ABSTRACT

Climate change is causing shifts in the spatial distribution of species, and therefore community composition. On coral reefs, deep water can act as refugia for corals from the combined negative effects of heat and light stress. Phenotypically plastic generalists that can tolerate both low and high light could be disproportionately important on future reefs, both persisting in refugia and colonizing vacant shallow reefs. We experimentally investigated the effect of light on the abundant, depth-generalist coral *P. varians*. We measured the growth response and reaction norms of several other morphological and functional traits in full sunlight, 75%, and 90% shade. We also modelled the combined effects of light and temperature on growth. *P. varians* had positive growth in all three treatments, but grew most quickly in 90% shade, with a higher density of corallites, and a less rugose skeleton that may enhance light capture. Areas of the colony corresponding to new growth had thicker tissues and greater fluorescence of Symbiodiniaceae communities in the darkest treatment. Light did not alter the functional lipid ratio, nor did communities of Symbiodiniaceae vary with light treatments. The model revealed additively negative, but not synergistic, effects of light and temperature on growth. The results from our model are consistent with the hypothesis that reductions in bleaching at depth could be the product of reduced light stress at depth rather than reduced temperature stress. Light-associated plasticity likely allows this species to live in a wide variety of habitats and across a broad depth gradient. In reduced light conditions this species is able to mitigate some of the negative effects of bleaching temperatures on growth. We predict that *P. varians* is likely one of a minority of species that may benefit from deep reef refugia.

INTRODUCTION

Phenotypic plasticity allows multiple phenotypes to be expressed from a single genotype in response to different environments (Levins 1963; Bradshaw 1965; Sultan 2021 and references therein). Plasticity is particularly prevalent in autotrophic sessile invertebrates and plants, immobile as adults, yet persisting in spatially and temporally varying environments

(Lichtenthaler et al. 1981; Anthony et al. 2005; Markesteijn et al. 2007; Todd 2008; Padilla & Savedo 2013; Kaniewska et al. 2014; Padilla-Gamiño et al. 2019). Under low light, phenotypic shifts can allow autotrophs to maximize light capture in darker environments, such as deep water (Anthony et al. 2005) or the forest understory (Sterck et al. 2013); whereas under high light, species may alter phenotypes to reduce light capture (Werner et al. 1999; Anthony and Hoegh-Guldberg 2003). Plasticity likely facilitates overall community stability by allowing foundational autotrophs to maintain community structure in varying environments.

Plasticity may enable taxa to tolerate climate change (Parmesan et al. 2006; Nicotra et al. 2010; Pérez-Ramos et al. 2019). Greater phenotypic plasticity is often associated with species that are successful invaders (Funk 2008), have large ranges (Sheth & Angert 2014), and able to persist in heterogeneous environments (Chazdon & Kaufmann 1993; Valladares et al. 2000; Vázquez et al. 2017). Phenotypic plasticity may allow species to tolerate rapidly changing climates in two ways: sessile or modular species may alter their phenotypes in place over their lifespans, and for species with dispersive life-history stages, plasticity may facilitate range-shifts or extensions into less stressful habitats (Lande 2009; Chevin et al. 2010; Vitasse et al. 2010; Kingsbury et al. 2019).

Similar to altitudinal shifts observed in plants in response to climate change, corals may escape increasingly stressful shallow-water habitats on tropical reefs by shifting their distributions to deeper water. The Deep Reef Refugia Hypothesis (DRRH) proposes that mesophotic reefs, at depths of 30 m or more, may act as refuges for depth generalists locally extirpated from shallow reefs by a multitude of stressors such as storms, pollution, disease, and overfishing (Glynn 1996; Bongaerts et al. 2010; Kahng et al. 2010, but see Rocha et al. 2018). Climate change is causing oceans to warm, leading to more frequent heat waves, bleaching events, and mass mortality on coral reefs (Hughes et al. 2017a,b). However, coral bleaching, a breakdown in the symbiotic relationship between coral hosts and their intracellular zooxanthellae (Family: Symbiodiniaceae), is often caused by the combined stress of high temperature and light (Jokiel & Coles 1977; Warner et al. 2006; Roth 2014), both of which decline with depth. Accordingly, bleaching severity is often reduced under low light, such as at depth (García-Sais et al. 2017; Frade et al. 2018; Baird et al. 2018; Couch et al. 2017) and during periods of high cloud cover (Mumby et al. 2001; Donner and Carilli 2019) and increased turbidity (Golbuu et al. 2011;

van Woesik et al. 2012; Morgan et al. 2017; Teixeira et al. 2019). Although the low light which characterizes the mesophotic may slow coral growth, reduced irradiance of deep reefs likely reduces symbiont photosystem stress during high temperatures (Venegas et al. 2019).

The realized impact of deep reefs as refugia is limited by the disparity in coral community composition between deep and shallow reefs. Based on the distribution of their abundances, most corals are likely depth specialists: the dominant reef builders on both mesophotic and shallow reefs tend to be species with specialized, inflexible morphologies, limiting ecological exchangeability across depth gradients (Kahng et al. 2010; 2012; Pratchett et al. 2015; Rocha et al. 2018; Roberts et al. 2019;). In contrast, the handful of depth generalist species capable of persisting at demographically-significant densities from shallow to deep reefs, may do so via light-associated phenotypic plasticity (Roberts et al. 2019). These plastic generalists may be particularly important in a warming ocean as they are able to tolerate the broad range of light conditions needed to use deep reefs as refugia (Chow et al. 2019; Roberts et al. 2019).

The agaricid coral *Pavona varians* (Verrill 1864) is considered a depth generalist (Roberts et al. 2019; Montgomery et al. 2021), found at depths from 0.5 to >50 meters (Luck et al. 2013). It is one of the most common species in the Indo-Pacific (Sheppard 1998; Dietzel et al. 2021), ranging from the Red Sea to the Eastern Pacific (Veron 2000). *P. varians* is aptly named, exhibiting high variation in both microskeletal structure and gross colony morphology (Veron and Pichon 1980). Unrecognized cryptic diversity may be responsible for some morphological variation in this nominal species (Veron 2000); however, depth (Wells 1954), wave energy (Veron & Pichon 1980), and latitude (Veron 2000) may also explain inter-colony morphological variability of this species. Intracolony variation suggests *P. varians* is phenotypically plastic with respect to light because individual colonies can be more rugose on upward-facing surfaces than on downward-facing surfaces (Fig. 4.1).

To investigate the extent of light-driven phenotypic plasticity in *P. varians*, we conducted a common garden experiment. We were particularly interested in the effect of light on skeleton rugosity, because more and taller ridges may have functional importance for this species by modulating the internal light environment experienced by symbionts. We assessed this plasticity in the context of changes in several other morphological and functional traits that relate to the

ecology and fitness of corals (Darling et al. 2012; Padilla-Gamiño et al. 2019; Huffmyer et al. 2020). Assessing plasticity of functional traits, such as growth rate, is particularly important as it is likely a key means of tolerating a rapidly changing climate (Nicotra et al. 2010) and provides specific insight into how corals respond to changing environmental conditions and how they allocate energy to different physiological processes (Leuzinger et al. 2003; Madin et al. 2012). Growth rate is also the primary way that corals are classified into functional groups (Darling et al. 2012), which are used to make predictions about climate-driven changes in community structure on coral reefs (Côté and Darling 2010). Although coral growth depends fundamentally on environmental conditions (Buddemeier & Kinzie 1976), the impacts of spatial variation in light, temperature, and other environmental drivers are rarely considered in trait-based classifications, largely because of a lack of experimental data (Pratchett et al. 2015).

In addition to fragmenting and growing colonies under manipulated natural lighting, we then took advantage of natural variation in light and temperature over the experiment to model and statistically separate the effects of light and temperature on growth. Our approach allowed us to assess the proposed synergistic effects of heat and light on coral growth (e.g., Coles and Jokiel 1978), and understand the physiological mechanisms underlying the potential benefits of deep reefs for generalist species in an ever-warming ocean.

METHODS

Sample collection

We collected three colonies of *P. varians* with snorkel or SCUBA from Sand Island, O‘ahu for the experiment (21°17'54.40"N 157°52'22.33"W). Where possible, colonies were photographed *in situ* prior to collection using a camera (Canon G6) in underwater housing (Canon WP-DC34). One genotype was collected in winter 2015 from a depth of 1 m and kept at the nursery under two layers of 50% shade cloth (Coolaroo Shade Fabrics, Altamonte Springs, FL). The remaining two genotypes were collected in April 2017 from a depth of 3 m.

Molecular Analyses

To assess whether individuals of *P. varians* collected for this experiment form a single clade, 663-670 bp of the *cox1*-1-rRNA intron (Luck et al. 2013) was sequenced from the experimental colonies. We also sequenced a fragment of one other colony exhibiting high intracolony morphological variation from Kāneʻohe Bay (OAKB5), collected in 2016 (Fig. 4.1). The mitochondrial intron is variable enough to distinguish species within Agariciidae, and is consistent with morphological species (Luck et al. 2013, Waheed et al. 2015; Terraneo et al. 2017). DNA was extracted using a Qiagen DNeasy kit according to the manufacturer's recommendations. The intron was amplified from six colonies using primers and protocol described in Luck et al. (2013). PCR products were sequenced using an Applied Biosystems 3730XL DNA Analyzer at the University of Hawai'i at Mānoa's Advanced Studies in Genomics, Proteomics and Bioinformatics (ASGPB) sequencing facility.

Sanger sequences were manually checked and edited using Geneious R10 and aligned with other electronically-retrieved agaricids (Medina et al. 2006; Luck et al. 2013; Waheed et al. 2015) using ClustalW in Geneious with default parameters. A phylogeny was built using the Bayesian inference criterion implemented in the MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) Geneious R10 plug-in, under the HKY85 + G model, chosen with ModelFinder and BIC (Trifinopoulos et al. 2016; Kalyaanamoorthy et al. 2017). The phylogenetic analysis ran for 2,500,000 generations on four Markov chains, sampling every 1,000 generations. The first 100,000 generations were discarded as burn-in after examining the trace for convergence.

