

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

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Forsman, Z.H., E.C. Johnston, A.J. Brooks, T.C. Adam, and R.J. Toonen. 2013. Genetic evidence for regional isolation of *Pocillopora* corals from Moorea. *Oceanography* 26(3):153–155, <http://dx.doi.org/10.5670/oceanog.2013.58>.

DOI

<http://dx.doi.org/10.5670/oceanog.2013.58>

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Genetic Evidence for Regional Isolation of *Pocillopora* Corals from Moorea

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Pocillopora is one of the most abundant and widely distributed coral genera, with a geographic range spanning the entire tropical Pacific and Indian Oceans as well as the Red Sea and Arabian Gulf. Across this enormous geographic range, *Pocillopora* is a major reef builder (second in importance and abundance only to *Acropora*) that can dominate a wide variety of habitats, including marginal environments occupied by only a few other coral genera. Despite the ecological importance of this genus, species boundaries remain poorly understood. Species identification is extremely challenging in many corals, and *Pocillopora* is often cited as a prime example. Around 40 species in the genus have been named, while approximately 14 are considered valid and one (*P. elegans*) is currently under consideration for protection under the US Endangered Species Act. However, the evaluation and conservation of coral species remains problematic due to taxonomic uncertainty (Brainard et al., 2011). The genus consists mostly of fast-growing “weedy species” that are highly susceptible to mortality from bleaching and predation, and, due to past patterns of regional extinction, are considered to

be highly vulnerable (Van Woesik et al., 2012). *P. damicornis* is widely used as a model organism for research (a “lab rat”) because it is abundant, fast growing, and some varieties in some geographic regions brood planular (ciliated, free-swimming) larvae (Schmidt-Roach et al., 2012b). Several recent genetic studies have confirmed cryptic lineages (Flot et al., 2010; Pinzón and LaJeunesse, 2010; Souter, 2010; Schmidt-Roach et al., 2012a,b; Marti-Puig et al., in press), and a recent range-wide phylogeographic survey indicated that several genetic groups have highly limited geographic distributions (Pinzón et al., 2013).

Here, we place *Pocillopora* from the Moorea Coral Reef Long Term Ecological Research (MCR LTER) site

into a broad phylogeographic context by comparing new mitochondrial data with all known studies published as of June 2013 (Figure 1). There are clear biogeographical patterns that emerge within the genus *Pocillopora*. Samples from the MCR LTER site are genetically diverse, and several genetically distinct groups are unique to Moorea (Figure 1) when compared to the greater Pacific locations sampled thus far. Several haplotypes have a highly restricted geographic distribution (e.g., 1b, 6a, 6b, 3h, 9, 10, 11 in Figure 1). Other haplotypes occur over a broad geographic range (e.g., 1a, 3a, 4, 5 in Figure 1), although these ranges are still significantly smaller than reported ranges based on morphological species descriptions. For example, the nominal

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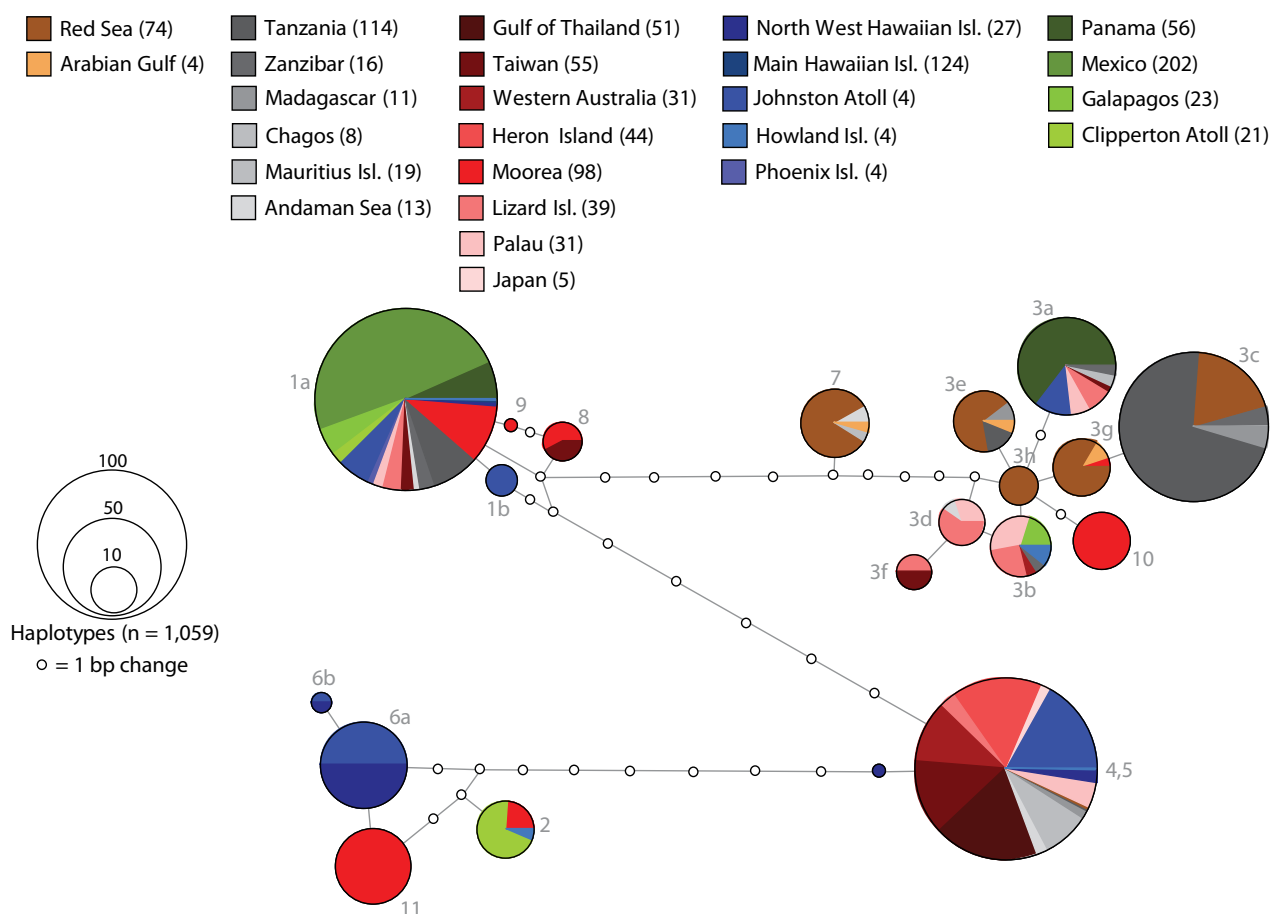


