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ORIGINAL ARTICLE

Complete Mitochondrial Genome of Great Frigatebird (*Fregata minor*): Phylogenetic Position and Gene Rearrangement

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Abstract

The complete mitogenome sequence of the Great Frigatebird, *Fregata minor* was sequenced for the first time in this study. The mitogenome (16,899 bp) comprises of 13 protein-coding genes (PCGs), two ribosomal RNA (rRNA) genes, and 22 transfer RNA (tRNA) genes, and a control region (CR). The mitogenome was AT-rich (55.60%) with 11 overlapping and 18 intergenic spacer regions. Most of the PCGs were started by a typical ATG initiation codon except for *cox1* and *nad3*. A maximum-likelihood phylogeny of concatenated PCGs resulted in a well-resolved phylogeny of all the species of Suliformes and illuminates the sister relationship of *F. minor* with *F. magnificens*. The present mitogenome-based phylogeny clearly enlightens the evolutionary position of Suliformes and Pelecaniformes species. Unique tandem repeats were identified in both *F. minor* and *F. magnificens*, which can be employed as a species-specific marker. To illuminate the population structure of this migratory seabirds, the present study advocate more sampling and the generation of additional molecular data to clarify their genetic diversity. The present study also rejects an earlier hypothesis on the mitochondrial gene order of Suliformes and corroborated the typical avian gene order in frigatebirds.

Keywords Seabirds · Mitogenome · Phylogeny · Gene order · Evolution

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Introduction

The members of Fregatidae were formerly grouped under the order Pelecaniformes along with other pelicans, cormorants, anhingas and darters, boobies and gannets, and tropicbirds (Nelson 2005). Later on, the cormorants, anhingas and darters, and frigatebirds are grouped under the order Suliformes (Christidis and Boles 2008; Gibb et al. 2013; Gill and Donsker 2021). The family Fregatidae (order Suliformes) comprises a single genus with five species which are distributed across all tropical and subtropical oceans (BirdLife International 2021). The frigatebird species have partially overlapping distributions but their behavior, breeding and foraging ecology are almost similar (Valle 1986). They spend most of the day in flight searching for food (fish and squid) and rest on trees or cliffs at night. They were tracked to the atmospheric conditions to understand the evolution of flight strategies and evidence for long-distance migrations over months-long transoceanic flights (Weimerskirch et al. 2016). Among all five extant species, the Great Frigatebird, *Fregata minor* is distributed throughout the world's tropical seas and is found foraging at low densities throughout the Indo-Malay archipelago during the non-breeding season (Rasmussen and Anderton 2012). Among the five species, the Ascension Frigatebird, *F. aquila* is Vulnerable, the Christmas Frigatebird, *F. andrewsi* is Critically Endangered, and the other three species (*F. magnificens*, *F. ariel*, and *F. minor*) are Least Concern in the IUCN Red List of Threatened species (IUCN 2021). This group of bird faces several threats such as, extreme atmospheric conditions, habitat alteration, and ecosystem degradation associated with climate change, marine pollution by heavy metals and industrial pollutants, and human persecution as well as accidental entanglement during fishing activities.

The taxonomic identification of this group of birds is challenging due to their phenotypic similarity and impressive plumage differences within the group (James 2004; Valle et al. 2006). Hence, molecular information tools are required for rapid and reliable species level identification and to resolve their phylogenetic relationships. Mitochondrial and nuclear DNA has been used to elucidate the phylogeny of various groups of birds, including frigatebirds (Hedges and Sibley 1994; Friesen and Anderson 1997; Kennedy and Spencer 2004; Paton and Baker 2006; Brown et al. 2008; Patterson et al. 2011). In addition, the mitogenome, the whole genome, and comparative genomics approaches have also been used to examine the relationships, divergence time, and classification of avian species (Harrison et al. 2004; Gibb et al. 2007, 2013; Hackett et al. 2008; Pacheco et al. 2011; McCormack et al. 2013; Jarvis et al. 2014). So far, the mitogenome of only a single species, *F. magnificens* was assembled and publicly available at GenBank (Feng et al. 2020). Another mitogenome (GenBank accession number AP009192) was not identified to species (Watanabe et al. 2006). To enrich the global database and help understand the phylogenetics of frigatebirds, the present study aimed to generate the complete mitogenome of *F. minor* and compared with other Suliformes.