Experimental design and coral sampling

To test the effect of light on coral growth, morphology, lipid content, fluorescence, and *Symbiodinaceae* community, a 6-month experiment was conducted at the Hawai'i Division of Aquatic Resources' Ānuenue Coral Restoration Nursery, Sand Island (21°18'14.6"N 157°52'16.1"W) on the island of O'ahu, Hawai'i. The experiment was conducted outside in two 3.9 m diameter flow-through tanks, supplied by running, unfiltered sea water. Each tank was divided into six equally-sized triangular segments to which three light treatments were applied using zero, two, and four layers of 50% shade cloth (corresponding to 0, 75, 90% shade

respectively, equivalent to descending 40 m in clear, tropical water, see Tamir et al. 2019) were randomly applied in duplicate, such that each treatment was replicated four times across the two tanks. On June 2nd, 2017, each of the three *P. varians* parent colonies were cut into twelve 1 cm² fragments using a diamond bandsaw, and then each fragment was glued to individual 5 cm² unglazed travertine tiles using IC-GEL ethyl cyanoacrylate gel glue (BSI Inc.) and left to recover under two layers of 50% shade cloth in running sea water. On the 19th of June, 2017, one fragment from each genotype was randomly placed in each of the twelve treatments/replicates, suspended 10 cm below the surface, in the middle of the treatment area. Each replicate included a HOBO pendant light (lux) and temperature (°C) logger, recording both variables every ten minutes for the duration of the experiment. The unoccupied portions of tiles were cleaned weekly using a toothbrush to maintain a uniform environment across treatments with respect to sediment and fouling communities.

At the beginning of the experiment and monthly thereafter, tiles (and attached corals) were buoyantly weighed (per Jokiel et al. 1978) to the nearest 0.025 g using an electronic balance, and calibrated photographs were taken from directly above the two-dimensional (2D) footprint of each coral. At the end of the experiment (approximately 6 months), photographs were taken for photogrammetry (described below), and the coral was divided into fragments for different analyses including: laser scanning confocal microscopy, lipid content, and symbiont community. Fragments for lipid content were immediately frozen on dry ice before being transported to a -80 °C freezer. Fragments for fluorescence and tissue thickness measurements were immediately preserved in Z-fix (Anatech Ltd, Battle Creek, MI) and stored at 4 °C in the dark.

For the purposes of this paper, the three parent corals will be referred to as genotypes, equivalent to genets, and fragments associated with each genotype will be referred to as fragments, equivalent to ramets (Heyward & Collins 1985). The portion of the colony originally glued to the tile (including vertical growth during the experiment) is the “original fragment”. New growth around this original fragment is referred to as “new lateral growth”.

Growth and corallite density

Change in skeletal weight was measured by subtracting the initial buoyant weight of the fragment + tile from the final buoyant weight at the end of the experiment (151 d). Change in the 2D footprint of living coral tissue was also measured from top-down photographs with a ruler for scale (Canon EOS 6D, 135 mm lens). 2D footprints were measured in Adobe Photoshop; images were scaled using the ruler and then *Quick Select tool* was used to calculate area in cm². To calculate lateral growth per day rate, the difference between the first and last measurements were divided by the time between the two measurements (151 days). To calculate 2D colony growth, area measurements were log transformed to account for the circular nature of growth, and the final measurement was taken slightly later (165 d). For the three colonies which had negative growth, the rate was fixed at 0.

Corallite (skeletal cup of one polyp) density was calculated in areas of new lateral growth because of the difficulty in counting corallites between ridges on the original fragments. Corallites were counted in ImageJ (v.1.8.0_77) using the multi-point tool. The number of corallites were then divided by the area of new growth, determined by subtracting the area of the original fragment subtracted from the final area measurement.

3D photogrammetry and colony rugosity

We characterized colony rugosity by dividing the final 2D footprint of each colony by the 3D surface area. Each colony was photographed 35 - 50 times (depending on colony size) in two concentric circles, with a ruler for scale and reflective disk for reference. 3D photomodels were created using Agisoft Photoscan Professional (v.1.2.6) (now Agisoft Metashape) using default settings (see Remondino et al. 2012; Burns et al. 2015; Ferrari et al. 2017). The 3D model was scaled twice from the ruler, and then exported as an .obj file for downstream analyses. For three colonies which had negative growth, photomodels were not created.

To calculate colony rugosity, the 2D surface area (i.e., the 2D colony footprint calculated earlier) was divided by the 3D surface area, and the difference scaled to the 2D surface area. The 3D surface area was always greater than the 2D, with increases in their ratio correlating with higher rugosity. To determine the 3D surface area, .obj files were loaded into GeoMagic Control X 64 (v.2018.0.1), and 3D surface area calculated using the *measurement* tool.

Coral and symbiont fluorescence

Change in tissue thickness and symbiont densities were calculated using laser scanning confocal microscopy (LSCM) (see Huffmyer et al. 2020). Briefly, LSCM measures Symbiodinaceae fluorescence and coral host fluorescence depth, from which symbiont density and tissue thickness can be inferred, respectively. Two pieces ($<1\text{ cm}^2$ each) of each coral, one from the original fragment and one from new lateral growth were fixed in 1:4 zinc-buffered formalin (Z-Fix Concentrate, Anatech, Ltd) in $1\text{ }\mu\text{m}$ filtered seawater, and stored at $4\text{ }^{\circ}\text{C}$ in darkness. Samples were imaged using a Zeiss LSCM 710 and Zen Black software (2011 v14.0.16.201), with an excitation wavelength of 405 nm with $2.5\times$ magnification. For tissue thickness, 3D models were sliced vertically at three randomly generated points across the x-axis; the mean of five depth measurements at each cross-section were averaged to generate a tissue depth score per sample. For symbiont densities, 3D models were generated (threshold 1.12 ± 0.2) and collapsed into 2D Maximum Intensity Projection maps. The average Symbiodiniaceae fluorescence score of three non-overlapping uniform ROI's ($n=3/\text{fragment}$) was then calibrated to a percent relative intensity score using the InSpeck Microscope Image Intensity Calibration Red Kit (Molecular Probes, Sigma-Aldrich, St. Louis, MO).

Dry weight and ash-free dry weight

Two fragments ($0.8\text{--}2\text{ g}$), or technical replicates, from each of the new lateral and original growth of each *P. varians* sample was placed in a mortar and pestle, crushed, and mixed into a homogeneous slurry by adding 1 ml DPEC water for every 1 g of coral (Conlan et al. 2017; Sale et al. 2019). Dry weight (DW) was measured from two technical replicates of $100\text{ }\mu\text{l}$ of the coral slurry in pre-ashed pans that were dried to a constant weight at $60\text{ }^{\circ}\text{C}$ for 3 h . Dried samples were then ashed at $450\text{ }^{\circ}\text{C}$ in a muffle furnace to a constant weight (AW). Ash-free dry weight (AFDW) for each sample was calculated as the difference between DW and AW. The mean of two technical replicates were used to estimate all weights.

Lipid analysis

To quantify lipid class abundance and composition, whole coral slurries were prepared as above and lipids were extracted and quantified as in Sale et al. (2019). Briefly, lipids were extracted from two replicate $100\text{-}\mu\text{l}$ aliquots of coral slurry from each of 29 colonies. Lipids were

extracted in 2:1 methanol/chloroform for 30 min at -20 °C, washed in 1:1 chloroform/water, dried under a N₂ gas stream, and resuspended in 30 µl chloroform. Two 1 µl subsamples of each of the two aliquots were spotted on quartz-impregnated chromatographic rods and run through a two-step development process (Rodrigues et al. 2008). Total lipid mass fraction was calculated as the mass of the summed lipid classes divided by the total AFDW of the sample (Sale et al. 2019). The functional lipid ratio (FLR) (Henrichs et al. 2013) of each sample was calculated by summing the mass of all non-polar lipids and dividing by the mass of all polar lipids.

PCA

To visualize trends in the different metrics, a Principal Component Analysis (PCA) was conducted using nine variables: growth rate, calcification rate, corallite density, rugosity, functional lipid ratio, tissue thickness (in the original fragment, and lateral growth), and Symbiodiniaceae fluorescence (in the original fragment, and lateral growth). To generate a full data matrix for PCA, missing data (34/324 cells) were imputed using MissMDA (v1.14, Josse and Husson 2016). PCA was created using FactoMineR (v1.42, Lê et al. 2008), and visualized using the factoextra package (v0.5-3.0) in R.

Photosynthetic symbiont community structure

Symbiodiniaceae communities were characterized at the end of the experiment with DNA extracted from excess lipid slurry using a Qiagen DNeasy kit. Libraries were also prepared for the top and bottom sections of a colony showing phenotypic plasticity in the field (OAKB5). The rRNA ITS2 region was amplified with primers ITSDINO-F (Pochon et al. 2001) and ITS2REV2 (Stat et al. 2009) that included adapters (Illumina, USA) added to the 5' end of each primer. Amplifications were conducted in 13 µl volumes consisting of 6.3 µl MyTaq 2x (Bioline, USA), 0.3 µl of each 10 µM primer, 0.65 µl 20 mg/mL BSA, 4.65 µl Ultrapure distilled water (Life Technologies), and 0.5 µl DNA. Thermal cycling consisted of an initial denaturation step of five min at 95 °C, followed by 35 cycles of 30 s at 95 °C, 30 s at 53 °C, and 45 s at 72 °C, with a final extension of 10 min at 72 °C. Nextera XT (Illumina, USA) index adapters were added to each library followed by purification with Agencourt[®] Ampure XP beads. Amplicons (including negative controls) were then (pair-end, 300 bp) sequenced on an Illumina MiSeq platform at the ASGPB. Sequences were analyzed using SymPortal (Hume et al. 2019).

Statistical analysis of endpoint sampling metrics

All growth and tissue metrics from the end of the experiment were analyzed with linear mixed effects models using lme4 (v1.21, Bates et al. 2015) and lmerTest (v3.1, Kuznetsova et al. 2017) in R (v3.5.2). Treatment and genotype were fixed effects with an interaction term, with tank as a random effect. Normality and homogeneity were confirmed using residual and q-q plots. Cook's Distance was used to remove between 0-3 outliers from each response variable. For datasets with significant treatment or genotype effects, post hoc pairwise comparisons were performed using a Tukey HSD test, using emmeans package (v1.3.5.1) in R.

