# Genetic and morphological characterization of a coral Species of Concern, *Montipora dilatata*, in Kaneohe Bay, Oahu, Hawaii

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**Executive Summary**

*Montipora dilatata* (a stony coral endemic to Hawaii) is one of the rarest corals known; only a few colonies have ever been found despite extensive surveys. The taxonomic status of *M. dilatata* is unclear, in part because coral species boundaries in general are poorly understood. In order to examine evolutionary relationships in *Montipora*, a suite of molecular markers (mitochondrial: COI, CR, Cyt-B,16S, ATP6; nuclear: ATPsβ, ITS-2) were tested for polymorphism on samples collected from Hawaii and the Phoenix Islands. ATPsβ and the putative mitochondrial Control Region (CR) were selected for a broad survey of 13 morphospecies, followed by a more focused analysis of 6 representative Hawaiian taxa with all markers. The mitochondrial markers consistently showed clear and statistically supported divisions that are likely to be ancient given the slow rate of evolution of Anthozoan mitochondrial DNA. Hawaiian samples generally sorted into three distinct clades: I) *M. patula/M. verrilli*; II) *M. dilatata/M. turgescens/M. flabellata*; and III) *M. capitata*. ATPsβ trees of all sequences resolved no groups, but when heterozygous and non-Hawaiian taxa were excluded from the analysis, four strongly supported groups emerged. Unexpectedly, all markers indicated that *M. dilatata*, *M. turgescens,* and *M. flabellata* share identical or very similar sequences, indicating that they are either close relatives, morphological variants of the same species, or members of the same "hybrid species complex". In order to distinguish among these competing hypotheses, it is necessary to focus on morphological variation and/or reproductive relationships. This preliminary study echoes findings of other molecular studies on reef building coral, indicating that morphology obscures genetic relationships and limits our understanding of coral evolution and biodiversity. Now that the closest relatives of *M. dilatata* have been identified, gene flow, morphological, and reproductive characteristics can be more closely examined to further elucidate the nature of coral species so they can be better understood and more effectively managed.

## Introduction

*Montipora dilatata* is thought to be one of the rarest corals known. It has only been found in two locations: Kaneohe Bay, Oahu, and Maro reef (*M. c.f.dilatata*) in the Northwestern Hawaiian Islands (Fenner 2005; NOAA 2007). In 2000, extensive surveys identified only three colonies of *M. dilatata* in Kaneohe Bay, where previously it was thought to be more abundant (NOAA 2007). The apparent decline of this species in Kaneohe Bay may be attributed to coral bleaching, freshwater kills, sedimentation/habitat degradation, overgrowth by alien algae (e.g., Figure 1), or anchor/boat damage, which remain significant threats given the limited distribution and small number of colonies (NOAA 2007). *M. dilatata* appears distinct from most other congeneric species; however, *Montipora*, like many coral genera, has a high degree of morphological variation that can make confident identification problematic. *M. turgescens*, which is not found in the main Hawaiian Islands, exhibits some similarities to *M. dilatata* and it is not known if they are the same biological species (i.e., freely interbreeding). It is also not clear if the *M. c.f. dilatata* reported from the Northwestern Hawaiian Islands is in fact the same "species" as reported in Kaneohe Bay (Fenner 2005).

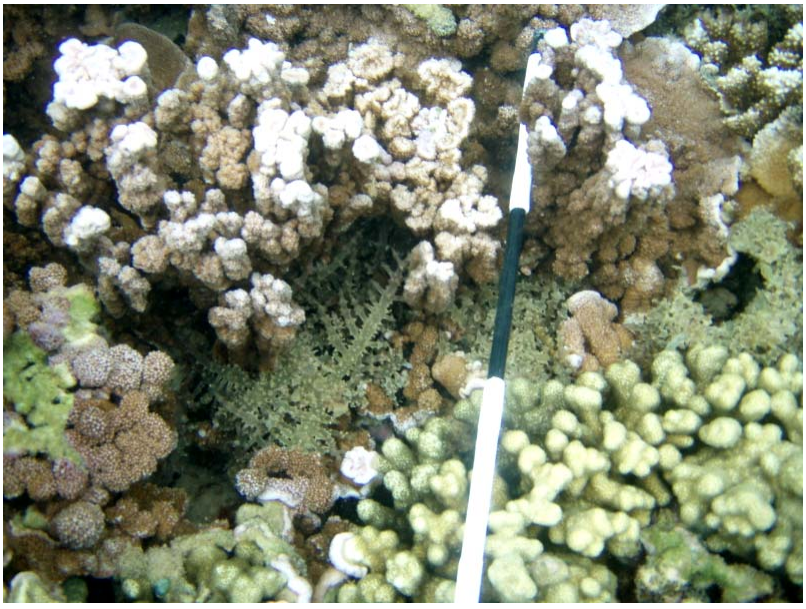

**Figure 1** *M. dilatata* in close proximity to *Kappahycus/ Eucheuma* spp., an invasive alien algae known to overgrow and smother coral.

The taxonomic uncertainty in *Montipora* is due to confusing patterns of morphological variation. *Montipora* taxonomy (as with all reef building coral) is based on skeletal morphology, which is known to be remarkably variable, responding to a wide variety of physical parameters such as light, sedimentation, water motion, water chemistry, and even many ecological interactions (Veron 2000; Todd *et al.* 2008). Recently, molecular studies have revolutionized our understanding of coral taxonomy, showing that the coral skeleton can be remarkably misleading, with surprising examples of convergent evolution (Fukami *et al.* 2004; Fukami *et al.* 2008), evolutionary plasticity (Forsman *et al.* in press), and phenotypic plasticity (Todd *et al.* 2008). Adding to taxonomic confusion, the conceptual nature of the coral species is a subject of intense debate, particularly regarding the permeability of reproductive boundaries between morphospecies (Veron 1995, 2000; Volmer & Palumbi 2002).

*Montipora* species are classified by traits that can vary within an individual colony, such as colony form (laminar, encrusting, massive, and branching), and on arrangement and size of protrusions between corallites (e.g., "papillae" are smaller than corallites, "tuberculae" are larger than corallites, and "verrucae" are very large "tuberculae"; in Figure 2 *M. capitata* has

large verrucae whereas *M. dilatata* has no conspicuous papillae). As colony form, size, and arrangement of microskeletal characters can be continuously variable, taxonomists disagree about the number and names of *Montipora* species that occur in Hawaii: for example, Veron (2000) lists 12 species, while Fenner (2005) and Maragos (1977) list 6, with disagreements about species ranges and nomenclature.