Remarkably, the mitogenome of Suliformes represent unique gene order with duplicated region due to pseudogenization or loss of selected genes and/or the

control region (Urantówka et al. 2020). The duplicated control regions with contiguous genes could enhance the effectiveness of replication and transcription (Kumazawa et al. 1996; Jiang et al. 2007). In this context, we revisited the mitochondrial gene order of both cormorants and darters as well as compared with frigatebirds mitogenome to assure the recent views on the organization and evolution of Suliformes mitogenome (Morris-Pocock et al. 2010; Gibb et al. 2013; Rodrigues et al. 2017; Zhang et al. 2017; Urantówka et al. 2020). The gene arrangement information will help to elucidate the evolution of studied avian groups as well as their evolutionary relationships.

Materials and Methods

Ethics Statement and Sample Collection

A dead sub-adult frigatebird was recovered by West Bengal Forest Department on 29 May 2020 from Basirhat (22° 37′ 53.12″ N, 88° 53′ 7.39″ E), North 24 Parganas, West Bengal, India. This about 80 km inland from the nearest sea coasts of Sunderban Biosphere Reserve and subsequently sent the specimen to Zoological Survey of India (ZSI) for its identification. The bird may have been driven inland due to the cyclonic storm 'Amphan' which hit eastern India in May 2020. Before preservation of the specimen in the National Zoological Collection's of the Bird Section, ZSI under the voucher number 41302/AVES, a tissue sample was collected from the hind leg using sterile surgical blade and forceps. No bird specimen was sacrificed in the present study.

The collected frigatebird species was identified as the sub-adult of Great Frigatebird, *Fregata minor* using the literature (James 2004; Rasmussen and Anderton 2012; Maheswaran and Alam 2014). The studied specimen had a pale and tawny head, white breast divided by a dark brown breast-band, slenderer in middle and white belly patch almost round in the anterior region and becoming narrower in its posterior region ending in cloaca. The alar bars are prominent but buff in colour and rounded to the posterior of the belly patch, and the absence of axillary spurs. The culmen of the studied specimen was 111 mm, which is congruent with the earlier report of *F. minor* (96–117 mm). The total length was 890 mm, while the length of head was 180 mm, tail and wing were 365 mm and 800 mm, respectively.

Mitochondrial DNA Extraction and Sequencing

The tissue sample was homogenized with 1 ml buffer comprising 0.32 M Sucrose, 1 mM EDTA, and 10 mM TrisHCl by the in-house WiseTis HG-15 homogenizer. The mixture solution was centrifuged at 700×*g* for 5 min at 4 °C to remove the nuclei and cell debris. The supernatant was collected in 1.5 ml tube and centrifuged at 12,000×*g* for 10 min at 4 °C to precipitate the mitochondrial pellet. The pellet was re-suspended in 500 µl of ATL buffer (50 mM TrisHCl, 25 mM of EDTA, 150 mM NaCl) and incubated overnight at 37 °C along with 20 µl of proteinase K

(20 mg/ml). Mitochondrial DNA was extracted using QIAamp DNA Investigator Kit (QIAGEN Inc.) with standard protocol. The sequencing of the *F. minor* sample was carried out on the Illumina platform (Illumina Hiseq 2500) with 150 bp paired-end read chemistry. Paired end libraries were constructed using TruSeq DNA Library Preparation kit with standard protocols. The high-quality reads were downsampled using Seqtk (https://github.com/lh3/seqtk) and assembled using NOVOPlasty v2.6.7 using default parameters (Dierckxsens et al. 2017). The mitogenome was submitted to the GenBank database.

