Chapter

Mitochondrial Group I Introns in Hexacorals Are Regulatory Genetic Elements

Steinar Daae Johansen and Åse Emblem

Abstract

Hexacoral mitochondrial genomes are highly economically organized and vertebrate-like in size, structure, and gene content. A hallmark, however, is the presence of group I introns interrupting essential oxidative phosphorylation (OxPhos) genes. Two genes, encoding NADH dehydrogenase subunit 5 (ND5) and cytochrome c oxidase subunit I (COI), are interrupted with introns. The ND5 intron, located at position 717, is obligatory in all hexacoral specimens investigated. The ND5-717 intron is a giant-sized intron that carries several canonical OxPhos genes. Different modes of splicing appear to apply for the ND5-717 intron, including conventional cis-splicing, backsplicing, and trans-splicing. Three distinct versions of hexacoral COI introns are noted at genic positions 884, 867, and 720. The COI introns are of the mobile-type, carrying homing endonuclease genes (HEGs). Some COI-884 intron HEGs are highly expressed as in-frame COI exon fusions, while the expression of COI-867 intron HEGs appear repressed. We discuss biological roles of hexacoral mitochondrial ND5 and COI introns and suggest that the ND5-717 intron has gained new regulatory functions beyond self-splicing.

Keywords: backsplicing, colonial anemone, mitochondrial genome, mtDNA, mushroom corals, sea anemone, stony corals

1. Introduction

Hexacorallia (hexacorals) represents an ecological important subclass of Anthozoa with about 4300 extant nematocyst-bearing species [1]. Well-known hexacoral orders include Actinaria (sea anemones), Zoantharia (colonial anemones), Scleractinia (stony corals), Corallimorpharia (mushroom corals), and Antipatharia (black corals). Ceriantharia (tube anemones) was previously considered to be a hexacoral order, but recent studies suggest tube anemones to represent a distinct subclass of Anthozoa [2].

Hexacorals have a global marine distribution pattern typically recognized in tropical seas at shallow waters living in close relationships with endosymbiotic photosynthetic alga. However, coral reefs and sea anemones in deep offshore waters have more recently been investigated [3–6]. These cold-water hexacorals occur in low temperatures at high latitudes or great depths. Among the approximately 1500 stony coral species known, 50% are located in cold-water habitats [7, 8]. A common
feature among cold-water deep-sea hexacorals is that they are non-endosymbiotic in respect to the photosynthetic alga.

Mitochondria are essential organelles of animal cells, involved in processes like cell metabolism, cell signaling, and cell death [9, 10]. Hexacorals, like all other animals, contain mitochondrial genomes (mtDNAs) encoding a subset (approximately 1%) of the gene products involved in mitochondrial structure and function [11]. Complete mtDNA sequences have been determined from approximately 200 hexacoral specimens representing 133 species and 51 families from sea anemones, colonial anemones, stony corals, mushroom corals, and black corals (Appendix Table 1). In general, hexacoral mitochondrial genomes are vertebrate-like in size (17–22 kb), structure, and coding capacity (Figure 1A). The circular and economically organized mtDNA encodes the same set of 2 ribosomal RNAs and 13 hydrophobic proteins involved in the oxidative phosphorylation (OxPhos) system [11]. However, noncanonical and optional mitochondrial genes may occur in some hexacoral species [11–16]. More unusual features, however, are the highly reduced tRNA gene repertoire (only 1–2 tRNA genes) and the presence of complex group I introns [11, 17–20].

Group I introns are intervening sequences interrupting functional genes in eukaryotic (mitochondrial, chloroplast, nuclear, viral) and prokaryotic (eubacterial, archaeal, phage) genomes [21]. Like other mobile genetic elements, horizontal transfer of a group I intron can affect the host by altering the function of surrounding genes, potentially interrupting vital processes but also creating diversity and beneficial alterations. Mitochondrial group I introns in metazoans are rare and restricted to some orders within the basal phyla of Placozoa, Porifera, and Cnidaria [11, 22]. Unlike spliceosomal introns, which are abundant in the nuclear genome of eukaryotes, group I introns encode catalytic RNAs (ribozymes) with the unique

![Figure 1. Mitochondrial genome and group I intron.](image)

(A) Circular map presenting gene content and organization of the sea anemone Urticina eques mtDNA. The mitochondrial genome harbors 14 protein coding genes, 2 rRNA genes, and 2 tRNA genes. All genes are encoded by the same DNA strand. The tRNA genes M and W (tRNA^{Met} and tRNA^{Thr}) are indicated by the standard one-letter symbols for amino acids; SSU and LSU, mitochondrial small- and large-subunit rRNA genes; ND1–6, NADH dehydrogenase subunit 1–6 genes; COI–III, cytochrome c oxidase subunit I–III genes; Cyb, cytochrome b gene; ATP6 and 8, ATPase subunit 6 and 8 genes; and HEG, homing endonuclease gene. The ND5–717 and CO–884 introns are indicated. Photo: SD Johansen. (B) A general diagram of group I ribozyme secondary and tertiary structure, according to the representation by [23]. The nine conserved secondary structure paired segments of the catalytic core (P1–P9) are shown, and the three tertiary domains (scaffold, substrate, catalytic) are indicated by blue, yellow, and green boxes, respectively. Essential nucleotide positions in P2 (U, G), P7 (G, C), and P9 (G) are indicated in red. 5', upstream exon sequence; 3', downstream exon sequence.
ability to self-splice as naked RNA. These introns sometimes even code for homing endonucleases, giving additional mobility to the ribozymes. The intron RNA processing reaction is catalyzed by the ribozyme, which folds into at least nine conserved paired segments (P1–P9), further organized into hallmark helical stacks named the catalytic domain, the substrate domain, and the scaffold domain (Figure 1B) [23–25]. Group I intron sequences are removed from precursor transcripts in a guanosine-dependent two-step transesterification reaction, leading to exon ligation and intron excision [21].

This chapter reviews recent developments in the characterization of hexacoral mitochondrial genomes with a focus on gene organization and rearrangements, complex obligatory group I introns in the NADH dehydrogenase subunit 5 (ND5) gene, and mobile-type group I introns in the cytochrome c oxidase subunit I (COI) gene.