Effect of light and temperature on lateral growth

We leveraged natural variation in environmental conditions to investigate the effects of light and temperature on growth measurements taken approximately every 30 d. We calculated average temperature and average peak light (between 10am-3pm) from data logged by hobo loggers for each one-month time period between photographs (five in total). Lateral growth was used for shorter-term intervals because it responded more rapidly to the environment than buoyant weight, where tissue death may not result in skeletal loss for many months. Growth, temperature and light data for 36 tiles and from five time periods were included (180 data points); 3 data points were identified as statistical outliers due to likely logger malfunction and removed from further analysis, for a total of 177. Growth was measured as the log difference in area. Light and temperature were both scaled to one to account for extreme differences in variation between the two metrics (e.g. 2,000 - 40,000 lux vs. 26 - 28°C).

Because we expected lateral growth to be influenced by the original size of the fragment (the growing edge increased as the colonies got larger), the previous month's area was included in the model (LaggedArea). Further, the time periods were not equal so Days between measurements were included, as were Tank and Tile, as random effects. We explored increasingly complex models with additive and/or interactive effects between light, temperature, and genotype, and selected the model with the lowest AICc (Akaike Information Criterion with a small sample-size correction).

We compared the best Linear Mixed Effect models to a Generalized Additive Model with the same fixed effects to account for potential nonlinear responses in growth rates to predictors.

Because AICc cannot directly compare models with and without random effects, we used cross-validation to assess each model's mean-squared predictive error, the ability to predict data that has been held out of the fitting process. The predicted effects of light and temperature on growth under an LME model were visualized using sjPlot (v2.7.2), with distribution of input data overlain as a rug plot using ggplot2 (v3.2.1, Wickham 2016) in R.

RESULTS

Phylogeny

Analysis of *cox-1*-rRNA intron sequences showed all the experimental colonies, plus OAKB5, formed a clade with six colonies identified by Luck et al. (2013) as *P. varians*; and these sequences are > 99.5% identical (Fig. S4.1). This clade included electronically-retrieved sequences from samples collected from shallow (2 m) to mesophotic depths (73 m). *P. varians* was placed in the tree as sister to *P. duerdeni*, a massive coral, highly morphologically distinct from *P. varians*.

Experimental conditions

Temperature and light varied seasonally over the 6-month duration of the experiment (Fig. S4.2). Peak light levels ranged from 40,453 to 71,311 lux (mean= 34,685 lux), 8468 to 14,959 lux (mean=10,438 lux), and 2,935 to 5,014 lux (mean= 3,495 lux) in the 0, 75 and 90% shade treatment levels, respectively. Temperature ranged from 26.9 to 28.1°C (mean= 27.1°C), 26.6 to 27.8°C (mean=26.9°C), and 26.6 to 27.7°C (mean= 26.9°C) in the 0, 75 and 90% shade treatments, respectively. Four colonies bleached in the first month of the experiment and suffered partial mortality. These colonies were in the 0% shade treatment and from Genotype 3; all were growing and had recovered pigmentation by the end of the experiment.

Growth and skeletal morphology

On average corals had a positive growth rate in all treatments, and there was an overall significant negative effect of light level on growth and growth-related traits. Calcification rate was significantly affected by light (LMM: df = 2, F = 11.3, p = 0.0003) and genotype (df = 2, F =

6.9, $p = 0.004$). Colonies laid down twice as much skeleton in the darkest treatment (mean = $0.011 \text{ g day}^{-1} \pm 0.0012$) compared to full sun (mean = $0.005 \text{ g day}^{-1} \pm 0.001$) (Fig. 4.2, 4.3a).

Lateral coral growth rate was also affected significantly by light (LMM, light: $df = 2$, $F = 42.6$, $p < 0.0001$, genotype: $df = 2$, $F = 30.0$, $p < 0.0001$), and the interaction between light and genotype was also significant (light*genotype: $df = 4$, $F = 3.5$, $p = 0.02$). Colonies grew more than twice as fast laterally in the 90% shade treatment (mean = $0.085 \text{ cm}^2 \text{ day}^{-1} \pm 0.00369$) compared to the full sun treatment (mean = $0.039 \text{ cm}^2 \text{ day}^{-1} \pm 0.00369$), and this effect was particularly strong for Genotype 3 (Fig. S4.3a).

Colonies not only grew more in the darkest environment, they also grew differently with respect to colony morphology and organization. First, whole colony rugosity was significantly affected by light (LMM, light: $df = 2$, $F = 19.4$, $p < 0.001$) and genotype (genotype: $df = 2$, $F = 22.2$, $p < 0.0001$): the ratio of 3-dimensional to 2-dimensional surface area was twice as large in full sun (46.24 ± 3.54) as in the darkest treatment (21.5 ± 3.34) (Fig. 4.2, 4.3c).

Second, corallite density in areas of new lateral colony growth was significantly affected by light (LMM, light: $df = 2$, $F = 14.5$, $p = 0.0001$) and genotype (genotype: $df = 2$, $F = 4.9$, $p = 0.018$), and there was a significant interaction between the two (light*genotype: $df = 4$, $F = 4.3$, $p = 0.012$). Corallites were 50% more dense in areas of new lateral growth in the darkest light treatment (mean = $14.42 \text{ cm}^2^{-1} \pm 1.01$) than in the full sun treatment (mean = $8.83 \text{ cm}^2^{-1} \pm 1.18$) (Fig. 3b). Although all genotypes showed the same density trend from full sun to 90% treatment, the reaction norms of individual genotypes differed (Fig. S4.3d). For Genotype 1 the full sun and 75% shade treatments were visually similar, while for Genotypes 2 and 3 the 75% and 90% shade treatments were visually similar (Fig. S4.3).

Coral condition metrics

In areas of new lateral growth, mean tissue thickness was significantly affected by light (LMM, light: $df = 2$, $F = 4.9$, $p = 0.017$) and genotype (genotype: $df = 2$, $F = 34$, $p < 0.0001$). Tissue in areas of new lateral growth was significantly thicker in the darkest treatment (mean = $1517 \mu\text{m} \pm 86.9$) than in full sunlight (mean = $1522 \mu\text{m} \pm 95$) (Fig. 4.4c). Mean Symbiodiniaceae fluorescence in areas of new lateral growth, was also significantly affected by light (LMM: $df = 2$, $F = 10.4$, $p = 0.00056$) and genotype ($df = 2$, $F = 58.3$, $p < 0.0001$). Fluorescence attributed to

Symbiodiniaceae was approximately twice as high in the darkest treatment (mean = 9.79 RI 100% $\pm$ 0.599) compared to under 0% shade (mean = 5.66 RI 100% $\pm$ 0.739) (Fig. 4.4a).

In contrast to areas of new lateral colony growth, light did not affect tissue thickness or Symbiodiniaceae fluorescence in the original fragment. There was no significant effect of light on tissue thickness of the original fragment, but there was a significant effect of genotype (LMM, genotype: df = 2, F = 51.1, p = <0.0001), and a significant interaction (light*genotype: df = 4, F = 3.7, p = 0.019). Similarly, there was no significant effect of light on fluorescence in the original fragment, but genotype was significant (LMM, genotype: df = 2, F = 26.1, p = <0.0001).

For the entire colony, total lipids were not significantly different among light treatments and genotypes. The ratio of nonpolar to polar lipids was also not significantly different among light treatments but there was a significant genotype effect (LMM, genotype: df = 2, F = 4.8, p = 0.022) (Fig. 4.4e).

Symbiodiniaceae community

Symbiodiniaceae communities generally did not vary by light environment. All samples contained communities dominated by symbionts from the genus *Cladocopium*, but phylotype varied between genotypes. Genotype 1 communities predominantly contained C1 symbionts, with no variation across light treatment. Genotypes 2 and 3 were dominated by C3, with the exception of the full sunlight sample of Genotype 3 which has a mixture of C1 and C3. Finally, the OAKB5 (Fig. 4.1) symbiont community was different from experimental corals, dominated by C27, but again community composition did not vary across colony surfaces exposed to different light levels, i.e., experimental conditions or top and bottom of the colony OAKB5 (Fig. 4.5).

Model of additive effects of light and temperature

The best linear mixed effects model did include the effects of temperature, light, and genotype but not interactions between these predictors. The next best model included an interaction between light and genotype, but support for this model was weak (Δ AICc 5.31). Therefore, the best-fitting model showed that light and temperature each had negative, additive (and independent) effects on growth (Fig. 4.6). Further, cross-validation between the best model LMM and the Generalized Additive Model showed these effects were linear, with no significant

difference in the mean squared predictive error (<1%), and otherwise similar error distributions between the two models. Under the LMM, lateral growth was reduced by both increasing temperature (LMM: Estimate = $-0.1092 \text{ cm}^2 \pm 0.024$, $t = -4.567$, $p < 0.0001$) and increasing light (LMM: Estimate = $-0.09047 \text{ cm}^2 \pm 0.026$, $t = -3.997$, $p = 0.0002$), and both had similar effect sizes (ΔAICc 8.68). Lateral growth was consistently 0.3 cm less at 28 °C than at 26.5 °C, and this difference was offset by the 0.29 cm increase in growth in the darkest to brightest light recorded (2,000-80,000 lux).

Other variables also had a significant effect on growth, consistent with the rest of the experiment. Genotype had a significant effect on growth, with Genotype 1 having a significant positive effect on growth (LMM: Estimate = $0.5746 \text{ cm}^2 \pm 0.084$, $t = 6.88$, $p < 0.0001$), whereas Genotype 3 had a significant negative effect on growth (LMM: Estimate = $-0.2448 \text{ cm}^2 \pm 0.048$, $t = -5.132$, $p < 0.0001$). Unexpectedly, the area of the colony at the previous time point also had a negative effect on growth (LMM: Estimate = $-0.05890 \text{ cm}^2 \pm 0.048$, $t = -5.132$, $p < 0.0001$).