Sequence Identity

Following Sangster and Luksenburg (2021), we verified the identity of our mitogenome sequence of *F. minor* with reference sequences of three commonly used mitochondrial markers in waterbird systematics: NADH dehydrogenase subunit 2 (*ND2*, 1041 bp; $n=416$, incl. four of *F. minor*), part of cytochrome c oxidase subunit I (*COI*, 696 bp; $n=1681$, incl. ten of *F. minor*), and cytochrome *b* (*Cyt b*, 1141 bp; $n=636$, incl. four of *F. minor*).

Data Set Construction and Comparative Analysis

The circular representation of the generated *F. minor* mitogenome was plotted by CGView Server (http://stothard.afns.ualberta.ca/cgview_server/) with default parameters (Grant and Stothard 2008). The direction and arrangements of protein-coding genes (PCGs), transfer RNA (tRNA), and ribosomal RNA (rRNA) were confirmed through MITOS online server (http://mitos.bioinf.uni-leipzig.de) (Bernt et al. 2013). On the basis of taxonomic hierarchy, five Suliformes species mitogenomes were downloaded from GenBank to construct the phylogenetic dataset (Table S1). The genome size and nucleotide composition of the studied species were calculated using MEGA X (Kumar et al. 2018). The overlapping regions and intergenic spacers of the studied mitogenome were calculated manually. Further, the structural characteristics and duplication of CR act a crucial role in regulating transcription and replication in the mitogenome (Ruokonen and Kvist 2002; Hanna et al. 2017). Hence, the present study evaluated the tandem repeats in the CR of both *F. minor* and *F. Magnificens* by online Tandem Repeats Finder web tool (https://tandem.bu.edu/trf/trf.html) (Benson 1999).

Phylogeny and Gene Order (GO) Analyses

To assess the phylogenetic relationships, the PCGs were aligned and concatenated using TranslatorX (with MAFFT algorithm with L-INS-i strategy and GBlocks parameters) and SequenceMatrix v1.7.84537 (Abascal et al. 2010; Vaidya et al. 2010). The best fit model (GTR+I+G) was calculated by PartitionFinder 2 using lowest BIC criterion (Lanfear et al. 2016) and the maximum-likelihood (ML) tree was constructed using the IQ-Tree web server with 1000 bootstrap replicates (Trifinopoulos et al. 2016). The mitogenome of *Ardea cinerea* (accession No.

NC_025900) of the family Ardeidae was used as an out-group. Further, to screen the genearrangement scenario, the TreeREx analysis was acquired to understand the evolutionary pathways within the Suliformes, considering to the detected diversity of the GOs. TreeREx can definitely discriminate the putative GOs at the internal nodes of a reference topology as the mechanism in a bottom-up manner through the iterative investigation of triplets or quadruplets of GOs to determine all the GOs in the entire topology (Bernt et al. 2008). We applied the default parameters of TreeREx indicated on the website (http://pacosy.informatik.uni-leipzig.de/185-0-TreeREx.html) to examine each node of the reference phylogenetic tree.