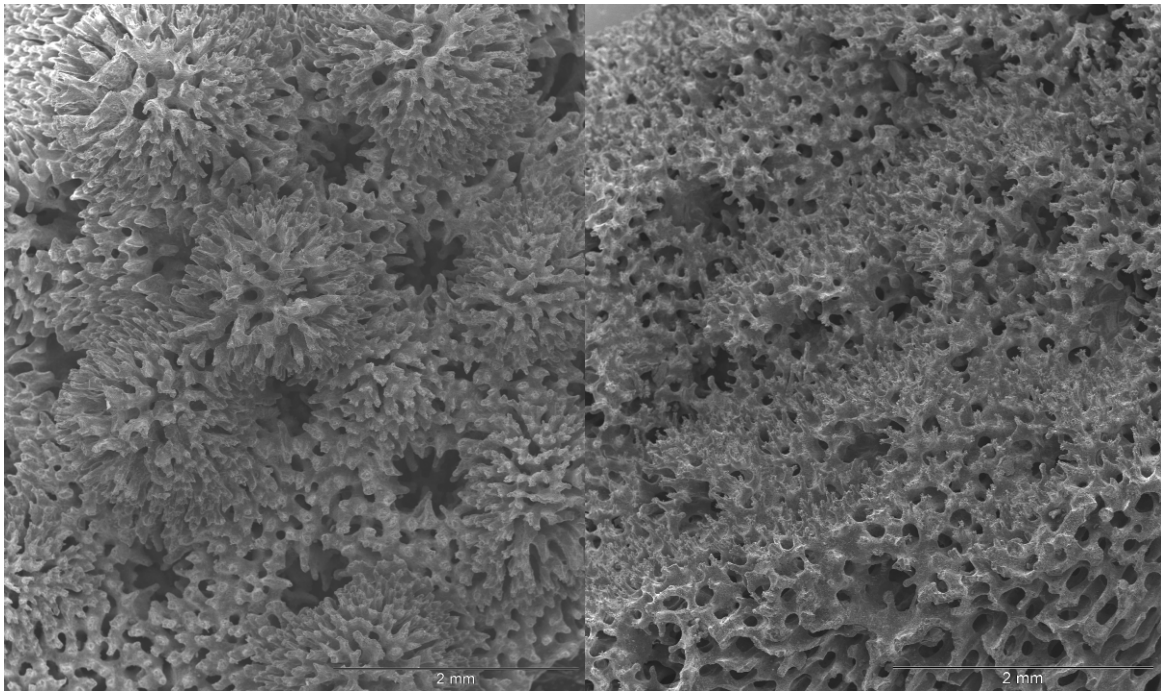


**Figure 2** Scanning electron microscope (SEM) images of *Montipora*; **left:** *M. capitata* from Pukoo, Molokai, Hawaii; **right:** *M. dilatata* from Kaneohe Bay, Oahu, Hawaii.

Based in part on studies in the related coral genus *Acropora*, there are three primary hypotheses for the confusing range of morphological variation observed in *Montipora.* One is that several "morphospecies" are capable of interbreeding. There may be up to 12 *Montipora* morphospecies in Hawaii (depending on the taxonomic source), creating many possibilities for hybrid combinations (Veron 2000). A second possibility is that *Montipora* individuals are highly polymorphic for skeletal morphology, although it is not clear how such differences would be maintained, unless mating is not as random as widely assumed. The final possibility is that *Montipora* species exhibit phenotypic plasticity depending on environmental conditions such as light, water motion, turbidity, etc. This hypothesis is difficult to fully reconcile with the observation that distinct morphotypes are frequently observed to occur side by side in the same habitat. Gross skeletal morphology may be a poor indicator of reproductive isolation, and other diagnostic information (such as genetic or microskeletal traits) may reveal more biologically meaningful species boundaries.

To determine the taxonomic status of *M. dilatata*, and to build a foundation for future work on *Montipora* in Hawaii, we conducted a genetic survey of most known Hawaiian *Montipora* species. The goal of this work was: 1) to develop a suite of molecular markers for genetic analysis of *Montipora*, 2) to identify the closest relatives of *M. dilatata*, and 3) perform a preliminary examination of evolutionary relationships of Hawaiian *Montipora*.

**Methods**

A set of 98 samples were examined for this study, representing 13 *Montipora* species (Appendix 1). Samples were collected throughout the main Hawaiian Islands (n=54), the Northwestern Hawaiian Islands (n=6), Tokelau (n=7), and the Phoenix Islands (n=31). To ensure consistency, a leading coral taxonomist (Dr. Jim Maragos) collected or confirmed the identification of the samples to species level. DNA extractions were accomplished following coral DNA extraction protocols previously developed in our laboratory (Concepcion *et al.* 2006), briefly: DNA was extracted from small pieces of coral tissue (5 $mm^3$) by digestion for 2–3 h in 200µL of DNAB (0.4m NaCl, 50 mm $Na_2$ EDTA pH 8.0) + 1% SDS+ 10µL proteinase K (10µg/mL) on a shaker at 55°C. An equal volume of 2X CTAB (cetyltrimethyl ammonium bromide) + 10µL/mL β -mercaptoethanol is then added, and the tube is vortexed before being incubated at 65°C for an additional 30–60 min. Samples are allowed to cool, and an equal volume of chilled chloroform is added prior to vortexing. The samples are then left on a rotating platform for 2-3 h. Finally, the supernatant is precipitated with 95% EtOH, pelleted by centrifugation, and subsequently washed with 70% EtOH. DNA is resuspended in 50µL deionized water before making 1–50 dilutions (approximate final concentration of 5 ng/µL) in dI for subsequent use as template for subsequent Polymerase Chain Reaction (PCR).

In order to provide evidence of genealogical concordance, multiple loci were examined. PCR primers were based on conserved portions of aligned sequences from the National Center for Biological Information's (NCBI) GenBank database, and designed with the aid of Primer 3 v 0.4.0 (Rozen & Skaletsky 2000), or based on previously published primers (Table 1). PCR reactions were performed on a Bio-Rad MyCycler Thermal Cycler. Each 25µL PCR contained 1µL of DNA template, 2.5µL of 10X ImmoBuffer, 0.1µL IMMOLASE DNA polymerase (Bioline), 3 mm MgCl2, 10 mm total dNTPs, 13 pmol of each primer, and deionized $H_2O$ to volume. Hot-start PCR amplification conditions varied slightly depending on the primer set used, but was generally: 95°C for 10 min (1 cycle), 95°C for 30s, annealing temperature (2 degrees less than primer melting temperature, ranging between 50 and 60°C) for 30s, and 72°C for 60s (35 cycles) followed by a final extension at 72°C for 10 min (1 cycle). PCR products were visualized using 1.0% agarose gels (1X TAE) stained with Gelstar. PCR products were treated with 2 U of exonuclease I and 2 U of shrimp alkaline phosphatase (Exo:SAP) using the following thermocycler profile: 37°C for 60 min, 80°C for 10 min. Cleaned PCR products were then cycle-sequenced using BigDye Terminators (PerkinElmer) run on an ABI-3100 automated sequencer at the EPSCoR core genetics facility at HIMB. Resulting sequences were inspected and aligned by eye using Sequencher version 4.5 (Gene Codes).

Sequences were aligned with ClustalW (Tompson *et al.* 1994) as implemented in BioEdit (Hall 1999) or with Muscle (Edgar 2004). All phylogenetic analyses were performed with MEGA4 (Tamura 2007), using the Neighbor Joining (NJ) method, with distances calculated with the p-distance option, and "pairwise deletion" selected for treatment of gaps, with 1000 bootstrap pseudoreplications. The phylogenetic analyses reflect uncorrected genetic distance and should be considered preliminary (although robust regarding major patterns and conclusions) as unequal patterns of nucleotide substitution are not modeled or accounted for.

