



## Original article

Characterization of the complete mitochondrial genome of *Diploastrea heliopora* and phylogeny of the scleractinia species which have group I introns in their COI genesJianguang Xiao<sup>a</sup>, Peng Tian<sup>a</sup>, Feng Guo<sup>a</sup>, Shuanggen Yu<sup>b</sup>, Wei Wang<sup>a</sup>, Xiaolei Wang<sup>a</sup>, Wentao Niu<sup>a,\*</sup><sup>a</sup> Laboratory of Marine Biology and Ecology, Third Institute of Oceanography, Ministry of Natural Resources, Xiamen 361005, China<sup>b</sup> Fisheries College, Ocean University of China, Qingdao 266003, China

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## ABSTRACT

Mitochondrial genome DNA is a powerful marker for resolving phylogenetic relationships among scleractinian corals. Here, we decode the complete mitochondrial genome of *Diploastrea heliopora* (Lamarck, 1816) for the first time. The general features are 18 363 bp in length, and conventionally, with 13 protein coding genes, two ribosomal RNAs, and two transfer RNAs. Gene arrangement and distribution are similar to other scleractinian corals. Moreover, the COI gene of *D. heliopora* is broken up into two parts by a complex group I intron. This intron is 1076 bases in length and contains helical structures (P1-P10, except P2) and four conserved regions (P, Q, R, and S). The mitochondrial genome of *D. heliopora* has asymmetric base composition (13.03% C, 20.29% G, 25.91% A, and 40.77% for T). Based on concatenated protein coding genes, ML and BI trees show similar phylogenetic relationship: *D. heliopora* clustered closely with *Sclerophyllia maxima* and *Echinophyllia aspera* into the robust branch. The data and conclusion in this study are reference for further phylogenetic studies of corals.

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## 1. Introduction

One main study discipline of mitochondrial DNA (mtDNA) is molecular evolution. Based on the excellent characters, e.g., maternal inherited, independent extranuclear genetic code, brief molecule structure, and slow evolutionary rate, mtDNA is usually used in genetic diversity analyses and phylogenetic studies. The mitochondrial genomes of Anthozoa are atypical with a few distinguishing characteristics. It is manifested in the presence of conventional two tRNAs; All protein-coding genes (PCGs) stop the protein biosynthesis process with complete termination codons (Fukami and Knowlton, 2005; Niu et al., 2020); A DNA mismatch repair mechanism benefiting from the slow mutation rates (Shearer et al., 2002); The relatively loose gene packing, featured by a series of noncoding regions (Kitahara et al., 2014); And group

I introns interrupting functional genes (Beagley et al., 1998; Emblem et al., 2011).

Group I introns are ribozymes (catalytic RNAs), and they can catalyze self-splicing from the mRNA, tRNA and rRNA precursors (Emblem et al., 2011). In general, the core secondary structure of a typical group I intron consists of 10 conserved paired regions (P1-P10) and a series of peripheral elements (Nielsen and Johansen, 2009). The core structure is organized into three helical stacks, including the substrate domain (P1, P2, P10), the catalytic domain (P3, P7-P9), and the scaffold domain (P4-P6) (Vicens and Cech, 2006). A putative Goddard-Burt cyclical model (Goddard and Burt, 1999), indicates that group I intron is not a fixed element. Group I introns undergo a recurrent evolutionary feature of gain and loss, and sometimes get new functions when they insert again (Nielsen and Johansen, 2009). At present, two different transfer mechanisms (both vertical and horizontal) have been suggested for explaining the embedded process of introns (Fukami et al., 2007; Emblem et al., 2011). It has a sporadic distribution throughout the metazoans, a few of mitochondrial genes of scleractinian corals are interrupted by group I introns.

In all coral species analyzed to date, the ND5 gene of mitogenome is interrupted by an obligatory group I intron at position 717, and a few of other functional genes embed in (Nielsen and Johansen, 2009; Lin et al., 2014). It's not a coincidence but we

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are still oblivious to its biological functions. Moreover, some coral species have another kind of group I intron in their COI gene. This type of group I intron can cut double-stranded DNA at specific recognition sites by coding mega nuclease or more often known as homing endonuclease. It performs an entirely different function from restriction enzyme, homing endonuclease facilitates horizontal transmit of genetic elements within a host (Dujon, 1989; Belfort and Roberts, 1997). Previous study summarized the COI group I intron in 13 genera of scleractinian corals, and divided them into four types by the insertion site, sequence length, and sequence similarity. The possible sources of COI group I introns were discussed, but little description on the biological roles (Fukami et al., 2007).