DISCUSSION

The common garden experiment, symbiont metabarcoding, and growth rate modeling revealed four main findings. First, *P. varians* is phenotypically plastic, changing its morphology in direct response to light conditions. Second, growth rates of *P. varians* were maximized under the darkest experimental conditions. Third, in contrast to the plasticity of the host's morphology, Symbiodiniaceae community was not affected by light; instead, community composition varied across genotypes. Finally, light and temperature had equal and additive negative effects on growth, indicating that low light partially mitigated the negative effects of high temperatures on growth. Taken together, these findings indicate that phenotypic plasticity is a key mechanism by which generalists achieve a broad realized niche; either by persisting in place through changing conditions, or by allowing range shifts to newly vacant habitats or use of refugia.

Morphological plasticity

The growth experiments indicate that much of the inter- and intracolony morphological variation observed in *P. varians* on natural reefs is due to phenotypic plasticity. In high light, experimental colonies grew more slowly (by either mass or 2D footprint) but had more rugose

skeletons (taller and more ridges), and a lower density of corallites (Figs. 4.2,4.3; Figs. S4.3,4.4). In low light, colonies grow more quickly and have flatter skeletons with shorter ridges, and a higher density of corallites.

This morphological phenotypic plasticity is likely adaptive, with a probable advantage of expanding the range of habitats available to individual colonies in a number of ways. First, increased ridge formation potentially enhances self-shading of zooxanthellae (in the furrows between ridges) from excess light, while in low light conditions, flatter skeletons maximize light capture by zooxanthellae (Todd 2008; Anthony and Hoegh-Guldberg 2003; Anthony et al. 2005; Todd et al. 2004a; Padilla-Gamiño et al. 2012). Second, plasticity in corallite density may be an integrated phenotypic response to variation in light availability because greater corallite (i.e., polyp) densities under low light conditions may increase the potential for colonies to offset reductions in photosynthesis by feeding on zooplankton (Crabbe and Smith 2006, but see Studivan et al. 2019). As light diminishes and the energy obtained by autotrophy declines, increased heterotrophy may extend the depth niche at light levels that cannot support positive growth through autotrophy alone. Although mixotrophy has not been established for *P. varians*, several other species of *Pavona* and *Leptoseris* are mixotrophic, with greater reliance on heterotrophy at depths from 70 to 120 m (Padilla-Gamiño et al. 2019; Conti-Jerpe et al. 2020). Traits related to increased resource acquisition, such as branching frequency and rhizome formation, are similarly plastic in plants, maximizing resource capture in heterogeneous light environments (de Kroon & Hutchings 1995).

Skeletal plasticity in *P. varians* could provide other advantages under different light environments. Increased colony rugosity may increase movement of metabolites away from (and oxygen towards) the colony surface due to increased shear stress from turbulent flow generated by the skeletal ridges (Finelli et al. 2006; Stocking et al. 2016). Similarly, colonies with irregular surfaces transfer more heat from water flow, potentially beneficial in warm, shallow water (Stocking et al. 2018). Greater corallite density in corals may have other advantages, as more polyps may enhance autotrophy because more space is devoted to gastrovascular cavities, which in turn can accommodate larger numbers of photosynthesizing symbionts (see Fig. 4.4f).

Genotypic variation was also significant for all metrics and in some instances genotype had as large an effect as light (Fig. S4.3). Of the three genotypes, Genotype 3 grew more slowly,

was less rugose, and had thinner tissues and fewer corallites than Genotypes 1 and 2 (Fig S4.3 & S4.4). In contrast, genotype by environment interactions were uncommon, indicating less genetic variation in plasticity itself. Therefore, there was considerable genetic variation underlying these morphological traits, consistent with other studies on light-associated phenotypic plasticity (e.g., Todd et al. 2004b; Ow & Todd 2010; Fong et al. 2021) and agreeing with the prevalence of individual effects in corals for other traits, such as stress tolerance (Edmunds 1994; Dilworth et al. 2021). High underlying genetic diversity could have ramifications for the response of *P. varians* to climate change, as greater standing genetic variation can lead to rapid adaptation (Barrett & Schluter 2008; Bay et al. 2017). Genotypic effects may also be important for coral restoration, where targeted propagation efforts on individuals known to be hardier or faster growing (such as Genotype 1) may be the best use of scarce resources (Drury et al. 2017).

Plasticity of functional traits

Light is an important variable affecting coral growth. Light attenuates exponentially with depth, and is the main factor delineating the mesophotic zone (Tamir et al. 2019; Laverick et al. 2019). The order-of-magnitude variation in light in this experiment encompasses the full spectrum of irradiance that can sustain shallow-water, coral reef accretion (Kleypas et al. 1999). Although the growth rate of *P. varians* was greatest at the lowest light levels in our experiment, colonies had positive growth in each treatment, highlighting the broad light niche of *P. varians*. Few coral species can persist across such a broad depth gradient, and the most abundant species (from Roberts et al. 2019 e.g. *Porites rus*, *Goniastrea pectinata*, and *Echinopora lamellosa*) are all, like *P. varians*, plastic in morphology or physiology with respect to light (Jaubert 1977 in Padilla-Gamino et al. 2012; Titlyanov et al. 2002; Ow & Todd 2010). Light-driven plasticity may also allow *P. varians* to exploit other dark environments, such as turbid reefs, and shallow, cryptic, shaded microhabitats that could similarly serve as refuges for corals.

Although *P. varians* maintained positive growth under a wide range of light, plasticity in other important traits such as functional lipid ratio (FLR), the ratio of structural to storage lipids, may provide an additional and more nuanced views of how light impacted coral health (Saunders et al. 2005; Cooper et al. 2009). In plants altered lipid concentrations can be indicative of stressful temperatures (Degenkolbe et al. 2012; Mueller et al. 2017) and drought (Hatzig et al.

2018). During times of stress for corals, such as bleaching, the relative amount of non-polar storage lipids can similarly decline, as energy reserves are depleted to account for the nutritional shortfall (Saunders et al. 2005; Bachok et al. 2006). However, storage lipids may also decline when used to either fuel rapid growth (Yamashiro et al. 2001; Sale et al. 2019) or offset energy demands under less photoefficient conditions (Cooper et al. 2011). The overall lack of a relationship between FLR and light gradient in our data might reflect the inability to separate similar changes in FLR in low light due to rapid coral growth, and in high light due to reduced photosynthesis. Alternatively, the absence of a relationship between FLR and light may indicate that *P. varians* can maintain FLR under a range of conditions that, in other species, drive substantial changes in energy use and storage (Saunders et al. 2005; Cooper et al. 2011; Henrichs et al. 2013). FLR may also provide a measure of genotype vigor in *P. varians*, because storage lipid was consistently low in Genotype 3, which also bleached and had the slowest growth rate of all the colonies (Fig. S4.2,4.3ab).

Symbiodiniaceae fluorescence and tissue thickness also both decline during bleaching, as symbionts are compromised and coral condition deteriorates (Huffmyer et al. 2020). In our experiment, the response of these metrics depended on the part of the colony analyzed. In portions of the colony corresponding to the original fragment, tissue thickness and fluorescence did not differ among light treatments; however these traits were plastic in areas of new lateral growth in *P. varians*. Areas of new lateral growth had thinner tissues and reduced symbiont fluorescence in full sun than in the 90% shade treatment. In contrast, the original coral fragment had an older, more rugose skeleton (Fig. S4.5) with more pronounced ridges. Increased rugosity may protect symbionts from light stress in full sun via self-shading, and prevent a noticeable decline in symbiont density and tissue thickness in the original fragment. In new lateral growth in *P. varians*, the skeleton is thinner and ridges are less developed, offering little protection from the stressful high light experienced in the full sun treatments, subsequently symbiont fluorescence and tissue thickness decline. Further, in darker conditions higher symbiont fluorescence facilitates greater capacity for photosynthesis when light is otherwise limited.

We characterized the Symbiodiniaceae assemblages of *P. varians*, to determine if community structure and composition was affected by differing light conditions. Although we recovered three different symbiont communities among four genotypes (dominated by C3, C1,

and C27, similar to those in *Pavona* elsewhere, see LaJeunesse et al. 2004a; LaJeunesse et al. 2004b; Keshavmurthy et al. 2017), these communities were largely maintained across light treatments (Fig. 4.5). High symbiont community diversity among colonies in our analysis is consistent with previous findings that *P. varians* is highly labile in its associations with Symbiodiniaceae (Cunning et al. 2015), yet does not shuffle symbionts in response to light availability alone. The relative performance of Symbiodiniaceae phylotypes is hard to determine, but C3 appears more stress tolerant than C1 (Swain et al. 2017). In our experiment, the composition of the symbiont community was not related to the unusual growth pattern of Genotype 3 (Fig. S4.3i), as Genotype 2 and 3 were dominated by the same Symbiodiniaceae phylotype.

Light and temperature stress

Understanding the impacts of light and temperature and other stressors in a multifactorial framework is important for predicting the future spatial distributions of corals and for management initiatives (Darling et al. 2013; Côté et al. 2016). Although most hermatypic taxa are often restricted to clear, tropical water, the response of photosynthetic scleractinians to climate change depends on their tolerance to both light and temperature, as the negative effects of high light and temperature are evident from experiments (Jokiel & Coles 1977; Lesser et al. 1990; Lesser and Farrell 2004; Takahashi et al. 2004; Baird et al. 2009). Further, the severity of bleaching is often reduced by low light conditions, such as cloud cover (Mumby et al. 2001; Donner and Carilli 2019), turbidity (Golbuu et al. 2011; van Woesik et al. 2012; Morgan et al. 2017; Teixeira et al. 2019), and in shaded microhabitats such as crevices and overhangs (Hoogenboom et al. 2017). Indeed, deep reefs are often not a temperature refuge (Venegas et al. 2019, and references therein), yet bleaching is often reduced at depth (García-Sais et al. 2017; Frade et al. 2018; Baird et al. 2018; Couch et al. 2017).