Results and Discussion

Mitogenome Structure and Organization

The complete mitogenome of *F. minor* (accession no. MZ681908) was 16,899 bp with 44.40% GC content. The mitogenome of *F. minor* was 111 bp longer than that *F. magnificens*. This was due to variation in length within the control regions of both species. The *F. minor* mitogenome contained 37 genes, comprising 13 PCGs, 22 tRNAs, 2 rRNAs, and a major non-coding control region (CR). Among them, nine genes (*nad6* and eight tRNAs) were identified on the negative strand, while the remaining 28 genes were identified on the positive strand (Table 1, Fig. 1). The total length of PCGs was 11,390 bp, that of ribosomal RNA was 2531 bp, transfer RNA was 1548 bp, and the control region was 1320 bp. The gene order of *F. minor* was identical to that of *F. magnificens*. A total of 18 intergenic spacer regions with a total length of 136 bp were observed with the longest region (38 bp) between tRNA-Valine (*trnV*) and Large Ribosomal subunit (rrnL) (Table 1). Further, 11 overlapping regions with a total length of 39 bp were distinguished in *F. minor*. The longest overlapping region (10 bp) was observed between the ATP synthase F0 subunit 8 (*atp8*) and ATP synthase F0 subunit 6 (*atp6*). Most of the PCGs of *F. minor* initiated with an ATG start codon; however, the GTG initiation codon was found in *cox1* and ATC in *nad3*. Six PCGs had TAA as their termination codon, while TAG was the termination codon of *nad2*, AGG that of *cox1* and *nad6*, GAA that of *nad3*, incomplete TA(A) by *nad1*, and T(AA) by both *cox3* and *nad4* respectively. A total of four tandem repeats, (105 bp)2, (10 bp)2.7, (21 bp)1.9, and (7 bp)13.3 were found in *F. minor*, while two tandem repeats, (10 bp)6.5 and (7 bp)8.1 were detected in *F. magnificens*. These distinguished genomic features could be used as a species-specific marker to identify the frigatebird species promptly.

Phylogeny and Mitochondrial Gene Arrangements

The partial mitochondrial markers-based phylogenyelucidates that the generated sequence of *F. minor* clustered with the reference sequences of *F. minor* available in the database, indicating that our sample was correctly identified through morphology (Fig. S1). The concatenated PCGs-based ML phylogeny distinctly

Table 1 List of annotated mitochondrial genes of *Fregata minor*

Gene	Strand	Start	Stop	Length (bp)	Anti-Codon	Start codon	Stop codon	Intergenic nucleotides
trnF	+	1	70	70	GAA	–	–	−1
rrnS	+	70	1045	976	–	–	–	−1
trnV	+	1045	1115	71	TAC	–	–	38
rrnL	+	1154	2708	1555	–	–	–	−1
trnL2	+	2708	2781	74	TAA	–	–	6
nad1	+	2788	3758	971	–	ATG	TA(A)	18
trnI	+	3777	3848	72	GAT	–	–	9
trnQ	−	3858	3928	71	TTG	–	–	−1
trnM	+	3928	3997	70	CAT	–	–	0
nad2	+	3998	5038	1041	–	ATG	TAG	−2
trnW	+	5037	5106	70	TCA	–	–	1
trnA	−	5108	5176	69	TGC	–	–	2
trnN	−	5179	5251	73	GTT	–	–	5
trnC	−	5257	5323	67	GCA	–	–	−1
trnY	−	5323	5393	71	GTA	–	–	1
cox1	+	5395	6945	1551	–	GTG	AGG	−9
trnS2	−	6937	7010	74	TGA	–	–	2
trnD	+	7013	7081	69	GTC	–	–	1
cox2	+	7083	7766	684	–	ATG	TAA	1
trnK	+	7768	7838	71	TTT	–	–	1
atp8	+	7840	8007	168	–	ATG	TAA	−10
atp6	+	7998	8681	684	–	ATG	TAA	−1
cox3	+	8681	9464	784	–	ATG	T(AA)	0
trnG	+	9465	9533	69	TCC	–	–	0
nad3	+	9534	9882	349	–	ATC	GAA	−5
trnR	+	9888	9958	71	TCG	–	–	1
nad4l	+	9960	10,256	297	–	ATG	TAA	−7
nad4	+	10,250	11,627	1378	–	ATG	T(AA)	0
trnH	+	11,628	11,697	70	GTG	–	–	0
trnS1	+	11,698	11,763	66	GCT	–	–	0
trnL1	+	11,764	11,834	71	TAG	–	–	0
nad5	+	11,835	13,652	1818	–	ATG	TAA	15
cytb	+	13,668	14,810	1143	–	ATG	TAA	4
trnT	+	14,815	14,883	69	TGT	–	–	23
trnP	−	14,907	14,976	70	TGG	–	–	8
nad6	−	14,985	15,506	522	–	ATG	AGG	3
trnE	−	15,510	15,579	70	TTC	–	–	0
D-loop	+	15,580	16,899	1320	–	–	–	–