Figure 1. Haplotype network of a 209bp fragment of the mitochondrial ORF gene across the geographic range of *Pocillopora*. Nomenclature for clades follows Pinzón et al. (2013), with clades 9, 10, and 11 unique to Moorea (added by this study). The photos are all representative voucher images from clade 6a, illustrating the range of morphological variation possible within each distinct genetic group. Most coral genera have uninformative mitochondrial markers, with extremely low levels of polymorphism, but the highly polymorphic mitochondrial ORF gene is a unique feature of Pocilloporidae (Flot and Tillier, 2007). Thus, we focus on this single marker because (1) it has been widely used and highly informative in *Pocillopora*, and (2) previous studies have found the marker to resolve more genetic groups (higher phylogenetic resolution) but still be concordant with other markers (Flot et al., 2010; Pinzón and Lajeunesse, 2010; Souter, 2010; Schmidt-Roach et al., 2012a,b; Marti-Puig et al., in press; Pinzón et al., 2013). Photo credits: James E Maragos and Frank Stanton. GenBank accession numbers KF381328-30

taxa “*P. damicornis*” and “*P. verrucosa*” are reported to occur across the entire Pacific and Indian Oceans (Veron and Stafford-Smith, 2000), but none of the genetic variants are found across this entire range (Figure 1).

During the past few years, genetic

studies have rapidly proliferated and challenged the understanding of species boundaries within this genus. Accumulating evidence now indicates that the range of phenotypic variation within each mitochondrial group of *Pocillopora* is underappreciated. For


example, clades 4 and 5 consist predominantly of colonies identified in the field as “*P. damicornis*”; however, this morphological variety has been identified (or misidentified) across most clades. Several clades exhibit a surprisingly wide range of morphological variation

(Figure 1). Phenotypic plasticity can have many underlying causes (reviewed by Todd, 2008), yet within a given geographic area, consistent and recognizable species of *Pocillopora* are often observed side by side in the same habitat; therefore, phenotypic and geographic variation in the context of coral genotype are fertile grounds for future work.

Genetic studies in general have resulted in rapid upheaval in coral taxonomy and systematics, and they are challenging longstanding paradigms based on skeletal morphology (reviewed by Stat et al., 2012). As a widely used experimental organism, *Pocillopora* is among the best studied of coral groups, yet much work remains to more accurately map patterns of biodiversity in this and other coral genera. Cryptic diversity and regional diversification were also recently discovered in *Stylophora pistillata*, another well-studied coral in the family Pocilloporidae (Keshavmurthy et al., 2013). Moorean *Pocillopora* corals are genetically diverse, but with a high proportion of sequence types that were sampled nowhere else. These results are consistent with reduced gene flow and high local retention (outlined by Leichter et al., 2013, in this issue). Even in this well-studied system, new discoveries are challenging the prevailing views of coral species boundaries, biodiversity, evolution, and ecology. Coral species boundaries and biogeography are increasingly important for understanding the past, present, and uncertain future of coral reefs in the face of biodiversity loss.

ACKNOWLEDGEMENTS

This work was supported by National Science Foundation grants OCE 1026851 and OCE 1236905, as well as by the

Gordon and Betty Moore Foundation. It represents a contribution of the NSF LTER Program's Moorea Coral Reef LTER site. This work was additionally supported by the University of Hawaii NSF EPSCoR program (Investing in Multidisciplinary University Activities, EPS-0903833, J. Gaines, PI) in support of the core functional genomics facility at the Hawaii Institute of Marine Biology, SOEST, University of Hawaii at Manoa. ZHF was supported by a fellowship from NOAA National Marine Sanctuaries Partnership MOA#2005-008/66882. This is HIMB contribution number 1558 and SOEST contribution number 8965. 

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