The results from our model are consistent with the idea that these reductions could be the product of primarily reduced light stress at depth (see Venegas et al. 2019). The model demonstrated that both light and temperature had linear, negative effects on growth, each with similar effect sizes but with no interaction or evidence of a synergistic effect (Fig. 4.6). Thus, for *P. varians*, low light can mitigate the negative consequences of high temperatures on coral growth, without impacting growth rates as seen in other species (Coelho et al. 2017). This could

be relevant at two scales for this species: within the colony, and across depth. First, by supporting the proposed adaptive role of increased ridge formation in high light conditions shading zooxanthellae, and thereby reducing the negative effects of increased irradiance. And second, by highlighting the importance of low light environments (such as deeper depths or overhangs) as refuges for *P. varians* (Camp et al. 2018). The lowest light treatment never became limiting for *P. varians* in our experiment, which contrasts with other species impacted by less modest light reductions (Forsman et al. 2012; Coelho et al. 2017). We found that *P. varians* would continue to grow at Hawai'i bleaching temperatures (28 °C) in 90% shade (~40 m depth), whereas growth would be halted in full sunlight (~0.5 m depth) at the same temperature.

Generalists in a warming world

Anthropogenic climate change is causing shifts in community composition of both terrestrial and marine biota (Pucko et al. 2011; Kopp & Cleeland 2014; McMahon et al. 2015; Mouthon and Daufresne 2015; Hughes et al. 2018; Fourcade et al. 2019). While exact responses differ between ecosystems, historical extinction events and niche theory predict that generalists are more likely than specialists to persist through the current human-induced stress event (Erwin 1998; Dennis et al. 2011; Colles et al. 2009). Shifts from specialists to generalists and functional homogenization in response to current climate change are already evident on land and in the sea (Clavel et al. 2011; Mangels et al. 2017).

Phenotypic plasticity plays an important role in shifts to higher altitudes observed in many montane plant species in response to warming temperatures at lower elevations (Byars et al. 2007; Midolo & Wellstein 2020). The DRRH offers a similar mechanism through which corals could persist through periods of heat stress. While other abiotic factors which can affect plant growth and survivorship change with elevation, in the marine environment, deeper depths correspond to not only lower temperatures but also declines in light, an essential resource affecting coral growth. Therefore light and depth generalist coral species may be able to use these temperature refugia, and be disproportionately important as early colonists on future reefs.

Our study focused on a “deep generalist” species that is more abundant at depth than on shallow reefs (Roberts et al. 2019; Montgomery et al. 2021). Although the extent to which the abundance of corals is limited by maximum growth rate or environmental constraints on growth (i.e., competition and disturbance) has been rarely tested (Pratchet et al. 2015), the outcome of

our experiment suggests that the growth rate reaction norms of *P. varians* may be a contributing factor to the depth-related abundance of this species. If restricted to deep reef refuges, deep generalists like *P. varians* may disproportionately contribute to future shallow water recruitment if faster growth translates into greater larval production at depth. But, potential increased relative abundance on shallow reefs may be diminished by intrinsically slower growth in high light. Comparative studies that relate growth rates under controlled conditions to field studies of realized growth on reefs for both deep and shallow generalists will be necessary to identify taxa most likely to benefit from the DRRH.

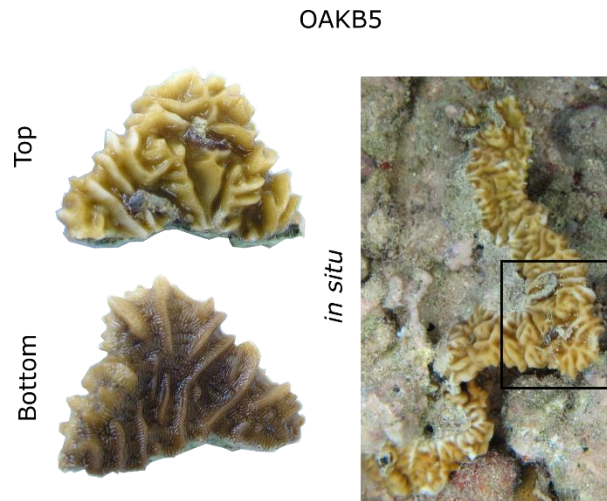


Figure 4.1. Colony of *Pavona varians*, OAKB5, *in situ* and top and bottom regions of collected fragment. Observation of intracolony variation in gross morphology between the exposed top and shaded bottom of a *P. varians* colony, suggesting light-associated phenotypic plasticity.

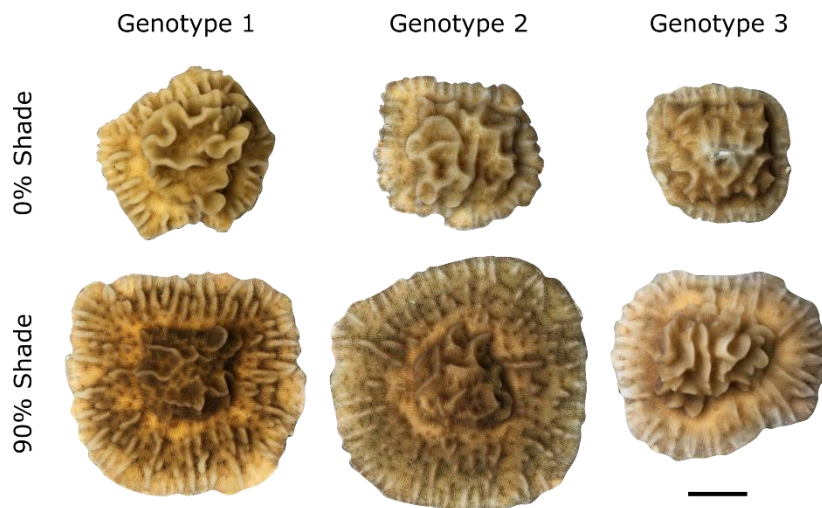


Figure 4.2. Photographs of fragments of the three genotypes of *Pavona varians* included in the experiment, from 0 and 90% shade treatments, scale bar 1 cm.

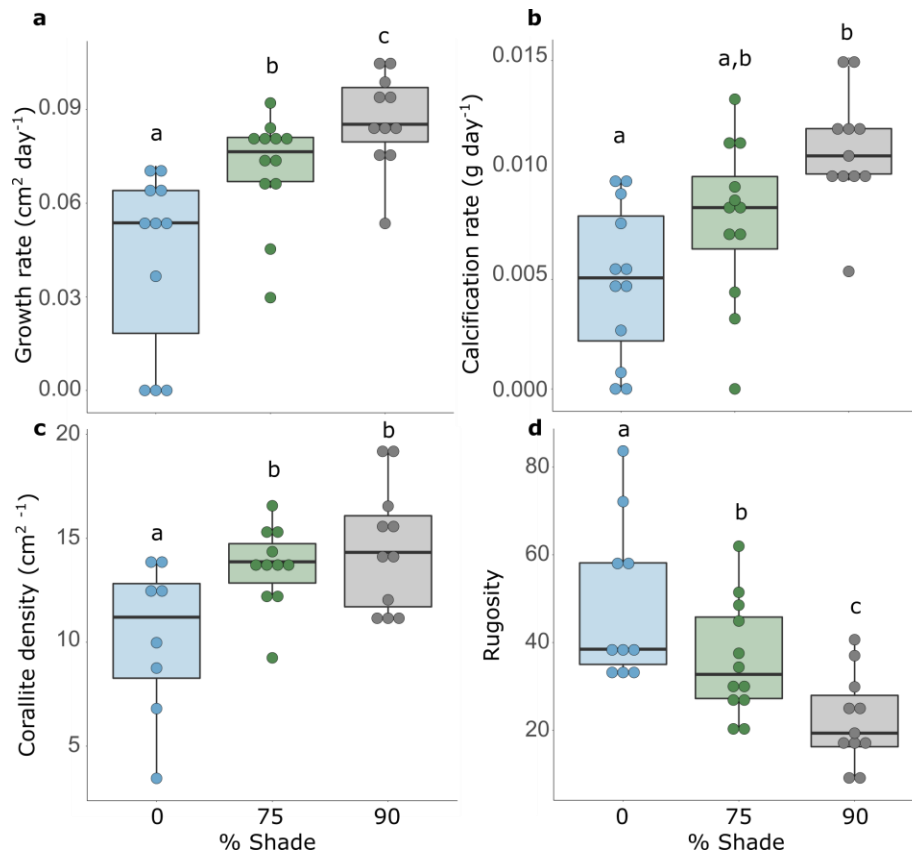


Figure 4.3. Growth and morphological metrics of *Pavona varians* across three light treatments: a) growth rate, b) calcification rate, c) corallite density on lateral growth, d) colony rugosity. Letters correspond to significant pairwise differences in post hoc analysis ($p < 0.05$).