2. Mitochondrial gene organization and expression in hexacorals

Five common features in the gene organization can be drawn from the 200 available mitochondrial genome sequences representing all five hexacoral orders (Appendix Table 1). (1) The 13 annotated OxPhos genes encode the same set of proteins as in vertebrate mtDNA [26], representing Complex I (ND1, 2, 3, 4, 4 L, 6, and 6), Complex III (CytB), Complex IV (COI, II, and III), and Complex V (ATPases 6 and 8). The additional approximately 70 OxPhos proteins are nuclear encoded [27]. (2) All canonical mitochondrial genes (OxPhos genes, rRNA, and tRNA genes) are encoded by the same DNA strand. (3) The tRNA gene repertoire is highly reduced, corresponding to tRNA^{fMet} and tRNA^{Trp} in sea anemones, stony corals, mushroom corals, and black corals, and only tRNA^{fMet} in colonial anemones [14, 28, 29]. This indicates extensive tRNA import into mitochondria [20]. (4) The ND5 gene is split into two exons at nucleotide position 717 (human ND5 gene numbering [19]) by a group I intron found in all hexacorals studied so far (see Section 3 below). (5) The mitochondrial gene synteny appears highly conserved within, but not between, different hexacoral orders.

2.1 Order-specific gene organization

Each hexacoral order harbors a closely related primary mitochondrial gene organization (Figure 2A). This is an interesting notion since the orders have been separated from each other for 100 million years or more [28]. Stony corals and mushroom corals share some mtDNA synteny [28, 30], and similarly, some segments of synteny appear conserved between sea anemones, colonial anemones, and black corals [30]. The only mitochondrial gene synteny common to all species in all five orders is the upstream proximity of the tRNA^{fMet} gene to the large-subunit (LSU) rRNA gene (Figure 2). This suggests co-expression similar to that of tRNA^{Val} and LSU rRNA genes in vertebrate mitochondria [26]. Recent studies in human and rat conclude that the mitochondrial encoded tRNA^{Val} has replaced the 5S rRNA and become an integrated component as a structural rRNA of the mitochondrial ribosome [31]. Thus, tRNA^{fMet} is considered as an interesting candidate for a similar dual function in hexacorals.

Deviations from the primary order arrangements have been reported in some sea anemones, stony corals, and mushroom corals and apparently confined to non-endosymbiotic deep-water species. Among the stony corals (Figure 2B), Madrepora has a rearrangement in the COII and COIII gene order, and Lophelia and Solenosmilia have a more dramatic rearrangement involving three genes (CytB, ND2, and ND6) [19, 32]. The latter example involves a dramatic shift in the size of
the ND5-717 intron from approximately 10 kb (primary arrangement) to 6 kb (see Section 3.1 about transfers of OxPhos genes into the intron). Two different deviations were noted in the mushroom corals *Corallimorphus* and *Corynactis* [30]. These rearrangements appear complex and involve a drastic size reduction of the ND5-717 intron from approximately 18 kb (primary arrangement) to 12 kb and 10 kb, respectively (Figure 2B).
The most dramatic mitochondrial genome rearrangement is seen in the deep-water sea anemone Protanthea [16]. Here, the 21 kb mtDNA is arranged along two circular mitochondrial chromosomes, MCh-I and MCh-II (Figure 2C). The mitochondrial gene order is heavily scrambled compared to the primary sea anemone arrangement. Different from all other hexacorals, genes at MCh-I are coded on both DNA strands. The ND5-717 intron size was increased from approximately 2 kb (primary sea anemone arrangement) to 15 kb in Protanthea (Appendix Table 1). Interestingly, the smaller MCh-II encodes the mitochondrial COII and one allele of the small subunit (SSU) rRNA. Phylogenetic analysis indicates that MCh-II is horizontally transferred into Protanthea from a distantly related sea anemone [16]. Not all deep-water hexacorals have mtDNA rearrangements. The Relicanthus sea anemone, sampled at a depth of 2500 m, [4] harbors the primary arrangement [33]. Similarly, Bolocera specimen samples at 40 m (Atlantic Ocean) [12] and at 1100 m (Pacific Ocean) [5] contain the same primary sea anemone arrangement.

2.2 Mitochondrial RNA in hexacorals

Mitochondrial RNAs have been investigated in a few hexacoral species representing sea anemones, colonial anemones, and mushroom corals [6, 12, 14–16]. RNAseq data were obtained from 454 pyrosequencing and Ion Torrent PGM sequencing. Several general features are noted: (1) ribosomal RNA constituted more than 90% of the reads and is found to be at least 10–20 times more abundant than most OxPhos gene transcripts; (2) all the conventional genes were transcribed, and the Complex IV OxPhos genes appeared most expressed; (3) group I introns were perfectly spliced out from ND5 and COI mRNA precursors; (4) COI-884 intron splicing appeared more efficient than that of the ND5-717 intron, suggesting intron retention of ND5 mRNA [16]; and (5) noncanonical mitochondrial genes, such as the intron-encoded HEG and non-annotated open reading frames (ORFs), were clearly expressed. One of these ORFs, corresponding to a 306-amino-acid unknown protein in the mushroom coral Amplexidiscus, was highly expressed and located at the opposite strand compared to canonical OxPhos genes [16].

3. An obligatory group I intron in the ND5 gene

All hexacoral mitochondrial genomes harbor ND5-717 introns (Appendix Table 1), making this group I intron an obligatory feature. Evolutionary analyses of ND5-717 introns have previously been performed and show a strict vertical inheritance pattern and a fungal origin [19]. Homologous group I introns at the ND5 insertion site 717 are frequently noted in the fungi Ascomycota, Basidiomycota, and Zygomycota [34], which include mobile-type versions with HEGs [35, 36]. This supports an ancient transfer with a subsequent progression into an obligatory strict vertical inherited intron. Interestingly, HEG-containing ND5-717 was also reported in the mitochondrial genome of choanoflagellates, species considered as the animal ancestors [37].