*Diploastrea heliopora* (Lamarck, 1816), was initially assigned to the family Diploastraeidae Chevalier and Beauvais (1987). However, Veron (2000) put this species into the family Faviidae Milne Edwards & Haime, 1857, based on Wells' (1956) skeletal taxonomy. Until recently, Diploastraeidae was revived according to a morphology-based phylogenetic analyses (Budd et al., 2012). It is widely distributed in the Indo-Pacific Ocean (Veron, 2000). It is easy to recognize according to the following characteristics: colonies dome-shaped, surface even, skeleton dense, columellae large, corallites plocoid, and septa equal. The colonies of *D. heliopora* can even grow up to 7 m in diameter and 2 m high. The color of *D. heliopora* usually uniform cream or grey, and sometimes greenish (Veron, 1986, 2000).

The group I introns of *D. heliopora* were described by Fukami et al. (2007). It was different from the COI introns of other coral species but similar to the COI intron of sponge *Tetilla* sp. The COI intron of *D. heliopora* belonged to the type 1 and this type could also be found in *Blastomussa wellsii*, *Oxypora lacera*, etc. The phylogenetic relationships based on the COI genes and the COI group I introns were similar, with *D. heliopora* embed in the ancestral clade. This hypothesis was supported by a succession of phylogenetic researches based on different gene combinations (Huang et al., 2011, 2014a, 2014b). This suggests that *Diploastrea* species may regain the COI group I intron after losing the original intron.

In this study, we report the structural characterization of the whole mitogenome and the COI group I intron of *D. heliopora*. Moreover, we reestablish the phylogeny based on the mitogenomes and COI group I introns of scleractinian corals and other hexacorals. It is hoped that the mitogenome of *D. heliopora* and relationships of scleractinian corals which have group I introns in their COI genes could be well clarified. This is a very significant study that will hopefully lead to the development of genetic researches of Scleractinia in the future.

## 2. Materials and methods

### 2.1. Sampling and taxonomic identification

The *D. heliopora* colony fragment used for complete mitochondrial genome sequencing was collected from Meiji Reef, Sansha, Hainan Province, China, in May 2018. All underwater morphological and color characteristics of *D. heliopora* are identical with the original description (Fig. 1A) (Lamarck, 1816). Skeletal morphology (Fig. 1B) and microscopic inspection (Fig. 1C) are in accordance with the published taxonomic descriptions (Veron, 1986, 2000).

### 2.2. General procedure for DNA extraction, amplification, and sequencing

Coral tissue was ground with mortar and pestle, then use DNeasy Blood & Tissue Kit (Qiagen China, Shanghai) for DNA rapid extraction. Thirty-two pairs of primers were designed to seg-



**Fig. 1.** Underwater photo in situ and skeleton features of *Diploastrea heliopora*. (A) the color of colonies is greenish, domed colonies is nearly 0.5 m across; (B) plocoid corallites and large columellae; (C) septa are equally and are thick at the wall and thin where joining the columellae, Scale bar represents 2 mm.

mented polymerase chain reaction (PCR) amplification (Table S1). PCR reaction mixture was totally 25  $\mu$ L, including template DNA 1  $\mu$ L, primers (forward and reverse) 2  $\mu$ L, dNTPs 2  $\mu$ L, *Taq* DNA polymerase 0.15  $\mu$ L, buffer solution 2.5  $\mu$ L, and sterile deionized water. The Eppendorf thermal cycler was used for PCR amplification following the standard procedures performed in Niu et al. (2020). The amplified products were purified and bidirectional sequenced in Personal Biotech. Co. Ltd. (Qingdao, China).