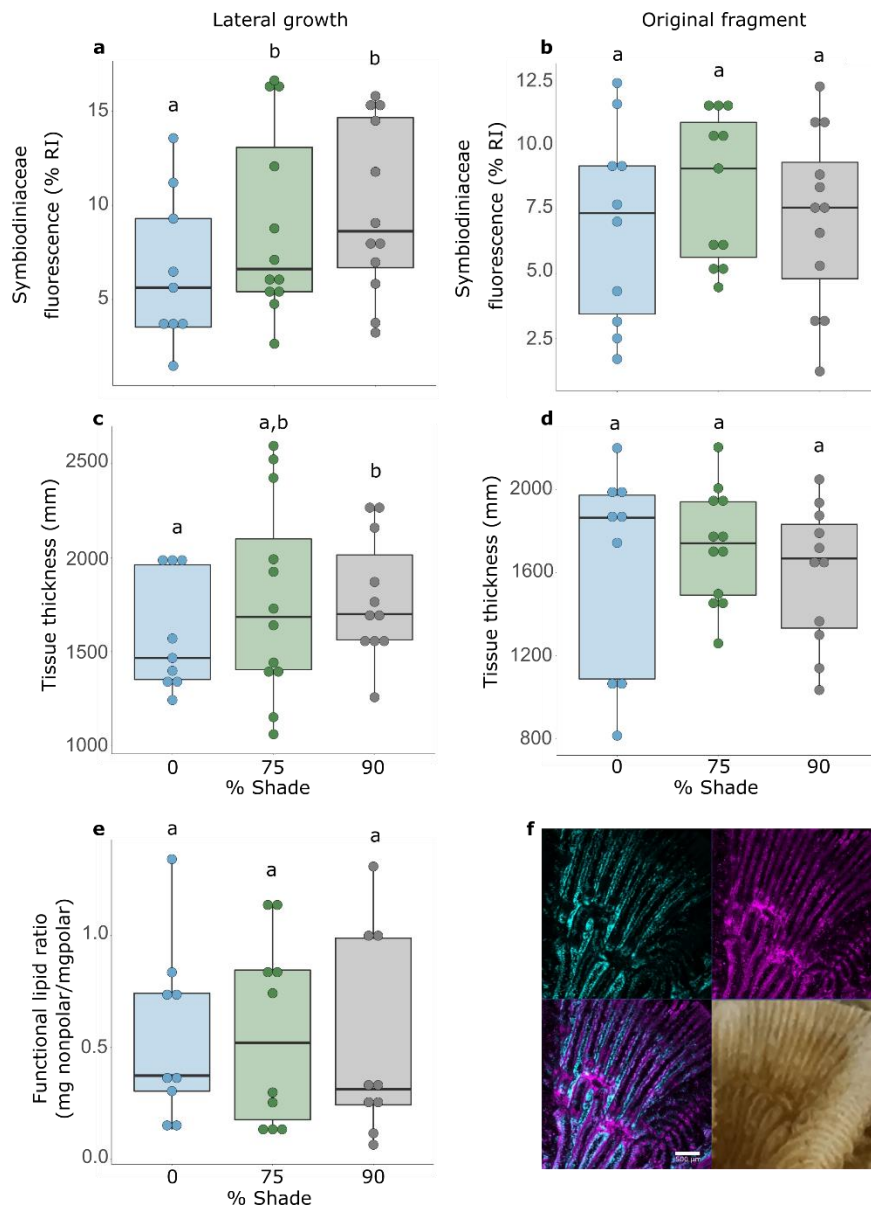


Figure 4.4. Physiological metrics of *Pavona varians* across three light treatments.

Symbiodiniaceae fluorescence (a,b) and tissue thickness (c,d) in the lateral growth (a,c), and original fragments (b,d) of *Pavona varians* across three light treatments. Functional lipid ratio of the whole fragment (e). Photograph and Laser Scanning Confocal Microscopy image of *P. varians* fragment (f). Cyan, coral tissue fluorescence; magenta, Symbiodiniaceae fluorescence. Scale bar, 0.5 mm. Letters correspond to significant pairwise differences in post hoc analysis ($p < 0.05$).

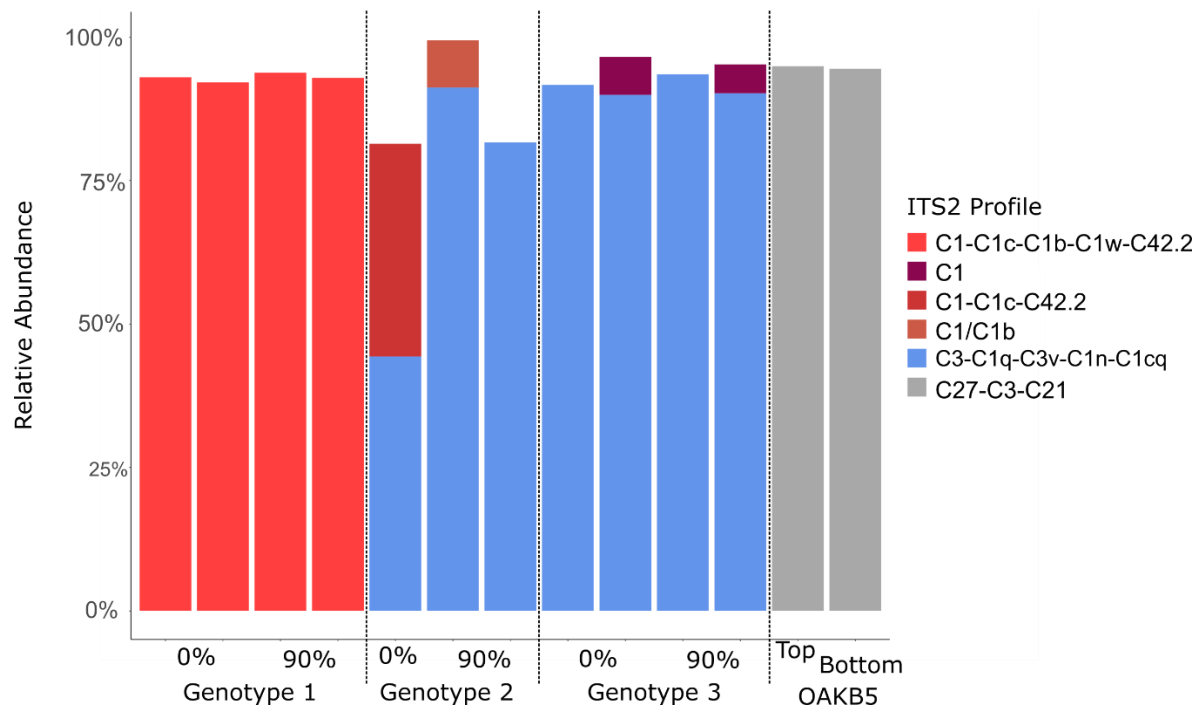


Figure 4.5. Symbiont communities of *Pavona varians* colonies from across three light treatments and from colony OAKB5. Relative abundance of ITS2 profiles for each genotype of *P. varians* included in analysis, from 0% and 90% shade, and from two samples of OAKB5, profiles generated in SymPortal (Hume et al. 2019).

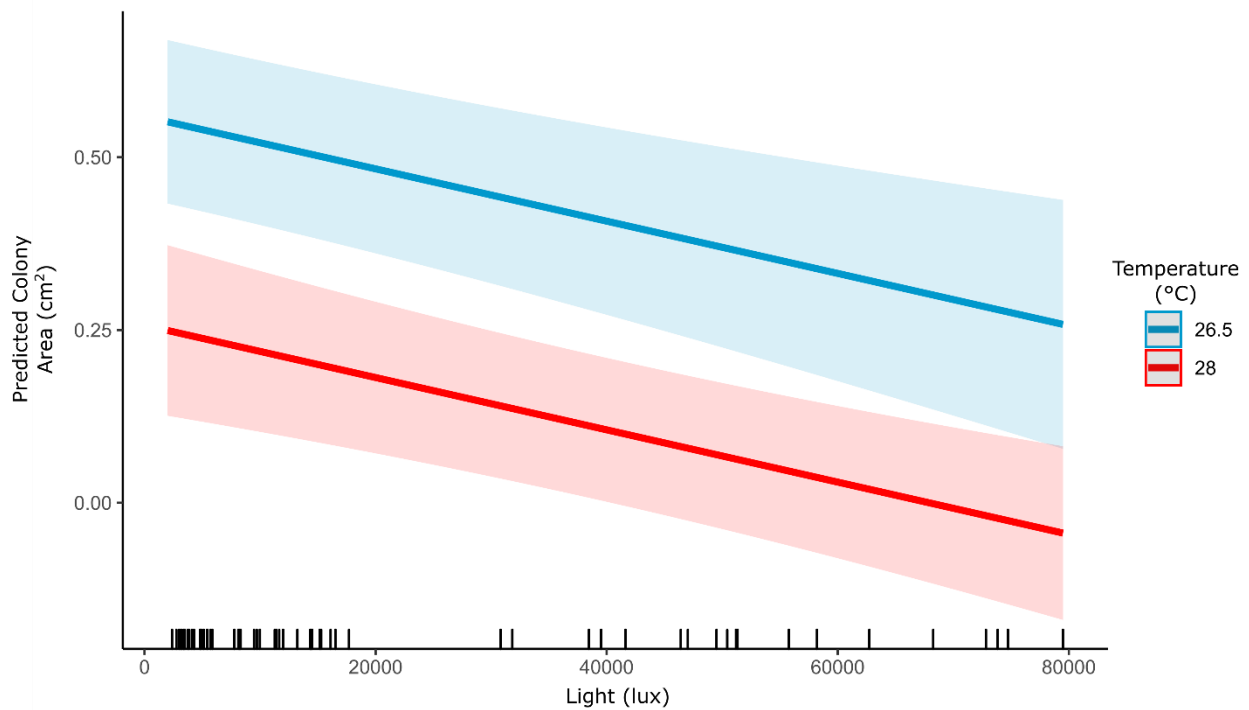


Figure 4.6. Combined effects of light and temperature on growth of *Pavona varians*. Predictions for lateral growth under normal (26.5 °C) and bleaching temperatures (28 °C) across light, from Linear Mixed Effects Model, shading indicates 95% confidence interval of the effects of light and temperature. Rug plot indicates distribution of experimental data.

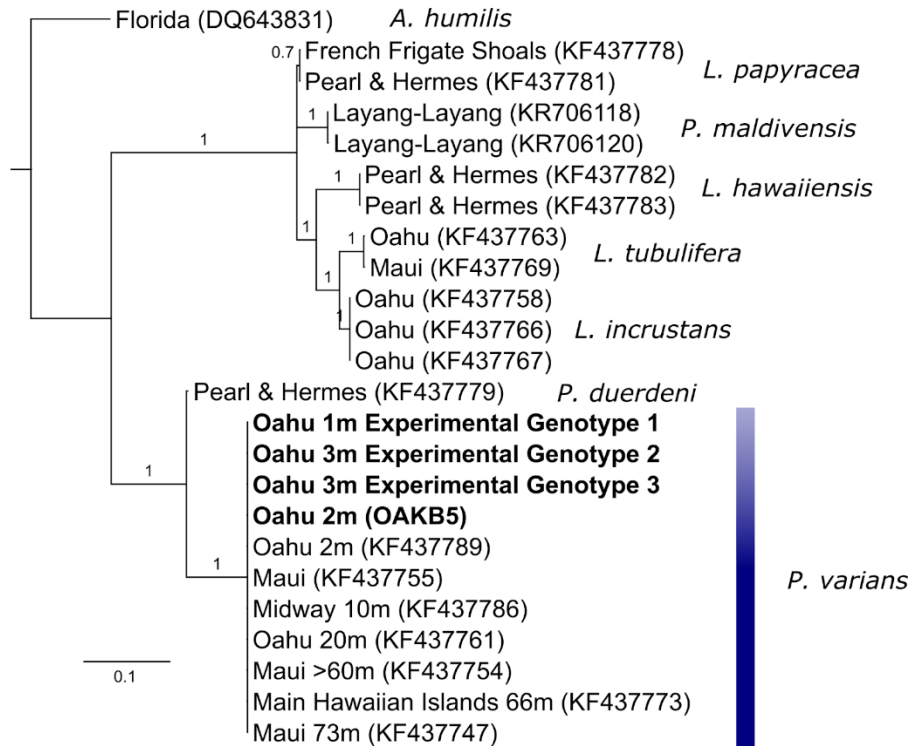


Figure S4.1. Bayesian phylogeny of Cox1-1-rRNA intron sequences from *Agaricia*, *Leptoseris*, and *Pavona*. Includes 18 published samples (DQ*,KF*, KR*:Medina et al. 2006; Luck et al. 2013; Waheed et al. 2015), the three genotypes collected for this study and OAKB5 (in bold). Tip labels indicate site, depth collected (m) where available, and sample code or GenBank accession number in parentheses. *P. varians* samples ordered by increasing depth of collection.