3.1 The ND5-717 intron is a giant group I intron

Phylogenetic analysis supports the early version of hexacoral ND5-717 introns to harbor two OxPhos genes (ND1 and ND3) in P8 [19]. This ancient organization is represented by sea anemones, colonial anemones, and black corals (Figure 2A). Insertions of ORFs into loop regions are a common feature in group I introns, and engulfing these compulsory genes might be a strategy for the intron in becoming
essential to the host genome. RNA secondary structure folding of the ND5-717 ribozyme reveals that the catalytically important ωG (last nucleotide of the intron) is replaced by ωA (Figure 3). This replacement is likely to have a dramatic effect on intron biology, leading to host-factor dependent splicing and inhibition of 3’ hydrolysis-dependent intron RNA circularization [38].

In some hexacoral orders, mitochondrial genome rearrangements resulted in additional transfers of canonical genes into the P8 segment. In stony corals two versions of 6 and 11 genes are intron-located (Figure 2A and B). Furthermore, it was noted that robust-clade species have developed a highly compact ribozyme core compared to complex-clade species (and all other hexacorals) [19]. The most complex ND5-717 introns are found in mushroom corals and in the Protanthea sea anemone [6, 16, 28, 30]. Whereas three versions of 9, 11, and 15 intron-located genes are noted in mushroom corals, 14 genes are present in P8 of Protanthea (Figure 2B and C). The ND5-717 intron in mushroom corals represent the largest group I intron known to date with an approximate size of 19 kb.

Figure 3.
Structure diagram of Urticina eques ND5-717 group I intron. Conserved helical segments (P1–P10) are indicated, and flanking ND5 exon sequences are shown in lowercase letters. The three helical stacks, named scaffold domain, substrate domain, and catalytic domain, are indicated by blue, yellow, and green boxes, respectively. The last nucleotide of the intron (ω), which is considered as a universally conserved guanosine (ωG) in group I intron, is ωA in hexacoral ND5-717 introns (red circle). The P8 segment harbors the two OxPhos genes ND1 and ND3.
3.2 Unconventional splicing of ND5-717 introns

Mitochondrial RNA sequencing reveals perfectly ligated ND5 mRNA exons in sea anemones [12, 15], colonial anemones [14], and mushroom corals [16], which support a biological splicing activity of ND5-717 introns. In the mushroom corals *Ricordea* and *Amplexodiscus*, the splicing efficiency of the ND5-717 intron was reported to be about 10% of that of the COI-884 intron located in the same mitochondrial genome [16]. The complex ND5-717 intron contains 2–15 mitochondrial genes within P8 that challenges its mode of splicing. The shortest forms of ND5-717 introns (approximately 1.6–2.4 kb) detected in sea anemones, colonial anemones, and black corals are likely to be excised by conventional group I intron *cis*-splicing from one single precursor RNA (Figure 4A).

![Diagram of ND5-717 intron splicing modes](image)

**Figure 4.** Different modes of ND5-717 intron splicing. A schematic group I ribozyme (Rz717; green box) is indicated above each precursor map, and ligated ND5 mRNA is shown below. Splice sites (5' SS and 3' SS), initiation codons (AUG/GUG), and stop codons (UAA) are indicated. (A) Cis-splicing performed from a single precursor RNA where both ND5 exons are in a conventional order (exon 1-exon 2). (B) Backsplicing performed from a single precursor RNA where both ND5 exons are in a non-conventional order (exon 2-exon 1). (C) Trans-splicing performed from two separate precursor RNAs, each containing one ND5 exon.

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DOI: http://dx.doi.org/10.5772/intechopen.91465
The longest forms of ND5-717 introns (approximately 15–19 kb), present in mushroom corals [28, 30] and the deep-water Protanthea sea anemone [6], contain almost the entire mitochondrial genome within P8. Recently, experimental support of intron removal by backsplicing in mushroom corals was reported [16]. It was found that the primary ND5 transcript contains a permuted exon arrangement where exon 2 is followed by exon 1 (Figure 4B). Correct ND5 exon ligation was achieved by involving a circular exon-containing RNA intermediate, which is a hallmark of intron backsplicing [16]. This is the first example of a natural group I intron removed by backsplicing and may explain why some hexacorals tolerate giant ND5-717 group I introns.

How the ND5-717 introns in stony corals are removed from their precursors by splicing is currently not known. These introns (sizes from approximately 6–12 kb) [19, 39] may be too large and complex to be removed by conventional cis-splicing, and the ND5 exons may be too distant apart for backsplicing. Thus, a more plausible alternative is trans-splicing that generates a ligated ND5 mRNA from two separate precursor RNAs (Figure 4C). An interesting notion is that group I intron trans-splicing has been reported in mitochondrial transcripts of placozoan animals [40].

4. Mobile-type group I introns in the COI gene

The gene encoding COI is a frequent host of group I introns in hexacoral mitochondrial genomes. Of the total 133 species inspected (Appendix Table 1), about 50% harbor an intron insertion. COI introns are present in all five hexacoral orders, but at different distribution patterns.

4.1 Three different insertion sites in the COI gene

The COI gene is interrupted by group I introns at three genic positions, where each intron site represents a unique evolutionary history [14, 41]. The intron insertion sites correspond to positions 720, 867, and 884 (human COI gene numbering [19]). The COI-884 introns are widespread in hexacorals, present in most investigated species of sea anemones, mushroom corals, and black corals, as well as a few stony corals (Appendix Table 1) [12, 41, 42]. Colonial anemones harbor COI-867 introns [14], and some Indo-Pacific stony coral species contain COI-720 introns [41, 43]. It appears that hexacorals are infected at least three times by COI introns or that this mitochondrial gene is subjected to recurrent group I intron invasion and extinction.

COI introns at different insertion sites are distinct in their ribozyme secondary structure, exemplified by the Urticina sea anemone and Zoanthus colonial anemone introns COI-884 and COI-867, respectively (Figure 5A and B). A common feature, however, is the large insertion within helical segment P8 harboring a HEG that codes for a homing endonuclease of the LAGLIDADG family. These HEGs extend beyond P8 and into the ribozyme domains [12, 14, 15, 43]. Thus, COI-720, COI-867, and COI-884 intron sequences possess dual coding potentials of catalytic RNAs and homing endonucleases. This integration of the endonuclease into the ribozyme core structure ties the two elements closer together, making the endonuclease less prone to degradation.