**Table 1** List of primers used for this study: mt = mitochondrial, n = nuclear.

| Gene | | Sequence | Aprox. size | Reference |
|---|---|---|---|---|
| mt16S | Z16Sf | CCTCGGCTGTTTACCAAAAA | 790bp | This study |
| | Z16Sr | AACATCGAGGTCGCAAACAT | | This study |
| mt12S | Z12sf | CCGAGGCAGCAGTAAAGAAT | 705bp | This study |
| | Z12sr | CCGTTATCTTCCAGGCACTT | | This study |
| mtATP-6 | ZATP6F | GGCTCTGATCGCCTTGACTA | 534bp | This study |
| | ZATP6R | GGCCCACTTGCAACTAACAT | | This study |
| mtCyt-B | ZMcytbf | GGGACAGATGTTGTGCAATG | 649bp | This study |
| | Zmcytbr | CCCCCAACAAAGGGATTAGT | | This study |
| mtCox-1 | ZCOIF | TCAACTAATCATAAAGATATTGGTACG | 609bp | Forsman et al. in press |
| | ZCOIR | TAAACCTCTGGATGCCCAAA | | Forsman et al. in press |
| mtCR | Ms FP2 | TAGACAGGGCCAAGGAGAAG | 650bp | van Oppen et al. 2004 |
| | MON RP2 | GATAGGGGCTTTTCATTTGTTTG | | van Oppen et al. 2004 |
| nITS | ZITS1 | TAAAAGTCGTAACAAGGTTTCCGTA | 750bp | Forsman et al. in press |
| | ZITS2 | CCTCCGCTTATTGATATGCTTAAA T | | Forsman et al. in press |
| nITS-2 | ITSZ3 | CCAGGAGCATGTCTGTCTGA | 290bp | This study |
| | ITSZ4 | AGCCTTGCCTGATCTGAGGT | | This study |
| nPax-C | paxRP1 | GGCGATTTGAGAACCAAACCTGTA | 180bp | van Oppen et al. 2004 |
| | PaxMonFP1 | GGATGTAGCCACGAGAGAG | | van Oppen et al. 2004 |
| nND51a | NAD5_700F | YTGCCGGATGCYATGGAG | 443bp | Concepcion et al. 2006 |
| | NAD1_157R | VCCATCYGCAAAAGGCTG | 443bp | Concepcion et al. 2006 |
| nATPsβ | atpsbF2 | CGTGAGGGAAATGATTTCTACCATGAGATGAT | 280bp | This study |
| | atpsbR2 | CGGGCACGGGCGCCGGGGGGTTCGTTCAT | | |
| | atpsbF3 | TGATTGTGTCTGGTGTAATCAGC | | |

Initial screening for polymorphism indicated that ATPsβ and CR were among the most polymorphic and readily amplifiable markers, therefore they were selected for a broad survey of 98 samples from 13 morphospecies. Once the putative close relatives of *M. dilatata* were determined, a more focused study was conducted on a subset of samples (18 samples from 6 Hawaiian morphospecies) with mitochondrial (16S, ATP-6, Cyt-B, Cox-1) and nuclear (ITS-2) markers. The entire ITS region, ATPsβ, and the Pax-C intron, contained multiple PCR products, likely due to intragenomic variation (multiple alleles or gene copies within the genome). ATPsβ contained relatively few single nucleotide polymorphisms, which allowed direct sequencing; however, the ITS region and Pax-C would require molecular cloning and were not examined further for this study. The following is a brief description of the markers used in this study. The putative mitochondrial control region (CR) functions primarily by enhancing the transition from transcription initiation to elongation in RNA and DNA synthesis. The CR is the most rapidly evolving region in mtDNA (Shearer *et al.* 2002). *ND51a* is a ~500 bp non-coding region of the mitochondrial Nicotinamide Adenine Dinucleotide ($NAD^+$) gene. 12S and 16S are mitochondrial ribosomal genes, encoding the small and large ribosomal subunit, respectively. The mitochondrial cytochrome c oxidase 1 (COX1) gene, Adenosine triphosphate synthase 6 (*atp6*), and Cytochrome b (*Cyt b*) all code for portions of transmembrane proteins crucial for

cellular respiration. Mitochondrial markers are known to evolve extremely slowly in Anthozoa (van Oppen *et al.* 1999; Shearer *et al.* 2002; Hellberg 2006), and have been commonly used to deduce genetic relationships between genera, but not species (Ramano & Palumbi 1997; Fukami *et al.* 2000). Nevertheless, mitochondrial markers have evolutionary properties that are well studied and advantageous for phylogenetic analysis. Furthermore, multiple markers increase the chances of detecting species-level differences, and inferences about genological concordance can be strengthened.

Adenosine triphosphate synthase β (ATPsβ) is an intragenic region (intron) in the nuclear DNA. ATPases are important enzymes that convert potential energy stored in ATP to kinetic energy within the cell. *Pax C* is a single copy homeobox gene of ~180 bp (van Oppen *et al.* 2004). Signal Recognition Particle 54 (*SRP54*) is a ~177 bp fragment of a single copy nuclear-encoded protein that has worked successfully for both stony and soft corals (Concepcion *et al.* 2008). The hypervariable nuclear ribosomal internal transcribed spacer (ITS) region has been used widely to address relationships among closely related coral groups, which cannot be distinguished using other molecular markers (reviewed in Concepcion *et al.* 2008). The ITS region is a multi-copy marker, that is thought to be homogenized by recombinant mechanisms. Although it has been widely used to distinguish species successfully (e.g., Hunter *et al.* 1997; Forsman *et al*. 1995, 1996; Lam & Morton 2003; Forsman *et al.* in press), it can be challenging in some groups due to intragenomic variation and alignment ambiguity (Vollmer & Palumbi 2004); however, these challenging taxa may be an exception than a general rule (Wie *et al.* 2006) and the marker is known to diverge rapidly in reproductively isolated groups (Coleman 2003, 2007; Müller *et al.* 2007).

**Results & Discussion**

A set of 98 samples were examined for an initial broad survey. The control region (CR) and ATBsβ were successfully sequenced for 95 and 84 of the samples, respectively (Appendix 1). Comparisons with the NCBI GenBank database confirmed that the correct gene region was amplified, with the highest sequence similarity to other *Montipora* sequences in the database. The CR sequences clustered into 12 significant clades, many of which were shallow with long branches (Figure 1a). Only *M. capitata*, *M. lobulata*, and *M. faveolata* were monophyletic groups. One clade consisted entirely of *M. aequituberculata*; however, this species also occurred in three other clades. All other clades contained an unexpected mix of species, many of which have a very distinctive morphological appearance. Interestingly, all samples from the Hawaiian Islands sorted into three distinct clades, which became particularly evident when other samples are excluded from the analysis (Figure 2a). *M. dilatata* sequences were 100% identical to *M. turgescens* and *M. flabellata*. *M. patula* and *M. verrilli* also shared identical sequences, with long branches and strong support.