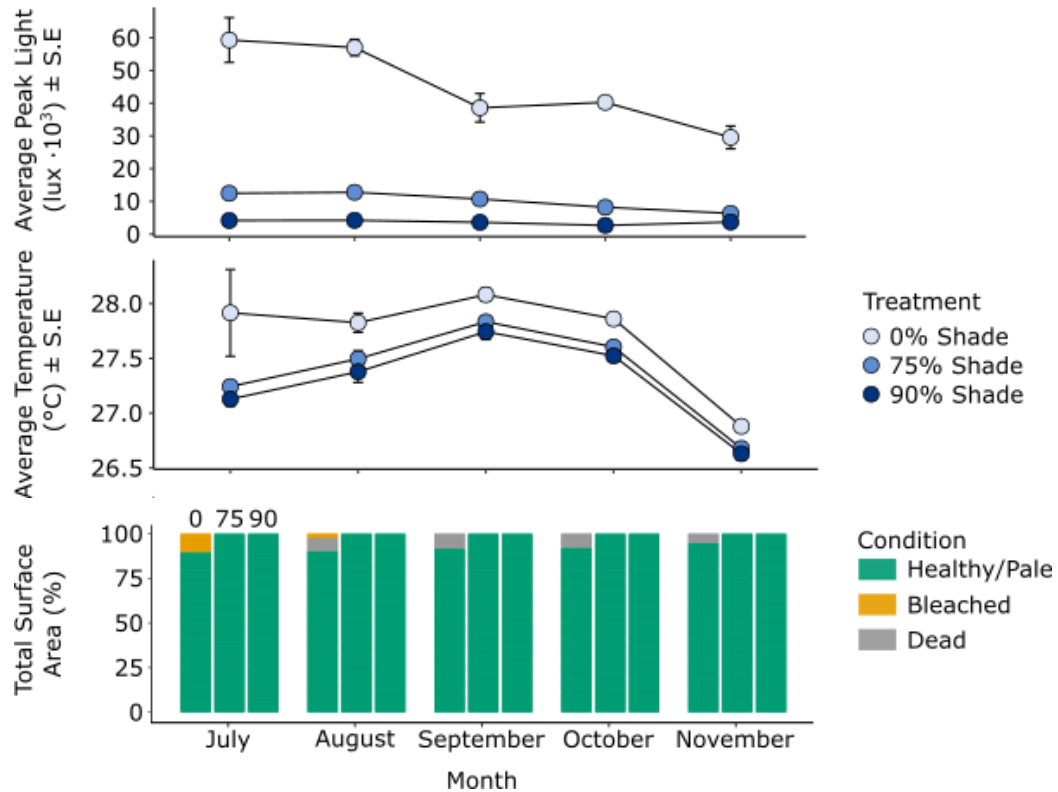


Figure S4.2. Experimental conditions of light and temperature, and prevalence of bleaching in each *Pavona varians* genotype, across the duration of the experiment. Average light and temperature through time, in three light treatments, with error bars for all points. And condition of coral colonies through time, as measured percent of total coral surface area. Each set of 3 bars corresponds to the light treatments.

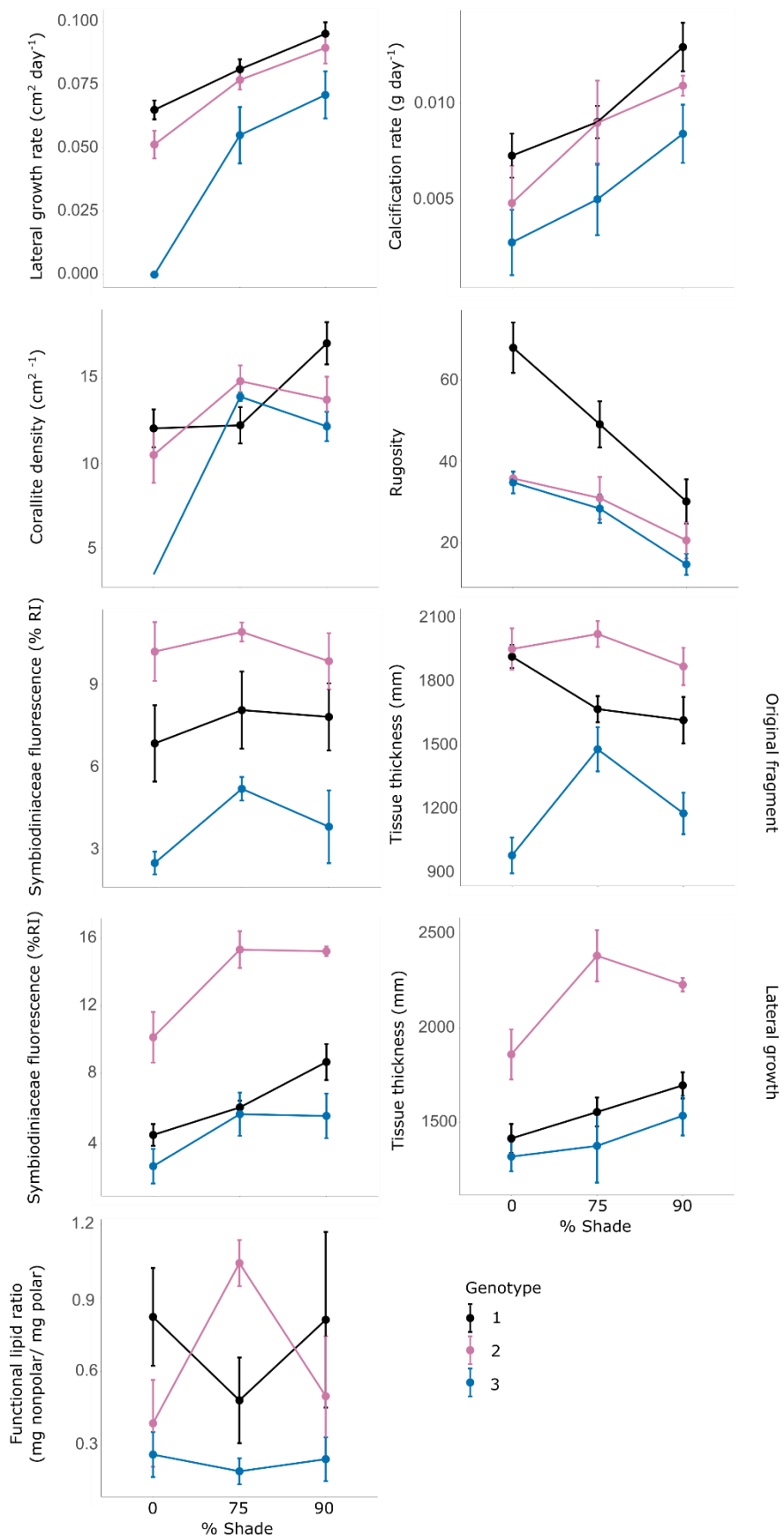


Figure S4.3. Genotype by light effects for all morphological and physiological metrics of *Pavona varians*. Genotype by a) lateral growth rate * b) calcification rate, c) rugosity, d) corallite density of lateral growth*, e) Symbiodiniaceae fluorescence in original fragment, f) tissue thickness in original fragment* g) Symbiodiniaceae fluorescence in lateral growth, h) tissue thickness in lateral growth, i) Functional lipid ratio in whole fragment. * denotes significant genotype by environment interaction.

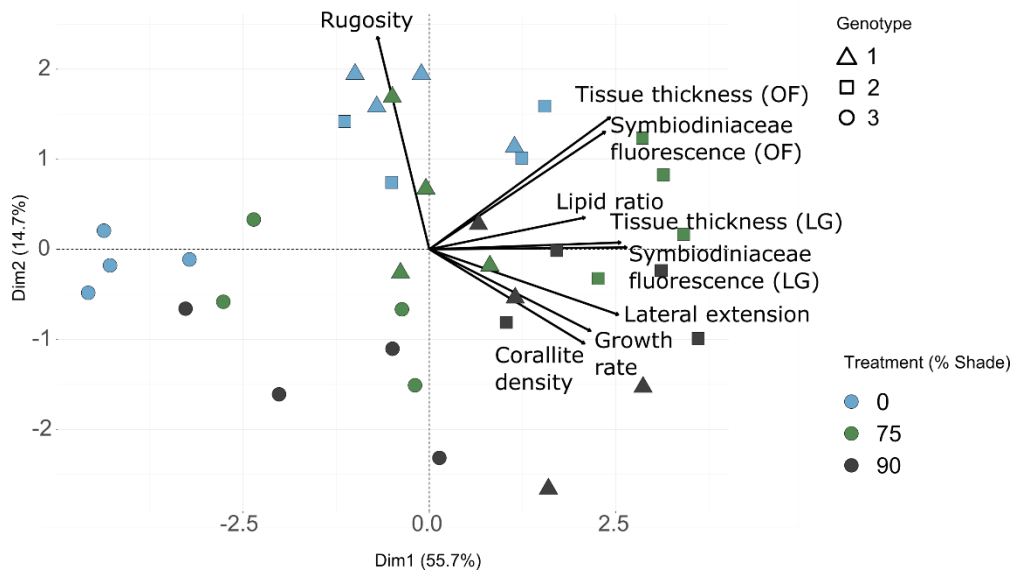


Figure S4.4. Principal Component Analysis of morphological and physiological metrics for three genotypes of *Pavona varians* across three light treatments. Dimensions 1 & 2, collectively 70% of variation, arrow length corresponds to contribution of each variable to dimensions.