4.2 Expression of intron-encoded homing endonucleases

Mobile-type introns, like the hexacoral mitochondrial COI introns, promote homing into cognate intron-less alleles by gene conversion [44, 45]. Intron homing
is initiated by a DNA double-strand break catalyzed by the intron-encoded homing endonuclease. Expression of HEGs has been studied in COI introns of sea anemones, colonial anemones, and mushroom corals [12, 14–16]. Two main versions were noted, leading to either highly expressed or repressed HEGs (Figure 5C). (1) The most successful mode of expression is the in-frame COI-HEG fusion strategy. The HEG, which covers most of the intron sequences (including the ribozyme encoded parts), is fused in-frame with the 5′ COI exon. Highly expressed in-frame HEGs are observed in the sea anemones Urticina and Bolocera [12], and similar in-frame organizations appear common in other sea anemones such as Isosicyonis, Phymanthus, Actinia, and Stichodactyla ([15, 46, 47]; our unpublished results). A COI fusion strategy for intron HEG expression in mitochondria, however, is not unique to sea anemones since several fungi are using this approach [44, 48]. (2) Truncated in-frame fusions or freestanding intron HEGs result in
significant lower expressions. This is observed for COI-884 introns of *Hormathia* and *Anemonia* sea anemones [12, 15], COI-884 introns of mushroom corals [16], and COI-867 introns of colonial anemones [14].

5. Concluding remarks

A hallmark of hexacoral mitochondrial genomes is the presence of self-catalytic group I introns. What is the biological role of these mitochondrial introns—are they purely selfish genetic elements, or could they have gained new regulatory functions beyond self-splicing? Current knowledge suggests a fungal origin of the hexacoral introns [19, 34, 49]. The group I introns in the COI gene encode LAGLIDADG-type homing endonucleases, consistent with intron mobility between cognate intron-less alleles [12, 45]. The hexacoral COI introns appear gained and lost in multiple cycles during the last 0.5 billion years [42], which supports a selfish intron behavior.

The ND5-717 intron is apparently obligatory in hexacoral mitochondrial genomes, making this genetic element an interesting candidate in gene regulation. Similar obligatory group I introns have been noted in the chloroplast tRNA^{Leu} gene of all green plants and in the nuclear LSU rRNA gene of all Physarales myxomycetes [50, 51]. These obligatory mitochondrial, chloroplast, and nuclear introns are considered domesticated group I introns that may have gained new host-specific functions beyond self-splicing [21, 25]. The mitochondrial ND5 mRNA stability has a key role in respiratory control in higher animals; it is tightly regulated and contains m1A base modification [52–54]. Intron retention of ND5 mRNA was recently reported in mushroom corals [16], suggesting possible host regulatory functions in hexacorals. Thus, further investigations on hexacoral mitochondrial intron functions and biological roles are needed and highly welcome.

Acknowledgements

We thank current and former members of the research teams at the Genomics Group (Nord University) and the RNA Group (UiT—The Arctic University of Norway) for discussion and support. A special thanks to the former PhD students Sylvia Ighem Chi and Ilona Urbarova for thoroughly investigating hexacoral genomics.

Conflict of interest

The authors declare that they have no conflict of interest.

A. Appendix

In January 2020 about 200 hexacoral mitochondrial genomes have been completely, or nearly completely, sequenced. These mitochondrial genomes represent all 5 hexacoral orders, 51 families, 77 genera, and 133 distinct species. All specimens (100%) harbor ND5-717 and approximately 50% harbor COI introns. Key features are summarized in Appendix Table 1.
| Species                  | Family                  | Accession no | Mt size ¹ | ND5 intron (size) ² | COI intron (size) ³ |
|-------------------------|-------------------------|--------------|-----------|---------------------|---------------------|
| *Synhaliactis elegans*  | Actiniaridae            | KR051009     | P11,445 bp| ND5+ (1635 bp)      | COI –               |
| *Actinia equina*        | Actiniidae              | MH545699     | C20,690 bp| ND5+ (2170 bp)      | 884_COI+ (857 bp)   |
| *Actinia tenebrosa*     | Actiniidae              | MK291977     | C20,691 bp| ND5+ (2170 bp)      | 884_COI+ (854 bp)   |
| *Anemone majano*        | Actiniidae              | KY860670     | C19,545 bp| ND5+ (1679 bp)      | 884_COI+ (853 bp)   |
| *Anemone sulcata*       | Actiniidae              | MN011067     | C20,390 bp| ND5+ (1725 bp)      | 884_COI+ (1053 bp)  |
| *Anemone viridis*       | Actiniidae              | KY860669     | C20,108 bp| ND5+ (1726 bp)      | 884_COI+ (853 bp)   |
| *Anthopleura midori*    | Actiniidae              | KT989511     | C20,039 bp| ND5+ (2174 bp)      | 884_COI+ (853 bp)   |
| *Bolocera tuediae*      | Actiniidae              | HG423145     | C19,143 bp| ND5+ (2055 bp)      | 884_COI+ (853 bp)   |
| *Bolocera sp.*          | Actiniidae              | KU507297     | C19,463 bp| ND5+ (2397 bp)      | 884_COI+ (854 bp)   |
| *Entacmaea quadricolor* | Actiniidae              | MN066616     | C20,960 bp| ND5+ (2052 bp)      | 884_COI+ (853 bp)   |
| *Epiactis japonica*     | Actiniidae              | MN076184     | C18,835 bp| ND5+ (1681 bp)      | 884_COI+ (853 bp)   |
| *Epiactis prolifera*    | Actiniidae              | Ref. [33]    | C19,752 bp| ND5+ (1737 bp)      | 884_COI+ (853 bp)   |
| *Isoscyonis striata*    | Actiniidae              | KR051006     | C19,001 bp| ND5+ (1695 bp)      | 884_COI+ (853 bp)   |
| *Urticina eques*        | Actiniidae              | HG423144     | C20,458 bp| ND5+ (1681 bp)      | 884_COI+ (850 bp)   |
| *Antholoba achates*     | Actinostolidae          | KR051002     | C17,816 bp| ND5+ (1884 bp)      | 884_COI+ (853 bp)   |
| *Stomphia selaginella*  | Actinostolidae          | Ref. [33]    | C18,349 bp| ND5+ (1784 bp)      | 884_COI+ (829 bp)   |
| *Aiptasia pulchella*    | Aiptasiidae             | HG423147     | C19,791 bp| ND5+ (1730 bp)      | 884_COI+ (847 bp)   |
| *Aiptasia pulchella*    | Aiptasiidae             | HG423148     | C19,790 bp| ND5+ (1730 bp)      | 884_COI+ (847 bp)   |
| *Bartholomea annulata*  | Aiptasiidae             | MN066614     | C19,615 bp| ND5+ (1754 bp)      | 884_COI+ (847 bp)   |
| *Alicia sanibirensis*   | Aliciidae               | KR051001     | C19,575 bp| ND5+ (2158 bp)      | COI –               |
| *Relicanthus daphneae*  | Boloceroididae          | MK947129     | C17,727 bp| ND5+ (1721 bp)      | 884_COI+ (926 bp)   |