The ATBsβ sequence data contained multiple peaks that are typical of heterozygous single nucleotide polymorphisms. These polymorphisms were treated as ambiguous characters, which can be problematic for inferring phylogenies (especially in closely related groups). The tree contained no monophyletic groups, although *M. dilatata* again shared identical sequences with *M. flabellata* (Figure 1b). When only taxa from the Hawaiian Islands were examined, several clades emerged with some resemblance to the CR tree (Figure 2b). When heterozygous individuals were excluded from the analysis, four strongly supported clades emerged, bearing closer resemblance to the CR tree (Figure 2c), with the exception of *M. flabellata* occurring in three very distinct clades. Also unlike the CR tree, *M. flabellata/M. dilatata* sorted into two strongly supported though not monophyletic clades: one clade with a majority of *M. dilatata* sequences, and one containing only *M. flabellata*. At the time of the writing of this report, sequencing of *M. turgescens* for ATBsβ has not yet been completed.

The focused study concentrated on a subset of 18 samples, 3 from each of the following Hawaiian species: *M. dilatata*, *M. flabellata*, *M. turgescens*, *M. verilli*, *M. patula*, and *M. capitata*, with the addition of outgroup sequences from Genbank (mostly *Acropora* species). The additional markers yielded the following number of sequences: ITS-2 (7), COI (13), ATP-6 (15), Cyt-B (15), and 16S (15) (Appendix 1). Trees from all of the additional mitochondrial markers exhibited similar patterns observed in the CR trees, although with varying levels of phylogenetic resolution. All clades that were resolved were consistent with the clades from the CR tree, with varying resolution of the same three clades. None of the mitochondrial markers exhibited consistent differences between *M. dilatata*, *M. flabellata*, and *M. turgescens* (Table 3, Figure 3a-d), which is not surprising given that no differences were observed in the CR tree, and it is among the most rapidly evolving portions of the highly conserved Anthozoan mitochondria. The additional mitochondrial genes provide further support for the three Hawaiian clades of *Montipora*, and they are alignable with outgroup taxa (unlike the CR) which allows for inferences about the order and age of some of the divisions. Less than half of the ITS-2 PCR products were successfully direct sequenced, and exhibited numerous double chromatogram peaks typical of a mixture of several sequence types of variable length. The ITS-2 marker showed differences between individual *M. dilatata* sequences that were greater than differences between *M. flabellata* and *M. turgescens*; however, the tree showed relationships that were generally similar to the mitochondrial trees. Molecular cloning of ITS PCR products is the next logical step to determine if there are fixed species level differences, or differences in frequencies of ITS sequence types among morphospecies. A more detailed analysis of ATBsβ heterozygosity may also offer insights into reproductive potential between morphospecies.

**Table 3** Comparison of polymorphisms between main Hawaiian Island *Montipora* species sampled; v = variable sites, pi = parsimony informative sites, d/f = nucleotide difference between *M. dilatata* and *M. flabellata*, d/t = *M. dilatata* and *M. turgescens*, A/M = nucleotide difference between *Montipora* and *Acropora* (some gene regions were unalignable between genera).

| Gene | Product size | v | pi | d/f | d/t | A/M |
|---|---|---|---|---|---|---|
| mt16S | 790bp | 3 | 3 | 0 | 0 | 11 |
| mt12S | 705bp | ~ | ~ | ~ | ~ | 14 |
| mtATP-6 | 534bp | 4 | 3 | 0-1 | 0-1 | 22 |
| mtCyt-B | 649bp | 3 | 3 | 0 | 0 | 33 |
| mtCox-1 | 609bp | 3 | 2 | 0 | 0 | 31 |
| mtCR | 650bp | 12 | 5 | 0 | 0 | ~ |
| nrITS | 750bp | ~ | ~ | ~ | ~ | ~ |
| nrITS-2 | 290bp | 17 | 11 | 1-7 | 3-6 | ~ |
| nATPsβ | 230bp | 19 | 19 | 0-8 | ~ | ~ |
| nPax-C | 180bp | ~ | ~ | ~ | ~ | ~ |
| nND51a | 443bp | ~ | ~ | ~ | ~ | ~ |

We can conclude that Hawaiian *Montipora* consists of three distinct mitochondrial lineages, and we have identified the putative closest relatives of *M. dilatata* for further work. We can further conclude that if *M. dilatata* is indeed a separate species, it has evolved fairly recently (e.g., within the last million years). Since Anthozoan mitochondrial genes evolve slowly, we have limited power to detect differences in recently diverged species. If we assume that mutations occur in a somewhat regular clock-like fashion, and that *Montipora* and

*Acropora* diverged approximately 54 mya in accordance with the fossil record (Wells 1956), then the rate of mitochondrial evolution is approximately 0.0005bp/$10^6$ years (which also corresponds to the rate estimated for Anthozoan mitochondrial genes in Helberg 2006). Since approximately 3232 bp of mitochondrial DNA was surveyed, we would expect to find only 1.6 mutations for species that have been separated by one million years. Furthermore, the mitochondrial gene regions would yield the following approximate diversification times for the three Hawaiian lineages: 4 mya (COI), 2.9 mya (16S), 3.1 mya (ATP6), 2.2 mya (Cyt-B), and 2.9 mya (ITS-2 assuming a rate of 0.004 bp/$10^6$ years based on Forsman *et al.* 2005). This date roughly coincides with the formation of the main Hawaiian Islands, although it is difficult to speculate on the possible origins of these mitochondrial lineages since members of two of the three clades (including the *M. dilatata* clade) can be found outside of Hawaii (Figure 1a).

**Conclusion**

Until very recently, the study of evolutionary relationships among coral species relied on morphological characters; however, recent genetic evidence has called the validity of morphological-based identification into question (Fukami *et al.* 2004; Fukami *et al*. 2008; Forsman *et al.* in press). In addition to genetics, studies on phenotypic plasticity in corals has revealed that two fragments taken from the same colony can exhibit strikingly different growth forms when grown in a different environments, and the extent of intraspecific variation (polymorphism) in corals is not known (Todd 2008). This is clearly problematic, because incorrect taxonomy results in misidentifications and erroneous statements of population and species distribution, abundance, and conclusions drawn regarding extinction risk. These factors complicate the understanding and management of potentially threatened coral species.

This study represents the first step in determining if *M. dilatata* is a unique species by identifying the likely closely related species for comparison. In addition, this study provides the first insights into genetic differentiation of Hawaiian *Montipora*, indicating that six morphospecies sort into only three mitochondrial lineages. No fixed genetic differences were found between *M. flabellata*, *M. turgescens*, and *M. dilatata*, indicating that they are either closely related (e.g., within one million years), or actively interbreeding. Now that the closest relatives have been identified, future work can examine gene flow between the morphospecies as well as a closer examination of morphological and reproductive characteristics.

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## Figure Legends

**Figure 1**

Neighbor Joining trees of the initial survey of specimens collected from Hawaii and the Phoenix Islands, *M. dilatata* is highlighted in red, bootstrap values below 50% are not shown. **A.** Putative mitochondrial control region (CR), **B.** ATPsβ

**Figure 2**

Neighbor Joining trees of Hawaiian specimens (other geographic regions excluded), *M. dilatata* is highlighted in red, bootstrap values below 50% are not shown. **A.** Putative mitochondrial control region (CR), **B.** ATPsβ, **C.** ATPsβ, with heterozygotes deleted.