### 2.3. Mitochondrial genome annotation and analyses

After we received the raw data, the target sequences were then pieced and assembled using software package programs from DNASTAR Inc. Firstly, we did a preliminary annotation referring to the results of software MITOS (Bernt et al., 2013), and finally annotated by other reported scleractinian species. We used the program ARWEN to detect the tRNA genes of *D. heliopora*, and tRNAscan-SE 2.0 was used to construct the cloverleaf secondary structures (Laslett and Canback, 2008; Lowe and Chan, 2016). MEGA 6.0 was used to analysis of nucleotide bias and codon usage (Tamura et al., 2013).

In this study, COI group I intron of *D. heliopora* was identified by the scaffolding domain, catalytic domain, substrate domain and conserved regions (P, Q, R, and S) based on existing research results (Fukami et al., 2007). Open reading frame (ORF) was identified and translated in the software package program from DNASTAR Inc. The secondary structure of COI group I intron was hand-drawn diagram according to predicting outcome using the online software RNAstructure Web Server (Reuter and Mathews, 2010).

### 2.4. Phylogenetic analyses

Phylogenetic topology was constructed based on 13 tandem mitogenome PCG sequences and COI group I introns of 16 Scleractinia species and 6 other hexacorals species (Table 1). There were different best-fitting models for different genes, which obtained from the scientific application jModelTest 2 (Darriba et al., 2012) (Table S2). To locate the phylogenetic position of *D. heliopora*, we performed two different phylogenetic trees including a Bayesian inference (BI) phylogenetic tree by MrBayes 3.12 under the Markov chain Monte Carlo sampling method, and a maximum likelihood (ML) estimation to estimate the parameters of a probability distribution by PAUP\* 4.0 (Huelsenbeck and Ronquist, 2001; Swofford, 2002). In ML tree, values on nodes represented support rates using 1 000 bootstraps. In BI analysis, three heated chains and one cold chain were set as: ngen 10 000 000 generations, samplefreq 1 000 samples, printfreq default 10 000. Set sump burnin 2500 (25% of ngen / samplefreq), and finally the 50% majority-rule con-

**Table 1**  
Species for phylogenetic analyses in this study.

Species	Family	Length	GenBank accession number
<b>Scleractinia</b>			
<i>Diploastrea heliopora</i>	Diploastraeidae	18363	MT560600
<i>Dendrophyllia arbuscula</i>	Dendrophylliidae	19069	NC_027590
<i>Tubastraea coccinea</i>	Dendrophylliidae	19070	NC_026025
<i>Turbinaria peltata</i>	Dendrophylliidae	18966	NC_024671
<i>Echinophyllia aspera</i>	Lobophylliidae	17697	NC_040169
<i>Sclerophyllia maxima</i>	Lobophylliidae	18168	FO904931
<i>Fungiacyathus stephanus</i>	Fungiacyathidae	19381	NC_015640
<i>Goniopora columna</i>	Poritidae	18766	NC_015643
<i>Goniopora djiboutiensis</i>	Poritidae	18765	NC_045931
<i>Porites fontanesii</i>	Poritidae	18658	NC_037434
<i>Porites harrisoni</i>	Poritidae	18630	NC_037435
<i>Porites lutea</i>	Poritidae	18646	NC_029695
<i>Porites porites</i>	Poritidae	18648	NC_008166
<i>Porites sverdrupi</i>	Poritidae	18628	KU956960
<i>Pseudosiderastrea formosa</i>	Siderastreidae	19475	NC_026530
<i>Siderastrea radians</i>	Siderastreidae	19387	NC_008167
Actiniaria			
<i>Anthopleura midori</i>	Actiniidae	20039	NC_030274
Antipatharia			
<i>Myriopathes japonica</i>	Myriopathidae	17733	NC_027667
Corallimorpharia			
<i>Corynactis californica</i>	Corallimorphidae	20715	NC_027102
<i>Corallimorphus profundus</i>	Corallimorphidae	20488	KP938440
<i>Ricordea yuma</i>	Ricordeidae	22015	NC_027106
Zoantharia			
<i>Savalia savaglia</i>	Parazoanthidae	20764	DQ825686