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2. DOI: http://dx.doi.org/10.5772/intechopen.91465
| Species | Family | Accession no | Mt size | ND5 intron (size) | ND5+ (size) | COI intron (size) | COI- |
|---------|--------|--------------|---------|------------------|-------------|-------------------|------|
| Edwardsia gilbertensis | Edwardsiidae | MN066615 | P17.661 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Edwardsia timida | Edwardsiidae | DQ283835 | C16.368 bp | ND5+ (1602 bp) | COI+ (1684 bp) |
| Nematostella sp. | Edwardsiidae | KR051003 | P17.320 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Halocampodia purpurea | Halocampodiidae | MG007747 | C18.343 bp | ND5+ (1622 bp) | COI+ (1684 bp) |
| Haloclydia | Haloclydiae | KF051004 | P17.320 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Hormodida | Hormodidae | MG007615 | C18.343 bp | ND5+ (1622 bp) | COI+ (1684 bp) |
| Lipometridae | Lipometridae | MG007615 | C18.343 bp | ND5+ (1622 bp) | COI+ (1684 bp) |
| Metridium | Metridiidae | AF000063 | P17.892 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Metridium calceum | Metridiidae | AF000063 | P17.892 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Phymanthus | Phymanthus | AF000063 | P17.892 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Palythoa heliodiscus | Sphenopidae | KY888767 | C20.361 bp | ND5+ (1604 bp) | COI+ (1684 bp) |
| Zoanthus sansibaricus | Zoanthidae | KY888767 | C20.361 bp | ND5+ (1604 bp) | COI+ (1684 bp) |

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| Species                        | Family             | Accession no | Mt size | ND5 intron (size) | COI intron (size) |
|-------------------------------|--------------------|--------------|---------|-------------------|-------------------|
| **C: Mushroom corals (Order Corallimorpharia)** |                    |              |         |                   |                   |
| *Corallimorphus profundus*    | Corallimorphidae   | KP938440     | 20,488 bp | ND5+ (12,389 bp)  | 884_COI+ (1182 bp) |
| *Corynactis californica*     | Corallimorphidae   | KP938436     | 20,715 bp | ND5+ (10,531 bp)  | 884_COI+ (1265 bp) |
| *Pseudocorynactis sp.*       | Corallimorphidae   | KP938437     | 21,239 bp | ND5+ (18,840 bp)  | 884_COI+ (1177 bp) |
| *Amplexidiscus fenestrafer*  | Discosomatidae     | MH308002     | 20,054 bp | ND5+ (17,960 bp)  | 884_COI+ (1206 bp) |
| *Amplexidiscus fenestrafer*  | Discosomatidae     | KP938435     | 20,188 bp | ND5+ (18,094 bp)  | 884_COI+ (1206 bp) |
| *Discosoma nummiforme*       | Discosomatidae     | KP938434     | 20,925 bp | ND5+ (18,791 bp)  | 884_COI+ (1208 bp) |
| *Discosoma sp.*              | Discosomatidae     | DQ643965     | 20,908 bp | ND5+ (18,803 bp)  | 884_COI+ (1207 bp) |
| *Discosoma sp.*              | Discosomatidae     | DQ643966     | 20,912 bp | ND5+ (19,807 bp)  | 884_COI+ (1206 bp) |
| *Discosoma sp.*              | Discosomatidae     | MH308003     | 20,288 bp | ND5+ (18,196 bp)  | 884_COI+ (1206 bp) |
| *Rhodactis indosinensis*     | Discosomatidae     | KP938438     | 20,100 bp | ND5+ (18,013 bp)  | 884_COI+ (1204 bp) |
| *Rhodactis musoides*         | Discosomatidae     | KP938439     | 20,826 bp | ND5+ (18,721 bp)  | 884_COI+ (1206 bp) |
| *Rhodactis sp.*              | Discosomatidae     | DQ640647     | 20,093 bp | ND5+ (18,001 bp)  | 884_COI+ (1206 bp) |
| *Ricordea florida*           | Ricordeidae        | DQ640648     | 21,376 bp | ND5+ (19,247 bp)  | 884_COI+ (1176 bp) |
| *Ricordea yuma*              | Ricordeidae        | MH308004     | 21,430 bp | ND5+ (19,301 bp)  | 884_COI+ (1198 bp) |
| *Ricordea yuma*              | Ricordeidae        | MH308005     | 21,566 bp | ND5+ (19,437 bp)  | 884_COI+ (1198 bp) |
| *Ricordea yuma*              | Ricordeidae        | KP938441     | 22,015 bp | ND5+ (19,886 bp)  | 884_COI+ (1198 bp) |
| **D: Black corals (Order Antipatharia)** |                    |              |         |                   |                   |
| *Cirrhipathes lucteni*       | Antipathidae       | JX023266     | 20,448 bp | ND5+ (2062 bp)    | 884_COI+ (1439 bp) |
| *Myriopathes japonica*       | Antipathidae       | JX456459     | 17,733 bp | ND5+ (1699 bp)    | 884_COI+ (924 bp)  |
| *Chryopathes formosa*        | Cladopathidae      | DQ304771     | 18,398 bp | ND5+ (1932 bp)    | COI−               |

