



Short Communication

Novel organization of the mitochondrial genome in the deep-sea coral, *Madrepora oculata* (Hexacorallia, Scleractinia, Oculinidae) and its taxonomic implicationsMei-Fang Lin^{a,c,g}, Marcelo Visentini Kitahara^b, Hiroyuki Tachikawa^d, Hironobu Fukami^e, David John Miller^{c,g}, Chaolun Allen Chen^{a,f,h,*}^a Biodiversity Research Center, Academia Sinica, Nangang, Taipei 115, Taiwan^b Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião 11600-970, Brazil^c School of Pharmacy and Molecular Sciences, James Cook University, Townsville 4810, Australia^d Natural History Museum and Institute, Chiba 955-2, Japan^e Department of Marine Biology and Environmental Science, University of Miyazaki, Miyazaki 889-2192, Japan^f Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan^g ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville 4810, Australia^h Taiwan International Graduate Program (TIGP)-Biodiversity, Academia Sinica, Nangang, Taipei 115, Taiwan

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ABSTRACT

Madrepora is one of the most ecologically important genera of reef-building scleractinians in the deep sea, occurring from tropical to high-latitude regions. Despite this, the taxonomic affinities and relationships within the genus *Madrepora* remain unclear. To clarify these issues, we sequenced the mitochondrial (mt) genome of the most widespread *Madrepora* species, *M. oculata*, and compared this with data for other scleractinians. The architecture of the *M. oculata* mt genome was very similar to that of other scleractinians, except for a novel gene rearrangement affecting only *cox2* and *cox3*. This pattern of gene organization was common to four geographically distinct *M. oculata* individuals as well as the congeneric species *M. minutiseptum*, but was not shared by other genera that are closely related on the basis of *cox1* sequence analysis nor other oculinids, suggesting that it might be unique to *Madrepora*.

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1. Introduction

Almost half of extant scleractinians are azooxanthellate (i.e. live without dinoflagellate symbionts) and are often referred to as cold- or deep-water corals because they generally occur in waters deeper than 50 m (Cairns et al., 1999; Cairns, 2007). Although less obvious than the shallow water coral reefs of tropical waters, the deep sea reefs constructed by some azooxanthellate scleractinians serve as habitat, feeding, recruitment, and nursery grounds for numerous marine organisms (Roberts et al., 2009) and have recently attracted the attention of both the scientific community and the general public, particularly the fishing industry. However, relatively few deep-water scleractinians – representatives of the genera *Lophelia*, *Solenosmilia*, *Goniocorella*, *Madrepora*, *Oculina*, and *Enallopsammia* – are considered to fulfill the ecological and geological criteria of true reef-building species (Stolarski and Vertino, 2007; Roberts et al., 2009).

Of the deep-sea reef-builders, *Madrepora* has a fossil record dating from the Lower Cretaceous (ca. 70 Mya; Stolarski and Vertino,

2007), and comprises five recent species (Cairns, 2009). *M. oculata* is the type species and is probably the most-widespread scleractinian species, being essentially ubiquitous in deep water except in the polar seas (Cairns and Zibrowius, 1997). *M. oculata* is highly polymorphic, six forms being recognized (*alpha*, *beta*, *gamma*, *galapagensis*, *vitiae*, and *formosa*; Cairns, 1991, 1995; Cairns et al., 1999) based on variations in color, branching patterns, the texture of the coenosteum and the size of septa; however, note that these characters are variable even within sympatric specimens (e.g., Galápagos specimens; Cairns, 1991).

Although traditionally classified in the Family Oculinidae (Cairns et al., 1999; Cairns, 2009), recent molecular phylogenetic analyses suggest that the family is polyphyletic (representatives were scattered across four different clades, these most likely representing four different families; Kitahara et al., 2010), and that the genus *Madrepora* should be elevated to a higher taxonomic level (Le Goff-Vitry et al., 2004; Kitahara et al., 2010). Molecular phylogenetics based on partial *cox1* data suggests that *Madrepora oculata* may be more closely related to *Caryophyllia* (family Caryophylliidae) and pocilloporids than to other oculinids (Kitahara et al., 2010; Stolarski et al., 2011).

Comparison of mitochondrial (mt) genomes has contributed to the clarification of phylogenetic relationships among animals (Boore,

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1999; van Oppen et al., 2002; Chen et al., 2008a,b), gene arrangement has been generally the most informative mt character (reviewed in Boore et al., 2005). Several well-established evolutionary lineages are defined by common organization of mt genes (reviewed in Boore and Brown, 1998) and unique arrangements distinguish subgroups within nematodes, mollusks (reviewed in Boore and Brown (1998)) and cnidarians (Hexacorallia; Beagley et al., 1998; Medina et al., 2006; Brugler and France, 2007). In terms of mt gene order, many scleractinians conform to a consensus first reported in *Acropora tenuis* (van Oppen et al., 2002; see Fig. 2A upper). Within the Scleractinia, only one example of apparent gene reorganization is known – the case of *Lophelia pertusa* (Emblem et al., 2011; see Fig. 2A lower) – but a number of minor variations have also been

reported, each with important phylogenetic implications. These variations include the presence of an idiosyncratic *atp8* in *Seriatopora* and a duplicated *trnW* in some pocilloporids (Chen et al., 2008b), the insertion of a distinct group I intron in the *cox1* gene of some “robust” corals (Fukami et al., 2007) and the extended 3'-end found of the *cox1* gene of *Euphyllia* (Lin et al., 2011).