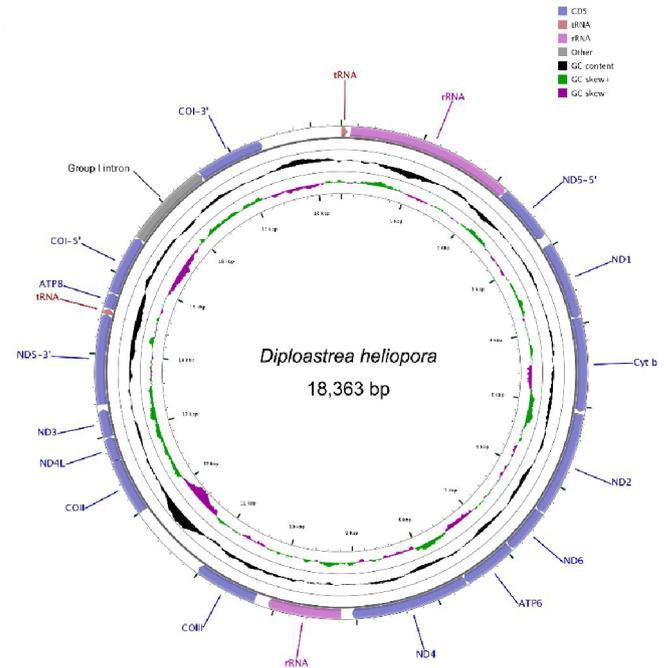
sensus tree was obtained. In BI tree, values on nodes represented support rates and over 70% were shown.

### 3. Results and discussion

#### 3.1. General characteristic

The complete mitogenome sequence of *D. heliopora* was a 18,363 bp circular molecule including 13 PCGs, 2 ribosomal RNA subunits, and 2 transfer RNA genes (Fig. 2, Table 2). It had been uploaded into the GenBank database with the authorization number MT560600. The general characteristic including gene arrangement and gene distribution was consistent with other species in Scleractinia (van Oppen et al., 2002). Moreover, the mitogenome of *D. heliopora* obtained in the present study also had a group I intron in COI gene, which observed sporadically in some complex and robust scleractinians (Fukami et al., 2007). The ND5 gene was broken into two parts by a group I intron and 11 genes embedded in (Fig. 2).

The mitochondrial genome of *D. heliopora* had asymmetric base composition (13.03% C, 20.29% G, 25.91% A, and 40.77% for T). The G + C content (33.32%) was distinctly lower than the A + T content (66.68%). According to different organizations, the A + T content was 67.48% in 13 PCGs, 68.47% in rRNA genes, 55.63% in tRNA genes, and 64.68% in COI group I intron, respectively. The mitochondrial genomes of hexacorallians and other metazoans had obvious AT-bias and negative C-bias on base composition (Perseke et al., 2010). This trait had resulted in a reduction in the DNA repair systems of scleractinian corals (Kitahara et al., 2014). Only five overlaps were identified and totally 24 bp in length. Thirteen intergenic sequences, which ranged from 1 to 1 076 bp, were identified. The longest intergenic sequence interrupted the COI



**Fig. 2.** Gene map of the complete mitochondrial genome for *Diploastrea heliopora* in the present study.

gene and included a group I intron. It was precisely due to the intergenic sequences that caused the difference in the length of scleractinian mitogenomes.

#### 3.2. Protein-coding genes

All PCGs were connected in series one by one up, and totally 11 751 bp in length. As the common initiation codons, ATG triggered polypeptide and protein synthesis of most PCGs, except ND2 gene, which started with the initiation codons ATA. All PCG's terminated the polypeptide chain by conventional stop codons TAA and TAG (Table 2). All 13 PCGs of *D. heliopora* comprised 3,904 codons, leucine (15.50%) had the highest percentage of amino acids and cysteine (0.01%) had the lowest (Fig. 3). In general, the species of Scleractinia, especially those "Robust" clade species, showed a strong bias to codons ending with thymine (Kitahara et al., 2014).