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DOI: http://dx.doi.org/10.5772/intechopen.91465
| Species                | Family     | Accession no | Mt size | ND5 intron (size) | COI intron (size) |
|-----------------------|------------|--------------|---------|-------------------|-------------------|
| E: Stony corals (Order Scleractinia) |            |              |         |                   |                   |
| Complex clade         |            |              |         |                   |                   |
| Acropora aculeus      | Acroporidae| KT001202     | C18,528 | ND5+ (12,116 bp)  | COI –             |
| Acropora acuminata    | Acroporidae| LC201815     | C18,586 | ND5+ (12,175 bp)  | COI –             |
| Acropora aspera       | Acroporidae| KF448532     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201816     | C18,346 | ND5+ (11,937 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201849     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201850     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201851     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201852     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201853     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201854     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora australis    | Acroporidae| LC201855     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora carduus      | Acroporidae| LC201813     | C18,373 | ND5+ (11,964 bp)  | COI –             |
| Acropora carduus      | Acroporidae| LC201814     | C18,372 | ND5+ (11,963 bp)  | COI –             |
| Acropora cytherea     | Acroporidae| LC201817     | C18,568 | ND5+ (12,158 bp)  | COI –             |
| Acropora cytherea     | Acroporidae| LC201818     | C18,568 | ND5+ (12,157 bp)  | COI –             |
| Acropora cytherea     | Acroporidae| LC201819     | C18,568 | ND5+ (12,158 bp)  | COI –             |
| Acropora digitifera   | Acroporidae| KF448535     | C18,479 | ND5+ (12,070 bp)  | COI –             |
| Acropora diviculata   | Acroporidae| KF448537     | C18,481 | ND5+ (12,072 bp)  | COI –             |
| Acropora echinata     | Acroporidae| LC201820     | C18,480 | ND5+ (12,071 bp)  | COI –             |
| Acropora echinata     | Acroporidae| LC201821     | C18,480 | ND5+ (12,071 bp)  | COI –             |
| Species          | Family       | Accession no | Mt size 1 | ND5 intron (size) 2 | COI intron (size) 3 |
|------------------|--------------|--------------|-----------|---------------------|---------------------|
| Acropora echinata | Acroporidae  | LC201822     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201823     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201824     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201825     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201826     | C18,482 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201834     | C18,481 bp | ND5+ (12,072 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201835     | C18,368 bp | ND5+ (11,959 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201836     | C18,482 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201837     | C18,368 bp | ND5+ (11,959 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201838     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201839     | C18,482 bp | ND5+ (12,073 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201840     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora echinata | Acroporidae  | LC201841     | C18,367 bp | ND5+ (11,958 bp)    | COI –               |
| Acropora florida | Acroporidae  | KF448533     | C18,365 bp | ND5+ (11,956 bp)    | COI –               |
| Acropora florida | Acroporidae  | LC201827     | C18,365 bp | ND5+ (11,956 bp)    | COI –               |
| Acropora grandis | Acroporidae  | LC201828     | C18,479 bp | ND5+ (12,070 bp)    | COI –               |
| Acropora humilis  | Acroporidae  | KF448528     | C18,480 bp | ND5+ (12,071 bp)    | COI –               |
| Acropora hyacinthus | Acroporidae | KF448531     | C18,566 bp | ND5+ (12,157 bp)    | COI –               |
| Acropora hyacinthus | Acroporidae | LC201829     | C18,567 bp | ND5+ (12,157 bp)    | COI –               |
| Acropora hyacinthus | Acroporidae | LC201830     | C18,567 bp | ND5+ (12,157 bp)    | COI –               |
| Acropora hyacinthus | Acroporidae | LC201831     | C18,567 bp | ND5+ (12,157 bp)    | COI –               |
| Species          | Family       | Accession no | Mt size | ND5 intron (size) | COI intron (size) |
|------------------|--------------|--------------|---------|-------------------|-------------------|
| Acropora hyacinthua | Acroporidae  | LC201832     | C18,568 bp | ND5+ (12,158 bp)  | COI –             |
| Acropora intermedia   | Acroporidae  | LC201833     | C18,479 bp | ND5+ (12,070 bp)  | COI –             |
| Acropora microphthalmal | Acroporidae | LC201842     | C18,479 bp | ND5+ (12,070 bp)  | COI –             |
| Acropora microphthalmal | Acroporidae | LC201843     | C18,481 bp | ND5+ (12,072 bp)  | COI –             |
| Acropora muriicata    | Acroporidae  | KF448529     | C18,481 bp | ND5+ (12,072 bp)  | COI –             |
| Acropora nasuta       | Acroporidae  | LC201844     | C18,480 bp | ND5+ (12,071 bp)  | COI –             |
| Acropora nasuta       | Acroporidae  | LC201845     | C18,374 bp | ND5+ (11,965 bp)  | COI –             |
| Acropora nasuta       | Acroporidae  | LC201846     | C18,484 bp | ND5+ (12,074 bp)  | COI –             |
| Acropora robusta      | Acroporidae  | KF448538     | C18,480 bp | ND5+ (12,071 bp)  | COI –             |
| Acropora selago       | Acroporidae  | LC201847     | C18,482 bp | ND5+ (12,073 bp)  | COI –             |
| Acropora selago       | Acroporidae  | LC201848     | C18,480 bp | ND5+ (12,071 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | AF338425     | C18,338 bp | ND5+ (11,928 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201856     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201857     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201858     | C18,343 bp | ND5+ (11,934 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201859     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201860     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201861     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201862     | C18,343 bp | ND5+ (11,934 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201863     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Acropora tenuis       | Acroporidae  | LC201864     | C18,342 bp | ND5+ (11,933 bp)  | COI –             |
| Species               | Family           | Accession no | Mt size | ND5 intron (size) | COI intron (size) |
|----------------------|------------------|--------------|---------|-------------------|-------------------|
| Acropora tenuis      | Acroporidae      | LC201865     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Acropora tenuis      | Acroporidae      | LC201866     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Acropora tenuis      | Acroporidae      | LC201867     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Acropora tenuis      | Acroporidae      | LC201868     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Acropora tenuis      | Acroporidae      | LC201869     | C18,341 bp | ND5+ (11,933 bp) | COI–              |
| Acropora tenuis      | Acroporidae      | LC201870     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Acropora valida      | Acroporidae      | MH141598     | C18,385 bp | ND5+ (11,976 bp) | COI–              |