**Figure 3**

Neighbor Joining trees of representative Hawaiian specimens for the focused study, *M. dilatata* is highlighted in red, bootstrap values below 50% are not shown. **A.** mitochondrial 16S, **B.** mitochondrial COI, **C.** mitochondrial Cyt-B, **D.** mitochondrial ATP6, **E.** nuclear ribosomal ITS region.

**Appendix 1** Table of sample collection and sequencing information. Check marks indicate successfully sequenced samples. Abbreviations: G.C.= Greg Concepcion, R.H.= Roxanne Haverkort, J.M.= Jim Maragos, Z.F.= Zac Forsman, E.C.= Evelyn Cox, C.H. = Cynthia Hunter, M.T.= Molly Timmers, I.B. = Iliana Baums.

| Code | Species | Location | Collector | CR | ATPsβ | ITS-2 | COI | ATP-6 | Cyt-B | 16S |
|---|---|---|---|---|---|---|---|---|---|---|
| M007 | *M.flabellata* | Lisianski | G.C. | | ✓ | | | | | |
| M008 | *M.flabellata* | Lisianski | G.C. | | ✓ | | | | | |
| M016 | *M.dilatata* | Oahu, Kaneohe bay | C.H. | | ✓ | | | ✓ | | |
| M058 | *M.flabellata* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| M059 | *M.capitata* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| M060 | *M.flabellata* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | | ✓ | | ✓ | ✓ | ✓ |
| M061 | *M.patula* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | | | ✓ | ✓ | ✓ | ✓ |
| M062 | *M.flabellata* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | ✓ | | | | | |
| M063 | *M.patula* | Oahu, Magic Isl. | G.C.;R.H. | ✓ | | | ✓ | ✓ | ✓ | ✓ |
| M065 | *M.patula* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M066 | *M.patula* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ |
| M067 | *M.patula* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M068 | *M.verrilli* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M069 | *M.sp.* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M070 | *M.sp.* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M071 | *M.capitata* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | ✓ | ✓ | ✓ |
| M072 | *M.patula* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M073 | *M.patula* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M074 | *M.verrilli* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M075 | *M.sp.* | Oahu, Lanikai | G.C.;R.H. | ✓ | ✓ | | | | | |
| M076 | *M.flabellata* | Oahu, Kaneohe bay | G.C.;R.H. | ✓ | ✓ | | | | | |
| M077 | *M.flabellata* | Oahu, Kaneohe bay | G.C.;R.H. | ✓ | ✓ | | | | | |
| M078 | *M.flabellata* | Oahu, Kaneohe bay | G.C.;R.H. | ✓ | ✓ | | | | | |
| M079 | *M.sp.* | Oahu, Kaneohe bay | J.S. | ✓ | ✓ | | | | | |
| M080 | *M.dilatata* | Oahu, Kaneohe bay | C.H.;Z.F. | ✓ | ✓ | ✓ | ✓ | | ✓ | ✓ |
| M081 | *M.sp.* | Molokai, Pukoo | C.H.;Z.F. | ✓ | | | | | | |
| M082 | *M.sp.* | Molokai, Pukoo | C.H.;Z.F. | ✓ | | | | | | |
| M083 | *M.flabellata* | Oahu, Kaneohe bay | E.C. | ✓ | ✓ | | | | | |
| M084 | *M.flabellata* | Oahu, Kaneohe bay | E.C. | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ |
| M085 | *M.flabellata* | Oahu, Kaneohe bay | E.C. | ✓ | ✓ | | | | | |
| M086 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| M087 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | ✓ |
| M088 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | ✓ | ✓ | ✓ | ✓ |
| M089 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M090 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M091 | *M.sp.* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M092 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M093 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M094 | *M.verrilli* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |

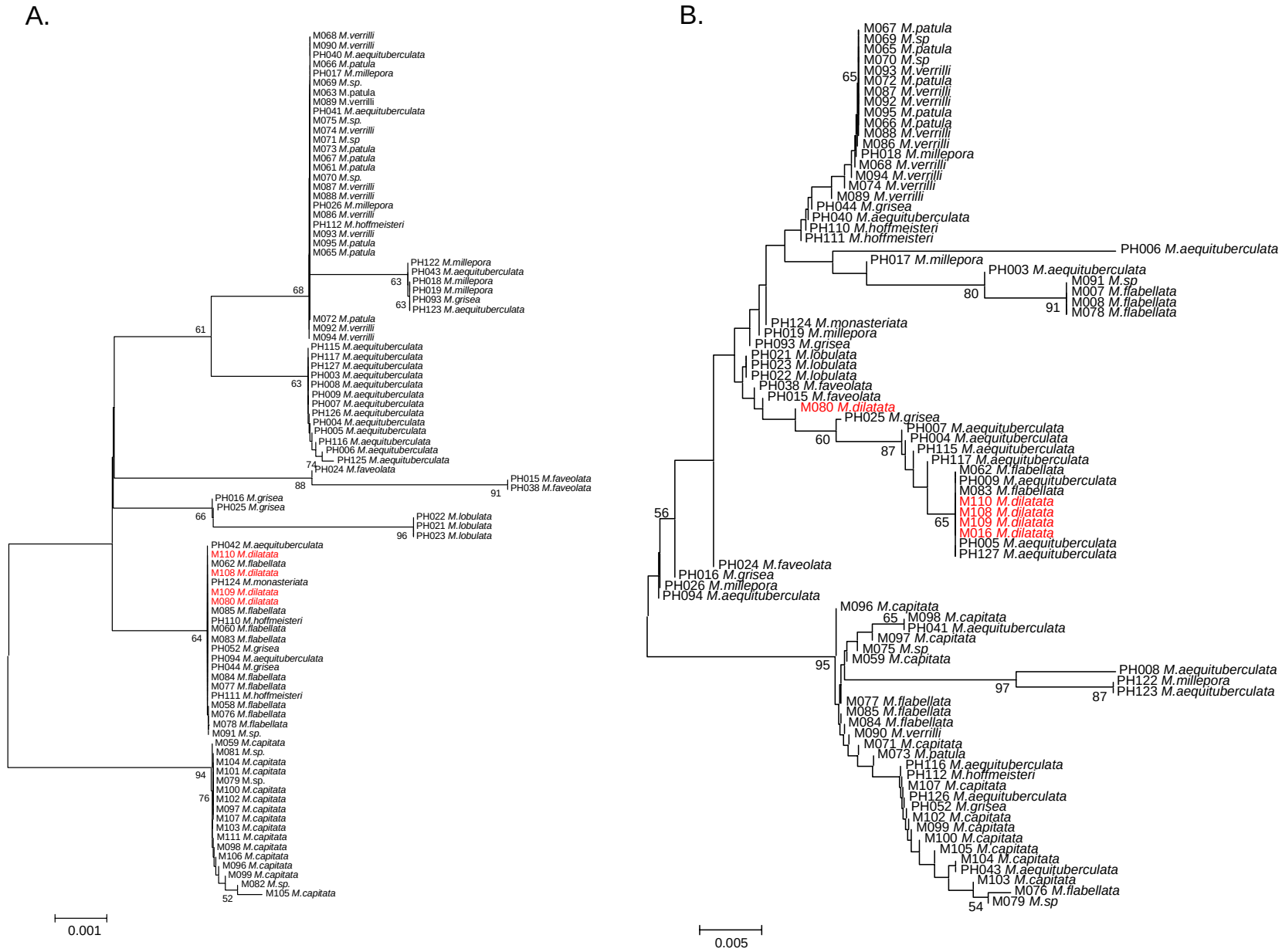
**Appendix 1 cont.**

| Code | Species | Location | Collector | CR | ATPsβ | ITS-2 | COI | ATP-6 | Cyt-B | 16S |
|---|---|---|---|---|---|---|---|---|---|---|
| M095 | *M.patula* | Oahu, Kaneohe bay | C.H.;Z.F.;R.H. | ✓ | ✓ | | | | | |
| M096 | *M.capitata* | Maro Reef, NWHI | I.B. | ✓ | ✓ | | | | | |
| M097 | *M.capitata* | Mare Reef, NWHI | I.B. | ✓ | ✓ | | | | | |
| M098 | *M.capitata* | Maro Reef, NWHI | I.B. | ✓ | ✓ | | | | | |
| M099 | *M.capitata* | Pearl and Hermes, NWHI | G.C. | ✓ | ✓ | | | | | |
| M100 | *M.capitata* | Kure Atoll, NWHI | G.C. | ✓ | ✓ | | | | | |
| M101 | *M.capitata* | Lisianski, NWHI | G.C. | ✓ | | | | | | |
| M102 | *M.capitata* | Lisianski, NWHI | G.C. | ✓ | ✓ | | | | | |
| M103 | *M.capitata* | Lisianski, NWHI | G.C. | ✓ | ✓ | | | | | |
| M104 | *M.capitata* | Pearl and Hermes, NWHI | G.C. | ✓ | ✓ | | | | | |
| M105 | *M.capitata* | Pearl and Hermes, NWHI | G.C. | ✓ | ✓ | | | | | |
| M106 | *M.capitata* | Pearl and Hermes, NWHI | G.C. | ✓ | | | | | | |
| M107 | *M.capitata* | Kure Atoll, NWHI | G.C. | ✓ | ✓ | | | | | |
| M108 | *M.dilatata* | Waikiki Aquarium | G.C. | ✓ | ✓ | ✓ | ✓ | ✓ | ✓ | |
| M109 | *M.dilatata* | Waikiki Aquarium | G.C. | ✓ | ✓ | | | | | |
| M110 | *M.dilatata* | Waikiki Aquarium | G.C. | ✓ | ✓ | | | | | |
| M111 | *M.turgescens* | PHR-26 | M.T. | ✓ | | | ✓ | ✓ | ✓ | ✓ |
| M112 | *M.turgescens* | LIS-10 | M.T. | ✓ | | | ✓ | ✓ | ✓ | ✓ |
| M113 | *M.turgescens* | PHR-31 | M.T. | ✓ | | ✓ | ✓ | ✓ | ✓ | ✓ |
| PH003 | *M.aequituberculata* | Tokelau, Swains | J.M. | ✓ | ✓ | | | | | |
| PH004 | *M.aequituberculata* | Tokelau, Swains | J.M. | ✓ | ✓ | | | | | |
| PH005 | *M.aequituberculata* | Tokelau, Swains | J.M. | ✓ | ✓ | | | | | |
| PH006 | *M.aequituberculata* | Tokelau, Nukunonu | J.M. | ✓ | ✓ | | | | | |
| PH007 | *M.aequituberculata* | Tokelau, Nukunonu | J.M. | ✓ | ✓ | | | | | |
| PH008 | *M.aequituberculata* | Tokelau, Nukunonu | J.M. | ✓ | ✓ | | | | | |
| PH009 | *M.aequituberculata* | Tokelau, Nukunonu | J.M. | ✓ | ✓ | | | | | |
| PH015 | *M.faveolata* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH016 | *M.grisea* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH017 | *M.millepora* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH018 | *M.millepora* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH019 | *M.millepora* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH021 | *M.lobulata* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH022 | *M.lobulata* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH023 | *M.lobulata* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH024 | *M.faveolata* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH025 | *M.grisea* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH026 | *M.millepora* | Phoenix Isl, Orona | J.M. | ✓ | ✓ | | | | | |
| PH038 | *M.faveolata* | Phoenix Isl, Birnie | J.M. | ✓ | ✓ | | | | | |
| PH040 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH041 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH042 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | | | | | | |

**Appendix 1 cont.**

| Code | Species | Location | Collector | CR | ATPsβ | ITS-2 | COI | ATP-6 | Cyt-B | 16S |
|---|---|---|---|---|---|---|---|---|---|---|
| PH043 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH044 | *M.grisea* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH052 | *M.grisea* | Phoenix Isl, Birnie | J.M. | ✓ | ✓ | | | | | |
| PH093 | *M.grisea* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH094 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH110 | *M.hoffmeisteri* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH111 | *M.hoffmeisteri* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH112 | *M.hoffmeisteri* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH115 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH116 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH117 | *M.aequituberculata* | Phoenix Isl, Kanton | J.M. | ✓ | ✓ | | | | | |
| PH122 | *M.millepora* | Phoenix Isl, Baker | J.M. | ✓ | ✓ | | | | | |
| PH123 | *M.aequituberculata* | Phoenix Isl, Baker | J.M. | ✓ | ✓ | | | | | |
| PH124 | *M.monasteriata* | Phoenix Isl, Baker | J.M. | ✓ | ✓ | | | | | |
| PH125 | *M.aequituberculata* | Phoenix Isl, Howland | J.M. | ✓ | | | | | | |
| PH126 | *M.aequituberculata* | Phoenix Isl, Howland | J.M. | ✓ | ✓ | | | | | |
| PH127 | *M.aequituberculata* | Phoenix Isl, Howland | J.M. | ✓ | ✓ | | | | | |