#### 3.3. Ribosomal and transfer RNA genes

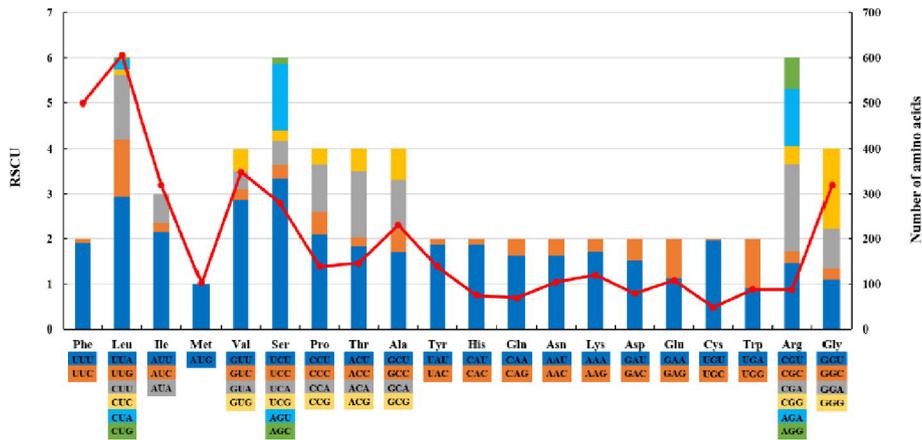
Two ribosomal RNA subunits were identified including 12S rRNA and 16S rRNA in *D. heliopora*, which were 901 bp and 2 045 bp in length, respectively. There were only two transfer RNAs in the mitogenome sequence. The cloverleaf structures of them were in accordance with the typical structure of other corals (Fig. 4). The length and structure characteristics of ribosomal and transfer RNA genes of *D. heliopora* accorded with the ordinary laws of other published scleractinian corals (Flot and Tillier, 2007; Capel et al., 2016).

#### 3.4. Group I intron in COI gene

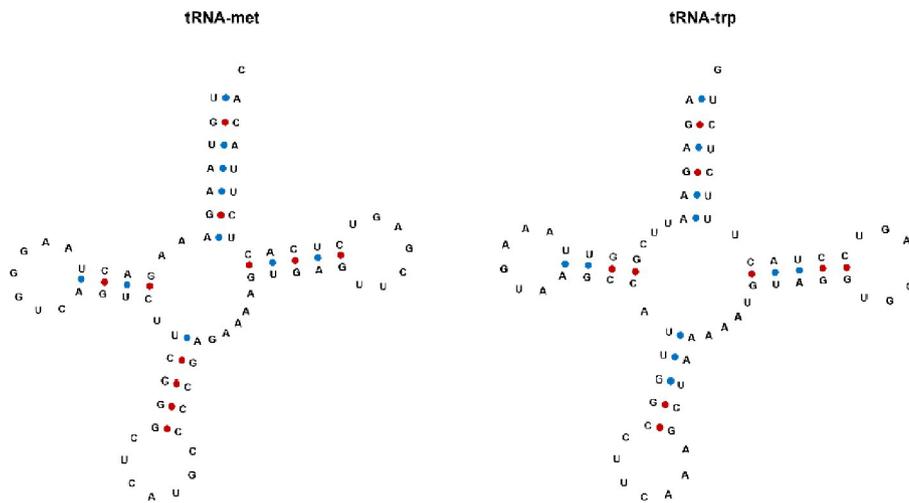
The COI group I intron of *D. heliopora* was 1 076 bases in length and contained helical elements (P1-P10, except P2) and four conserved regions P, Q, R, and S (Fig. 5). This result was consistent with previous results of *D. heliopora* as Fukami introduced (Fukami et al., 2007). The ORF in the COI intron extended from P5 to P9 and encoded 310 amino acids. But in contrast to Fukami's description

**Table 2**  
General features of mitochondrial genome of *Diploastrea heliophora*.

Gene	Position		Length	Anticodon	Codon		Intergenic nucleotides	Strand
	From	To			Start	Stop		
tRNA <sup>Met</sup>	1	72	72	UAC			977	H
16S rRNA	111	2155	2045				38	H
ND5 5'	2156	2866	711		ATG		0	H
ND1	2975	3922	948		ATG	TAG	108	H
Cyt <i>b</i>	3925	5064	1140		ATG	TAA	2	H
ND2	5090	6376	1287		ATA	TAA	25	H
ND6	6378	6938	561		ATG	TAA	1	H
ATP6	6938	7615	678		ATG	TAA	-1	H
ND4	7615	9054	1440		ATG	TAG	-1	H
12S rRNA	9186	10086	901				131	H
COIII	10246	11025	780		ATG	TAA	159	H
COII	11996	12703	708		ATG	TAG	970	H
ND4L	12685	12984	300		ATG	TAA	-19	H
ND3	12987	13328	342		ATG	TAA	2	H
ND5 3'	13385	14488	1104			TAG	56	H
tRNA <sup>Trp</sup>	14487	14556	70	ACU			-2	H
ATP8	14560	14757	198		ATG	TAA	3	H
COI 5'	14757	15485	729		ATG		-1	H
COI 3'	16562	17386	825			TAA	1076	H