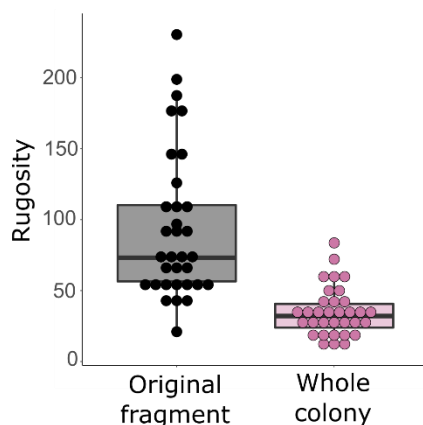


Figure S4.5. Comparison between whole fragment and original fragment rugosity of *Pavona varians* colonies. All measurements taken at the end of the experiment.

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CHAPTER 5. CONCLUSIONS

The aims of this dissertation were to investigate the phenotypic variation, phylogenomic and geographic diversity of species from the coral family Agariciidae. Agaricids are unusual among corals because of their wide-ranging species and broad depth distributions (Veron 2000; Hughes et al. 2002; Luck et al. 2013). These traits are exemplified in *P. varians*, a widely distributed, depth generalist, among the most abundant and common corals in the Indo-Pacific (DeVantier & Turak 2017; Roberts et al. 2019; Dietzel et al. 2021; Montgomery et al. 2021). To assess the phylogenetics and phylogeography of this family I applied two approaches. First, I used a traditional mitochondrial DNA barcoding approach that focused effort on a taxonomically and geographically broad sampling scheme (Chapter 2). Second, to test this approach I generated RAD libraries for a subset of individuals, which produced far more data from across the genome, albeit from fewer samples (Chapter 3). Lastly, I assessed the extent of light-associated phenotypic plasticity for the generalist species *P. varians* in a common garden experiment. From this experiment, I examined the impact of light and temperature on the growth of this species within a climate change context (Chapter 4).

BARCODING OF THE MITOCHONDRIAL INTRON

My second chapter represents the most comprehensive assessment of Indo-Pacific species from the family Agariciidae to date, sampling 77% of the currently recognized species in the region and across all five biogeographic provinces. This dataset involved combining new sequences from 208 corals with 191 previously published intron sequences to make a sweeping assessment of the mtDNA diversity and relationships within this family. There was minimal concordance between the clades recovered in the intron tree and the current taxonomy. The two richest genera in the family *Pavona* and *Leptoseris* were polyphyletic, and only 7/31 nominal species were monophyletic. This is consistent with previous work which found similar trends in geographically focused studies (Luck et al. 2013, Terraneo et al. 2017). Unlike other cryptic marine invertebrate groups, which recovered complexes of genetically distinct, but closely related lineages or cryptic species “complexes” (Knowlton 1993), many of the putative cryptic agaricids revealed in the intron study appeared distantly related to other morphologically similar

taxa. Unexpectedly, none of this cryptic diversity was associated with known phylogeographic breaks, and many species were still recovered as very widely distributed. This work recovered multiple putative cryptic species associated with the nominal taxa *P. varians* and *L. mycetoseroides*. And, this marker was nearly identical with respect to some morphologically disparate taxa, such as *P. varians* and *P. cactus*.

PHYLOGENOMICS

Given the potential for cytonuclear discordance, I generated a RAD-seq dataset of 120 colonies representing twenty nominal species, the first phylogenomic dataset generated for the Indo-Pacific agaricids. I assembled complete mitochondrial genomes for twenty species, eighteen of which are the first recorded for that taxon. I then assembled reads using three approaches, and from these assemblies I scored SNPs and generated phylogenies using a suite of tree-building methods. These different approaches consistently recovered three well-supported clades, which represent approximately generic level taxonomic structure. These clades did not correspond to the current genera of *Pavona* and *Leptoseris*, and indicate this family should be revised to include an additional genus.

The topologies recovered from the nuclear and mitogenome datasets were both well-supported but not concordant. This discordance was pervasive and affected all three of the main clades recovered from the SNP datasets, such that none were monophyletic in the mitogenome trees. One nominal taxon, *P. duerdeni*, which was monophyletic in all SNP trees, was polyphyletic in the mitogenome tree, recovered in three disparate clades. I found no evidence of introgression using D-statistics, suggesting hybridization and introgression may not be important in the agaricids, unlike other coral families (Mao et al. 2018, Cunha et al. 2019). Although the limited number of SNPs included in these analyses limits the power to detect potential introgression events, the strong discordance between the nuclear and mitogenome phylogenies suggests that mitochondrial introgression may have taken place several times.

Similar to the intron phylogeny of Chapter 2, the SNP phylogenies from Chapter 3 recovered multiple putative cryptic species associated with the nominal taxa *P. varians* and *L. mycetoseroides*. The two clades of *L. mycetoseroides* recovered in the SNP trees are each sister

to morphologically distinct nominal taxa, and therefore it is highly likely that one needs to be described as a new species. The eight cryptic clades of *P. varians* recovered from the coral holobiont SNP phylogeny are recovered in two separate generic level clades. Within the pink clade most of the putative *P. varians* cryptic species are more divergent from each other than morphologically disparate sister species in the same clade. Both of these species, *P. varians* and *L. mycetoseroides* have ridged morphologies, the repeat polyphyly of these two taxa suggests this morphology may have evolved multiple times across the agaricid tree or may represent the ancestral state of this family.

A surprising result from the increased data of the SNP phylogenies was the failure to clearly separate morphologically distinct species such as *P. venosa*, *P. frondifera*, and *P. cactus*, similar to the mitochondrial intron tree of Chapter 2. These three species were all more closely related to each other than to the other five clades of *P. varians* recovered within the pink clade. Although *P. venosa* and *P. cactus* are very different in colony morphology and corallite organization, the four species in that clade run a morphological spectrum from variable ridge formation (*P. varians*), to extensive well-developed ridges (*P. venosa*), to up-right chunky fronds (*P. frondifera*), to well-developed, delicate, bifacial fronds (*P. cactus*). To further complicate the issue, the intraspecific morphological variation of these species overlapped with the interspecific variation in form. Thus species delimitation in this group is extremely challenging without accurate information about which characters are liable to be plastic.

LIGHT-ASSOCIATED PHENOTYPIC PLASTICITY

Field observations indicated that the extent of ridge formation in *P. varians* was potentially affected by the light environment. In my fourth chapter I experimentally investigated the effect of light on phenotypic plasticity of one clade of *P. varians*. I used a common garden experiment to assess light-associated plasticity of morphological and growth metrics, the first such experiment in this species. I characterized the coral response using a combination of photogrammetry of individual coral colonies, laser scanning confocal microscopy, biochemical analysis of functional lipid ratios, and metabarcoding of the symbiont community.

I found that *P. varians* was able to grow across a light gradient representing a 90% reduction in available light, roughly equivalent to descending 40m in clear tropical waters (Tamir et al. 2019). Despite being capable of growth in full sun, I found that *P. varians* grew more quickly, with more densely packed corallites, and a flatter skeleton in darker environments. The ridges that characterize this species, and which are similar to those of numerous species across the family, became accentuated in high light, forming a more rugose 3D skeleton in lighter environments. This plasticity is likely adaptive: a more rugose skeleton creates pockets of shade across the colony surface which could protect symbionts from potentially damaging high light, whereas a flatter skeleton maximizes the surface area available for photosynthesis. Phenotypic plasticity may enable this species to exploit a wide variety of light and therefore depth niches (Roberts et al. 2019; Montgomery et al. 2021).

I further analyzed the growth data from the experiment by modeling the combined effects of light and temperature on growth of *P. varians*. Coral bleaching is strongly influenced by both of these factors and their combined, and potentially synergistic, effect has been noted since some of the earliest bleaching research (Jokiel & Coles 1977; Coles & Jokiel 1978). The model revealed a significant, additive but negative effect of each of light and temperature on growth of *P. varians*, but no interactive or synergistic effects. The additivity suggests that low light will mitigate some of the negative effects of high temperatures for this species.

Combined, the results from the experiment suggest that plasticity plays an important role enabling *P. varians* to utilize low light refugia, such as deep reefs that are potentially buffered from anthropogenic stressor (Glynn 1996; Bongaerts et al. 2010). Individuals living in low light habitats may be able to persist through bleaching events because these darker environments mitigate some of the negative consequences of high temperatures on growth. Put simply: *P. varians* is a generalist, and during times of stress, generalists persist while specialists perish (Erwin 1998).

FUTURE WORK

Future work on the evolution of *Pavona* and *Leptoseris* should focus on whole genome data. This would, most likely, enable confident and accurate delimitation of even the most

closely related species, as well as allowing for clear understanding of the nuclear gene tree discordance and rigorous testing for evidence of introgression. This would also enable the detection of genomic islands of differentiation which may be key for understanding species delimitation within the pink clade.

Expanded experimental assessment of light-associated phenotypic plasticity in other *P. varians* clades, i.e., testing for similar plastic responses in disparate taxa, could provide further insight into the convergent functional properties of ridge formation in this group. This combined with transcriptomic data could not only illuminate our understanding of the molecular pathways involved in ridge formation of this family, but calcification within corals as a whole.

FINAL THOUGHTS

Overall, my PhD work uncovered three major findings. First, the systematics and taxonomy of the agaricids is in need of major revision, the extent of which is beyond the scope of this study. Secondly, the current taxonomy is underestimating the diversity within this family, particularly with respect to the nominal ridged-morphology taxa *P. varians* and *L. mycetoseroides*. And lastly, light plays an important role in shaping the morphology of at least one clade of *P. varians*. This plasticity affects a trait which is known to vary continuously between closely related species. Thus I speculate that light may have played an important role in the speciation of those closely related taxa. This multi-disciplinary work has illuminated some of the complexity of this fascinating and understudied group of corals, and contributes to our growing understanding of coral diversity and evolution.

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