To clarify the phylogenetic status of *Madrepora*, the complete mt genome of *M. oculata* was sequenced, revealing a novel gene rearrangement that constitutes only the second known deviation from the scleractinian consensus. This pattern of mt genome organization appears to be common across *Madrepora*, but is not shared by genera that are closely related on the basis of *cox1* data (i.e. pocilloporids and some caryophyllids) or other

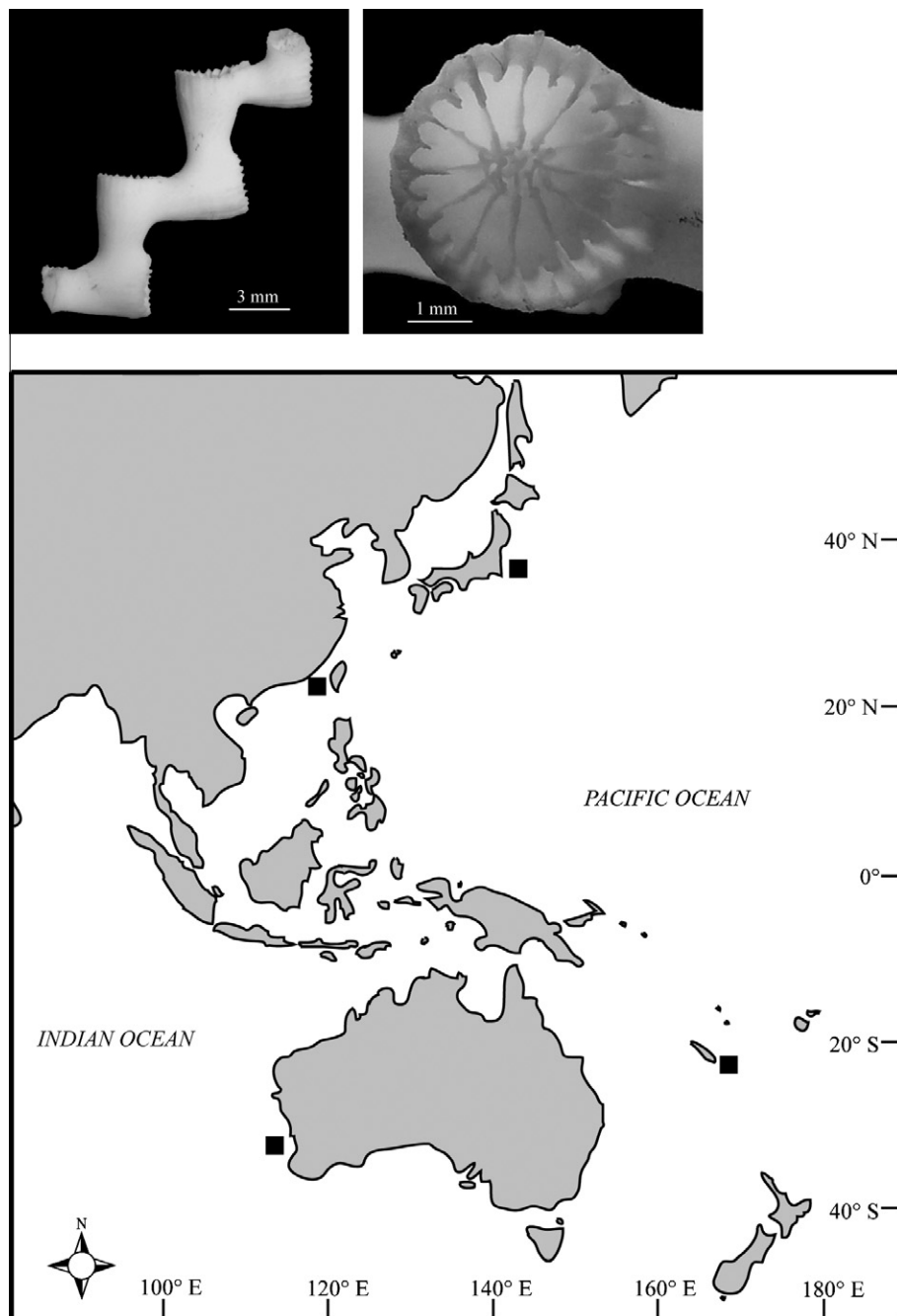


Fig. 1. *Madrepora oculata* branch fragment and calicular views of the specimen used for determination of the complete sequence of the mitochondrial genome, and the sampling locations examined in this study. Collection sites are indicated by solid black squares.

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