**Fig. 3.** RSCU (Relative Synonymous Codon Usage) and number of amino acids of mitochondrial genome for *Diploastrea heliophora* in the present study. The x-axis and left-y-axis were for histogram, the right-y-axis was for frequency polygon.



**Fig. 4.** Putative secondary structures of two tRNAs of *Diploastrea heliophora* in the present study.

“type 1 has a start codon at positions 58–60”, the ORF of COI group I intron of *D. heliophora* in the present study had a start codon at positions 49. This ORF included a signature sequence, the homing

endonucleases containing the LAGLI-DADG element of this type of COI group I intron played an important role in the gene transposition (Dalggaard et al., 1997).

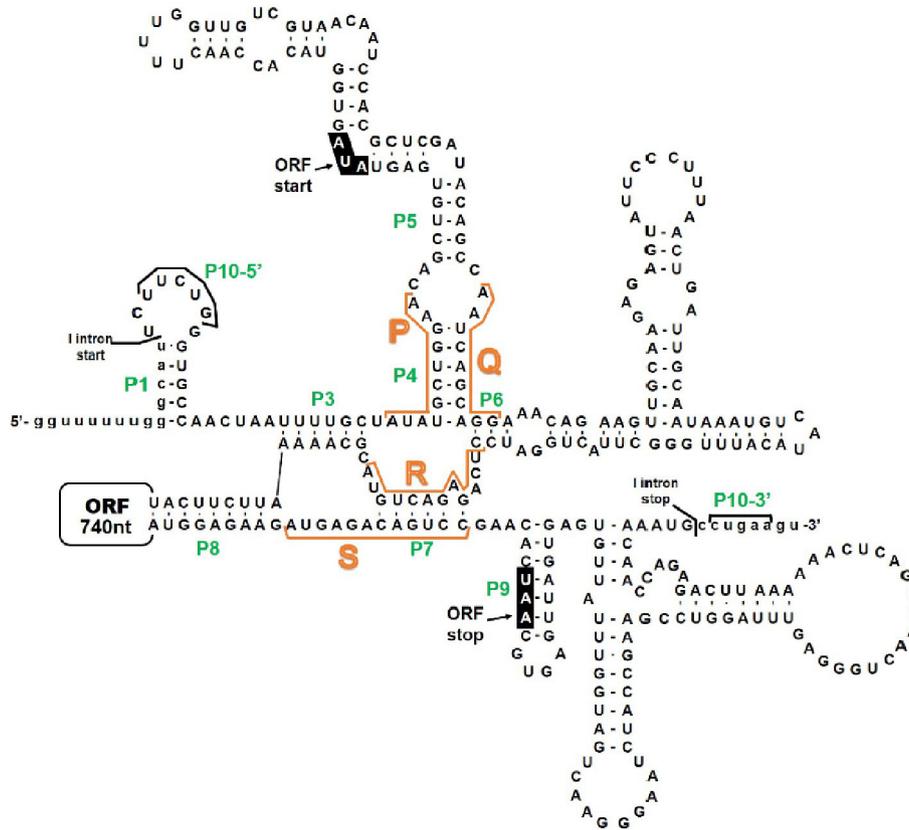


Fig. 5. Secondary structure model for the COI group I intron of *Diploastrea heliophora*.