| Acropora yongei      | Acroporidae      | KF448534     | C18,342 bp | ND5+ (11,933 bp) | COI–              |
| Anacropora matthai   | Acroporidae      | AY903295     | C17,888 bp | ND5+ (11,492 bp) | COI–              |
| Astreopora explanata | Acroporidae      | KJ634269     | C18,106 bp | ND5+ (11,795 bp) | COI–              |
| Astreopora myriophthalma | Acroporidae     | KJ634272     | C18,106 bp | ND5+ (11,795 bp) | COI–              |
| Montipora cactus     | Acroporidae      | AY903296     | C17,887 bp | ND5+ (11,485 bp) | COI–              |
| Montipora aequituberculata | Acroporidae    | KU762339     | C17,886 bp | ND5+ (11,488 bp) | COI–              |
| Montipora efflorescens | Acroporidae   | MG851914     | C17,886 bp | ND5+ (11,491 bp) | COI–              |
| Agaricia fragilis    | Agariciidae      | KM051016     | C18,667 bp | ND5+ (11,525 bp) | COI–              |
| Agaricia humilis     | Agariciidae      | DQ643831     | C18,735 bp | ND5+ (11,536 bp) | COI–              |
| Pavona clavus        | Agariciidae      | DQ643836     | C18,315 bp | ND5+ (11,129 bp) | COI–              |
| Pavona decussata     | Agariciidae      | KP231535     | C18,378 bp | ND5+ (11,129 bp) | COI–              |
| Dendrophyllia arbuscula | Dendrophyllida  | KR824937     | C19,069 bp | ND5+ (11,299 bp) | 884_COI+ (964 bp) |
| Dendrophyllia cribrosa | Dendrophyllida | JQ290080     | C19,072 bp | ND5+ (11,282 bp) | 884_COI+ (964 bp) |
| Tubastraea coccinea  | Dendrophyllida   | KX024566     | C19,094 bp | ND5+ (11,322 bp) | 884_COI+ (964 bp) |
| Tubastraea coccinea  | Dendrophyllida   | JQ290078     | C19,070 bp | ND5+ (11,300 bp) | 884_COI+ (964 bp) |
| Species                  | Family                   | Accession no | Mt size\(^1\) | ND5 intron (size)\(^2\) | COI intron (size)\(^3\) |
|--------------------------|--------------------------|--------------|----------------|--------------------------|--------------------------|
| *Tubastraea tagusensis*  | Dendrophyllidae          | KX024567     | C19,094 bp     | ND5+ (11,324 bp)         | 884_COI+ (964 bp)        |
| *Turbinaria peltata*    | Dendrophyllidae          | KJ725201     | C18,966 bp     | ND5+ (11,332 bp)         | 884_COI+ (964 bp)        |
| *Euphyllia ancora*      | Euphylliidae             | JF825139     | C18,875 bp     | ND5+ (11,866 bp)         | COI –                   |
| *Galaxea fascicularis*  | Euphylliidae             | KU159433     | C18,751 bp     | ND5+ (12,022 bp)         | COI –                   |
| *Fungiacyathus stephanus*| Fungiacyathidae          | JF825138     | C19,381 bp     | ND5+ (10,932 bp)         | COI+ (961 bp)           |
| *Alveopora japonica*    | Poritidae                | MG851913     | C18,144 bp     | ND5+ (11,621 bp)         | COI –                   |
| *Alveopora sp.*         | Poritidae                | KJ634271     | C18,146 bp     | ND5+ (11,621 bp)         | COI –                   |
| *Goniopora columna*     | Poritidae                | JF825141     | C18,766 bp     | ND5+ (11,175 bp)         | 884_COI+ (964 bp)        |
| *Porites fontanesii*    | Poritidae                | NC_037434    | C18,658 bp     | ND5+ (11,131 bp)         | 884_COI+ (965 bp)        |
| *Porites harrisoni*     | Poritidae                | NC_037435    | C18,630 bp     | ND5+ (11,133 bp)         | 884_COI+ (965 bp)        |
| *Porites lobata*        | Poritidae                | KU572435     | C18,647 bp     | ND5+ (11,133 bp)         | 884_COI+ (965 bp)        |
| *Porites lutea*         | Poritidae                | KU159432     | C18,646 bp     | ND5+ (11,130 bp)         | 884_COI+ (971 bp)        |
| *Porites okinavensis*   | Poritidae                | JF825142     | C18,647 bp     | ND5+ (11,133 bp)         | 884_COI+ (965 bp)        |
| *Porites panamensis*    | Poritidae                | KJ546638     | C18,628 bp     | ND5+ (11,117 bp)         | 884_COI+ (965 bp)        |
| *Porites poritii*       | Poritidae                | DQ643837     | C18,648 bp     | ND5+ (11,135 bp)         | 884_COI+ (965 bp)        |
| *Porites rus*           | Poritidae                | LN864762     | C18,647 bp     | ND5+ (11,133 bp)         | 884_COI+ (971 bp)        |
| *Pseudosiderastrea formosa* | Siderastreidae          | KP260632     | C19,475 bp     | ND5+ (11,524 bp)         | 884_COI+ (970 bp)        |
| *Pseudosiderastrea tayami* | Siderastreidae          | KP260633     | C19,475 bp     | ND5+ (11,524 bp)         | 884_COI+ (970 bp)        |
| *Siderastrea radians*   | Siderastreidae           | DQ643838     | C19,387 bp     | ND5+ (11,463 bp)         | 884_COI+ (988 bp)        |
| **Robust clade**        |                          |              |                |                          |                          |
| *Madracis decactis*     | Astrocoeniidae           | KX982259     | C16,970 bp     | ND5+ (10,435 bp)         | COI –                   |
| *Madracis mirabilis*    | Astrocoeniidae           | EU400212     | C16,951 bp     | ND5+ (10,415 bp)         | COI –                   |
| Species                  | Family          | Accession no | Mt size | ND5 intron (size) | COI intron (size) |
|-------------------------|-----------------|--------------|---------|------------------|------------------|
| Lophelia pertusa        | Caryophyllidae  | FR821799     | C16,150 bp | ND5+ (6460 bp)   | COI-             |
| Lophelia pertusa        | Caryophyllidae  | KC875348     | C16,149 bp | ND5+ (6460 bp)   | COI-             |
| Lophelia pertusa        | Caryophyllidae  | KC875349     | C16,149 bp | ND5+ (6460 bp)   | COI-             |
| Solenosmilia variabilis| Caryophyllidae  | KM609293     | C15,968 bp | ND5+ (6459 bp)   | COI-             |
| Solenosmilia variabilis| Caryophyllidae  | KM609294     | C15,968 bp | ND5+ (6459 bp)   | COI-             |
| Colpopyllia natans      | Flaviidae       | DQ643833     | C16,906 bp | ND5+ (10,445 bp) | COI-             |
| Pleistotrema versipora  | Flaviidae       | MH025639     | C15,320 bp | ND5+ (9398 bp)   | COI-             |
| Echinophyllia aspera    | Lobophylliidae  | MG792550     | C17,697 bp | ND5+ (10,136 bp) |    |
| Sclerophyllia maxima    | Lobophylliidae  | FO094931     | C18,168 bp | ND5+ (10,760 bp) |    |
| Dipsastrea rotulana     | Merulinidae     | MH119077     | C16,466 bp | ND5+ (10,149 bp) | COI-             |
| Flavites halicora       | Merulinidae     | MH794283     | C17,030 bp | ND5+ (11,150 bp) | COI-             |
| Hydnopora exesa         | Merulinidae     | MH086217     | C17,790 bp | ND5+ (10,243 bp) | COI-             |
| Orbicella annularis     | Merulinidae     | AP008973     | C16,138 bp | ND5+ (9540 bp)   | COI-             |
| Orbicella annularis     | Merulinidae     | AP008974     | C16,138 bp | ND5+ (9540 bp)   | COI-             |
| Orbicella faveolata     | Merulinidae     | AP008977     | C16,138 bp | ND5+ (9540 bp)   | COI-             |
| Orbicella faveolata     | Merulinidae     | AP008978     | C16,138 bp | ND5+ (9540 bp)   | COI-             |
| Orbicella faveolata     | Merulinidae     | AP008975     | C16,138 bp | ND5+ (9540 bp)   | COI-             |
| Orbicella faveolata     | Merulinidae     | AP008976     | C16,137 bp | ND5+ (9539 bp)   | COI-             |
| Polycyathus sp.         | Merulinidae     | JF825140     | C15,357 bp | ND5+ (9438 bp)   | COI-             |
| Platygrya carnosa       | Merulinidae     | JX91333      | C16,463 bp | ND5+ (10,164 bp) | COI-             |
| Musa angulosa           | Mussidae        | DQ643834     | C17,245 bp | ND5+ (10,636 bp) | COI-             |
| Madrepora oculata       | Oculinidae      | JX236041     | C15,841 bp | ND5+ (10,140 bp) | COI-             |