**Figure 1**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M066 M.patula
PH017 M.millepora
M069 M.sp.
M063 M.patula
M089 M.verrilli
PH041 M.aequituberculata
M075 M.sp.
M074 M.verrilli
M071 M.sp
M073 M.patula
M067 M.patula
M061 M.patula
M070 M.sp.
M087 M.verrilli
M088 M.verrilli
PH026 M.millepora
M086 M.verrilli
PH112 M.hoffmeisteri
M093 M.verrilli
M095 M.patula
M065 M.patula
PH122 M.millepora
PH043 M.aequituberculata
PH018 M.millepora
PH019 M.millepora
PH093 M.grisea
PH123 M.aequituberculata
M072 M.patula
M092 M.verrilli
M094 M.verrilli
PH115 M.aequituberculata
PH117 M.aequituberculata
PH127 M.aequituberculata
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PH008 M.aequituberculata
PH009 M.aequituberculata
PH007 M.aequituberculata
PH126 M.aequituberculata
PH004 M.aequituberculata
PH005 M.aequituberculata
PH116 M.aequituberculata
PH006 M.aequituberculata
PH125 M.aequituberculata
PH024 M.faveolata
PH015 M.faveolata
PH038 M.faveolata
PH016 M.grisea
PH025 M.grisea
PH022 M.lobulata
PH021 M.lobulata
PH023 M.lobulata
PH042 M.aequituberculata
M110 M.dilatata
M062 M.flabellata
M108 M.dilatata
PH124 M.monasteriata
M109 M.dilatata
M080 M.dilatata
M085 M.flabellata
PH110 M.hoffmeisteri
M060 M.flabellata
M083 M.flabellata
PH052 M.grisea
PH094 M.aequituberculata
PH044 M.grisea
M084 M.flabellata
M077 M.flabellata
PH111 M.hoffmeisteri
M058 M.flabellata
M076 M.flabellata
M078 M.flabellata
M091 M.sp.
M059 M.capitata
M081 M.sp.
M104 M.capitata
M101 M.capitata
M079 M.sp.
M100 M.capitata
M102 M.capitata
M097 M.capitata
M107 M.capitata
M103 M.capitata
M111 M.capitata
M098 M.capitata
M106 M.capitata
M096 M.capitata
M099 M.capitata
M082 M.sp.
M105 M.capitata
0.001
B.
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M069 M.sp
M065 M.patula
M070 M.sp
M093 M.verrilli
M072 M.patula
M087 M.verrilli
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M066 M.patula
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M086 M.verrilli
PH018 M.millepora
M068 M.verrilli
M094 M.verrilli
M074 M.verrilli
M089 M.verrilli
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PH110 M.hoffmeisteri
PH111 M.hoffmeisteri
PH006 M.aequituberculata
PH017 M.millepora
PH003 M.aequituberculata
M091 M.sp
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M008 M.flabellata
M078 M.flabellata
PH124 M.monasteriata
PH019 M.millepora
PH093 M.grisea
PH021 M.lobulata
PH023 M.lobulata
PH022 M.lobulata
PH038 M.faveolata
PH015 M.faveolata
M080 M.dilatata
PH025 M.grisea
PH007 M.aequituberculata
PH004 M.aequituberculata
PH115 M.aequituberculata
PH117 M.aequituberculata
M062 M.flabellata
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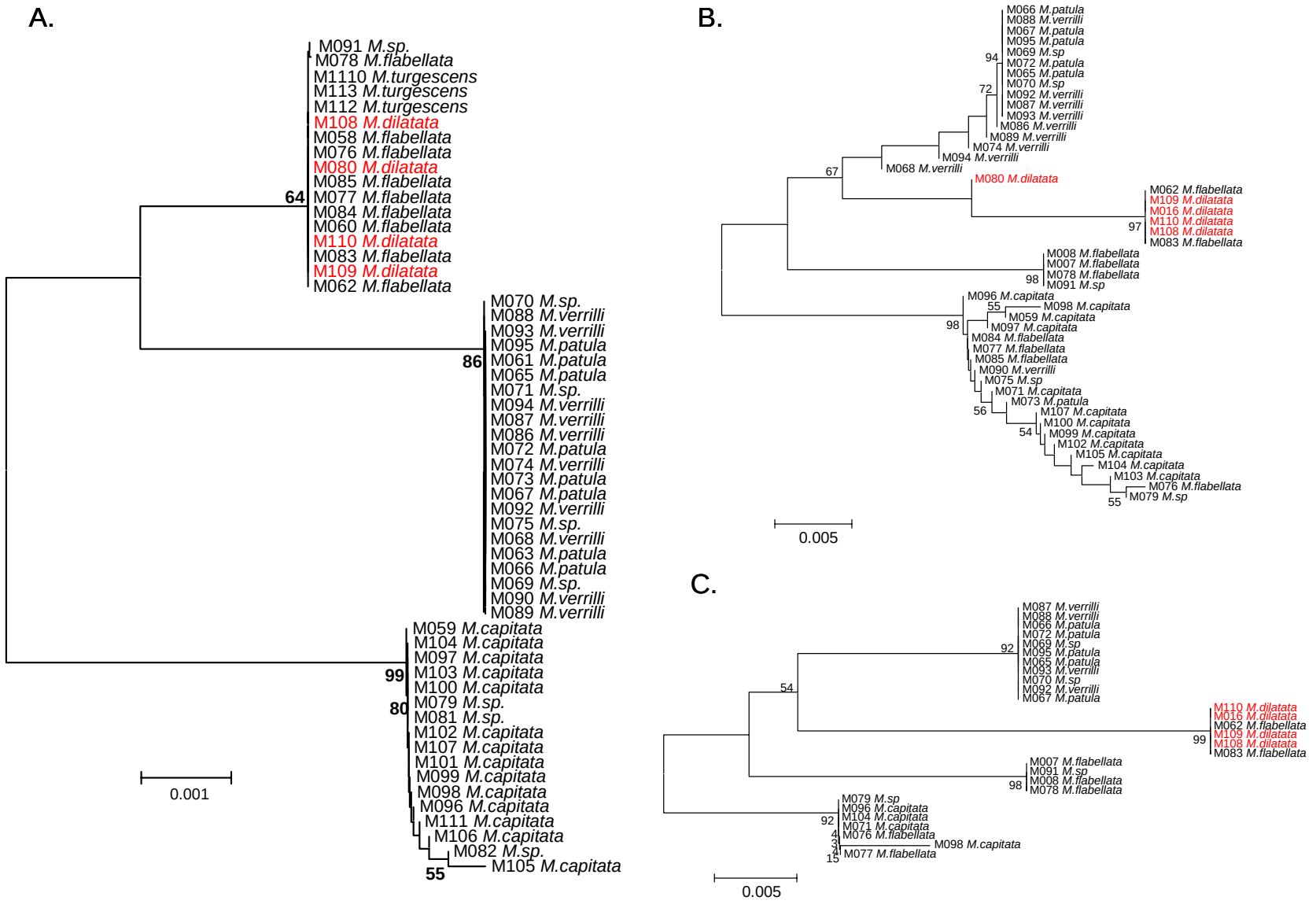
M083 M.flabellata
M110 M.dilatata
M108 M.dilatata
M109 M.dilatata
M016 M.dilatata
PH005 M.aequituberculata
PH127 M.aequituberculata
PH024 M.faveolata
PH016 M.grisea
PH026 M.millepora
PH094 M.aequituberculata
M096 M.capitata
M098 M.capitata
PH041 M.aequituberculata
M097 M.capitata
M075 M.sp
M059 M.capitata
PH008 M.aequituberculata
PH122 M.millepora
PH123 M.aequituberculata
M077 M.flabellata
M085 M.flabellata
M084 M.flabellata
M090 M.verrilli
M071 M.capitata
M073 M.patula
PH116 M.aequituberculata
PH112 M.hoffmeisteri
M107 M.capitata
PH126 M.aequituberculata
PH052 M.grisea
M102 M.capitata
M099 M.capitata
M100 M.capitata
M105 M.capitata
M104 M.capitata
PH043 M.aequituberculata
M103 M.capitata
M076 M.flabellata
M079 M.sp
0.005