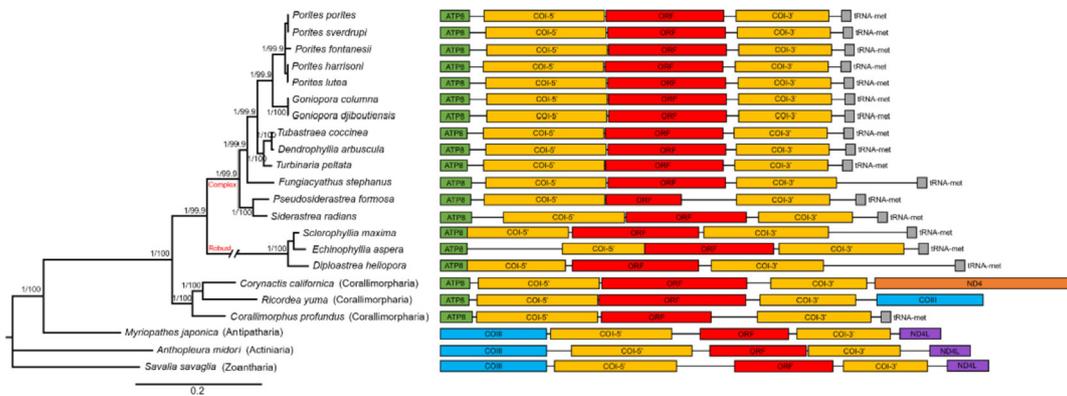


Fig. 6. BI and ML phylogenetic trees in the present study. The structure and gene arrangement of COI group I introns and adjacent genes are presented on the right.

COI group I introns was always under dispute. Whether vertical inheritance (acquire their introns from a common ancestor) or horizontal transfer (acquired their introns from surrounding fungi, sponges, and endosymbiotic dinoflagellate algae), all were short of credible evidence (Fukami et al., 2007). What is certain, though, is that the *Diploastrea* regain the COI group I intron after losing the original intron. Moreover, the high appearing frequency of introns in the corals may be related to the very slow rates of molecular evolution of anthozoan mitochondrial genomes (Fukami et al., 2007).

### 3.5. Phylogenetic analyses

Excepting the newly sequenced mitogenomes of *D. heliophora*, we also downloaded sequences of other 15 scleractinian corals

and 6 other hexacorals from GenBank for reconstructing phylogenetic BI and ML trees (Table 1). The two phylogenetic trees were almost identical: *D. heliophora* clustered closely with the robust species *Sclerophyllia maxima* and *Echinophyllia aspera* (Fig. 6). Antipatharia and Zoantharia species clustered into the ancestral clade. Moreover, we presented the COI group I introns and adjacent genes of these species. The structure and gene arrangement of Scleractinia were concordant comparing with the outgroup taxa. The BI tree basing on the COI intron sequences had come up with similar results (Fig. S1), but with an exception of *Savalia savaglia*, who clustered closely with the robust scleractinian clade. On all accounts, the complete mitochondrial genomes can provide more accurate phylogenetic information and an inspiration for modern taxonomy among scleractinian corals.

## 4. Conclusions

In this study, the results presented the detailed description of the complete mitogenome of *D. heliopora* (Scleractinia: Diploastraeidae), and particularly, we described the characteristics of COI group I intron of this widely-distributed species. In the mitogenome, gene arrangement and composition and general properties of PCGs, ribosomal and transfer RNA genes were consistent with other scleractinian corals. The COI group I intron of *D. heliopora* was identical to the intron as Fukami et al. (2007) introduced. The phylogenetic analysis indicated that *D. heliopora* clustered closely with *Sclerophyllia maxima* and *Echinophyllia aspera* into the robust branch. The mitogenome data and the phylogenetic relationships of *D. heliopora* provided a reference outline for further research.

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## Ethical approval

No animal testing was performed during this study.

## Sampling and field studies

All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities. The study is compliant with CBD and Nagoya protocols.

## Data availability

Genetic sequence data generated in this study were deposited in GenBank with Accession Number MT560600. All other data generated or analyzed during this study are included in this published article and its supplementary information files. **Fig. S1**: Bayesian inference (BI) tree inferred from the COI intron sequences of 16 Scleractinia species and six other hexacorals outgroup taxa. The numbers at the nodes showed the Bayesian posterior probabilities.

## Author Contribution Statement

JX and WN conceived and designed research. PT, FG and SY conducted experiments. WW and XW contributed to the field sampling. JX and PT extracted and analyzed the data. JX and WN wrote the manuscript. All authors read and approved the manuscript.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.sjbs.2021.07.086>.

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