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DOI: http://dx.doi.org/10.5772/intechopen.91465
### Appendix Table 1.
**Key features of group I introns in hexacoral mitogenomes.**

| Species            | Family          | Accession no | Mt size\(^1\) | ND5 intron (size)\(^2\) | COI intron (size)\(^3\) |
|--------------------|-----------------|--------------|---------------|-------------------------|-------------------------|
| *Pocillopora damicornis* | Pocilloporidae  | EU400213     | C17,425 bp    | ND5+ (10,864 bp)         | COI–                     |
| *Pocillopora damicornis* | Pocilloporidae  | EF526302     | C17,415 bp    | ND5+ (10,863 bp)         | COI–                     |
| *Pocillopora eydouxi*    | Pocilloporidae  | EF526303     | C17,422 bp    | ND5+ (10,863 bp)         | COI–                     |
| *Seriatopora caliendrum* | Pocilloporidae  | EF633601     | C17,010 bp    | ND5+ (10,463 bp)         | COI–                     |
| *Seriatopora hystrix*    | Pocilloporidae  | EF633600     | C17,059 bp    | ND5+ (10,465 bp)         | COI–                     |
| *Stylophora pistillata*  | Pocilloporidae  | EU400214     | C17,177 bp    | ND5+ (10,583 bp)         | COI–                     |
| *Astrangia sp.*           | Rhizangiidae    | DQ643832     | C14,853 bp    | ND5+ (9258 bp)           | COI–                     |

\(^1\)Size of mitochondrial genome. C, completely sequenced; P, partial/ almost completely sequenced.  
\(^2\)Size of ND5-717 group I intron.  
\(^3\)Size of COI group I intron. COI–, no COI intron present; 720, 867, or 884 introns indicated.  
\(^4\)The sea anemone *Aiptasia pulcella* may also be annotated as *Exaiptasia pallida*.  
\(^5\)Information from our unpublished complete mitochondrial genome sequence of *Stichodactyla helianthus*.  
\(^6\)The black coral *Cirrhipathes lutkeni* may also be annotated as *Strichpates lutkeni*.  
\(^7\)The stony coral *Lophelia pertusa* may also be annotated as *Desmophyllum pertusum*.  
\(^8\)The stony coral *Sclerophyllia maxima* may also be annotated as *Acanthastrea maxima*. 
Author details

Steinar Daæ Johansen1* and Åse Emblem2

1 Genomics Group, Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway

2 Research Laboratory and Department of Laboratory Medicine, Nordland Hospital, Bodø, Norway

*Address all correspondence to: steinar.d.johansen@nord.no

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