**Figure 2**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M113 M.turgescens
M112 M.turgescens
M108 M.dilatata
M058 M.flabellata
M076 M.flabellata
M080 M.dilatata
M085 M.flabellata
64
M077 M.flabellata
M084 M.flabellata
M060 M.flabellata
M110 M.dilatata
M083 M.flabellata
M109 M.dilatata
M062 M.flabellata
M070 M.sp.
M088 M.verrilli
M093 M.verrilli
M095 M.patula
M061 M.patula
M065 M.patula
M071 M.sp.
M094 M.verrilli
M087 M.verrilli
M086 M.verrilli
M072 M.patula
M074 M.verrilli
M073 M.patula
M067 M.patula
M092 M.verrilli
M075 M.sp.
M068 M.verrilli
M063 M.patula
M066 M.patula
M069 M.sp.
M090 M.verrilli
86
M089 M.verrilli
M059 M.capitata
M104 M.capitata
M097 M.capitata
99
M103 M.capitata
M100 M.capitata
80
M079 M.sp.
M081 M.sp.
M102 M.capitata
M107 M.capitata
M101 M.capitata
M099 M.capitata
M098 M.capitata
M096 M.capitata
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M106 M.capitata
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0.001
B.
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M067 M.patula
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M069 M.sp
94
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M065 M.patula
M070 M.sp
72
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M093 M.verrilli
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M089 M.verrilli
M074 M.verrilli
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97
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98
M078 M.flabellata
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55
M098 M.capitata
M059 M.capitata
98
M097 M.capitata
M084 M.flabellata
M077 M.flabellata
M085 M.flabellata
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M075 M.sp
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54
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M076 M.flabellata
55
M079 M.sp
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C.
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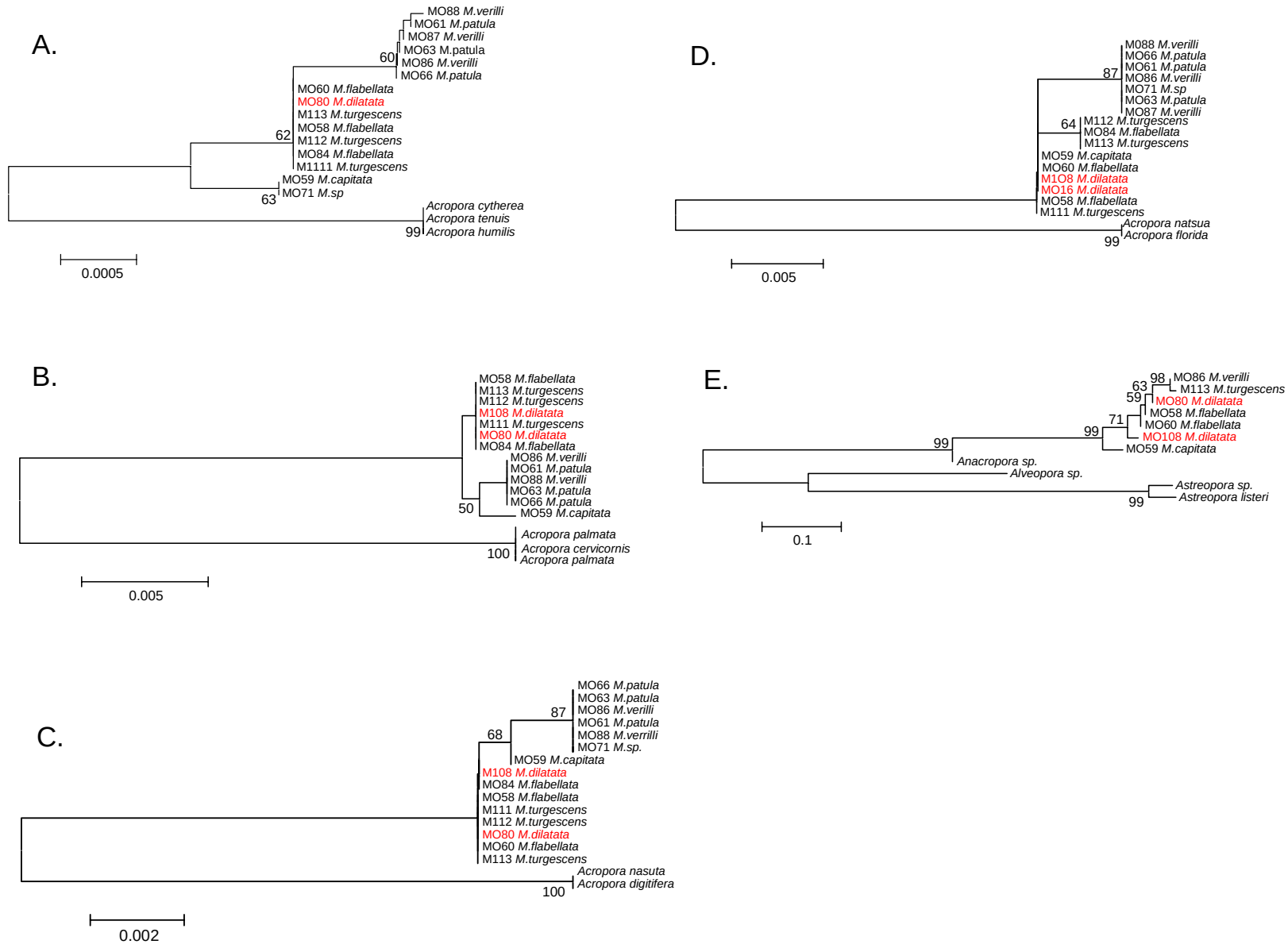
**Figure 3**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MO80 M.dilatata
M113 M.turgescens
MO58 M.flabellata
M112 M.turgescens
MO84 M.flabellata
M1111 M.turgescens
MO59 M.capitata
MO71 M.sp
Acropora cytherea
Acropora tenuis
Acropora humilis
60
62
63
99
0.0005
B.
MO58 M.flabellata
M113 M.turgescens
M112 M.turgescens
M108 M.dilatata
M111 M.turgescens
MO80 M.dilatata
MO84 M.flabellata
MO86 M.verilli
MO61 M.patula
MO88 M.verilli
MO63 M.patula
MO66 M.patula
MO59 M.capitata
Acropora palmata
Acropora cervicornis
Acropora palmata
50
100
0.005
C.
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MO63 M.patula
MO86 M.verilli
MO61 M.patula
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MO59 M.capitata
M108 M.dilatata
MO84 M.flabellata
MO58 M.flabellata
M111 M.turgescens
M112 M.turgescens
MO80 M.dilatata
MO60 M.flabellata
M113 M.turgescens
Acropora nasuta
Acropora digitifera
87
68
100
0.002
D.
M088 M.verilli
MO66 M.patula
MO61 M.patula
MO86 M.verilli
MO71 M.sp
MO63 M.patula
MO87 M.verilli
M112 M.turgescens
MO84 M.flabellata
M113 M.turgescens
MO59 M.capitata
MO60 M.flabellata
M1O8 M.dilatata
MO16 M.dilatata
MO58 M.flabellata
M111 M.turgescens
Acropora natsua
Acropora florida
87
64
99
0.005
E.
MO86 M.verilli
M113 M.turgescens
MO80 M.dilatata
MO58 M.flabellata
MO60 M.flabellata
MO108 M.dilatata
MO59 M.capitata
Anacropora sp.
Alveopora sp.
Astreopora sp.
Astreopora listeri
98
63
59
71
99
99
99
0.1