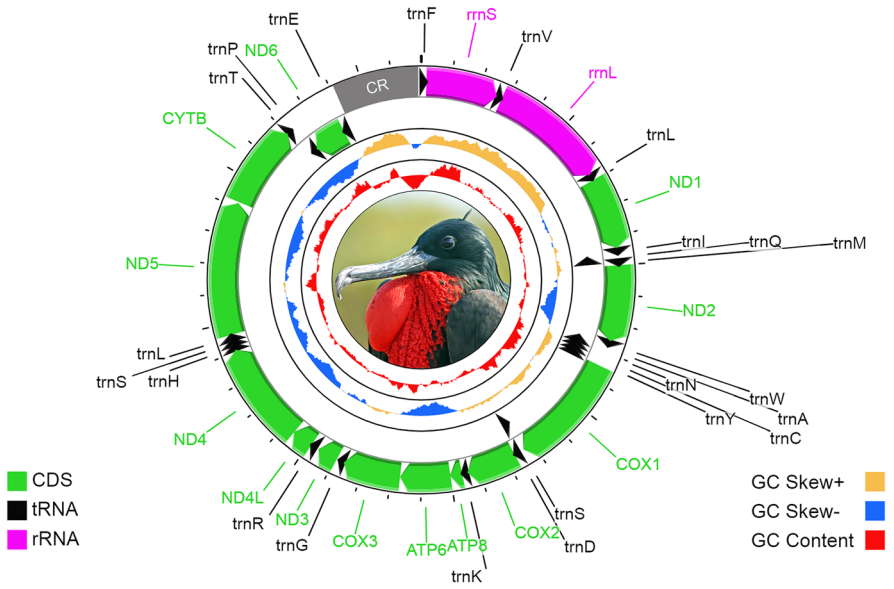

Fig. 1 The spherical representation of mitochondrial genome of *F. minor*. Direction of gene transcription is indicated by arrows. PCGs are shown as green arrows, rRNA genes as violet arrows, tRNA genes as black arrows, and non-coding control region as gray rectangle. The Gcskew is plotted using orange and blue colors, and GC content is plotted using red color sliding window as the deviation from the average in the complete mitogenome. The species photograph was acquired from the Wikimedia Commons, the free media repository under creative commons attribution-share alike 3.0 unported and edited manually in Adobe Photoshop CS 8.0

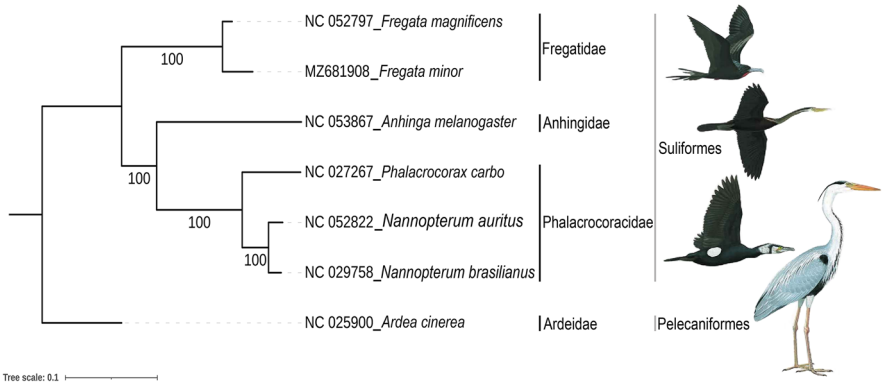

Fig. 2 The ML phylogeny based on the concatenated nucleotide sequences of 13 PCGs showing the phylogenetic relationship of *F. minor* with other Suliformes species. The bootstrap support values were superimposed with each node. The illustrations of representative birds were acquired from the digital edition of 'Birds of the Indian Subcontinent' by Grimmett et al. (2014) and edited manually in Adobe Photoshop CS 8.0

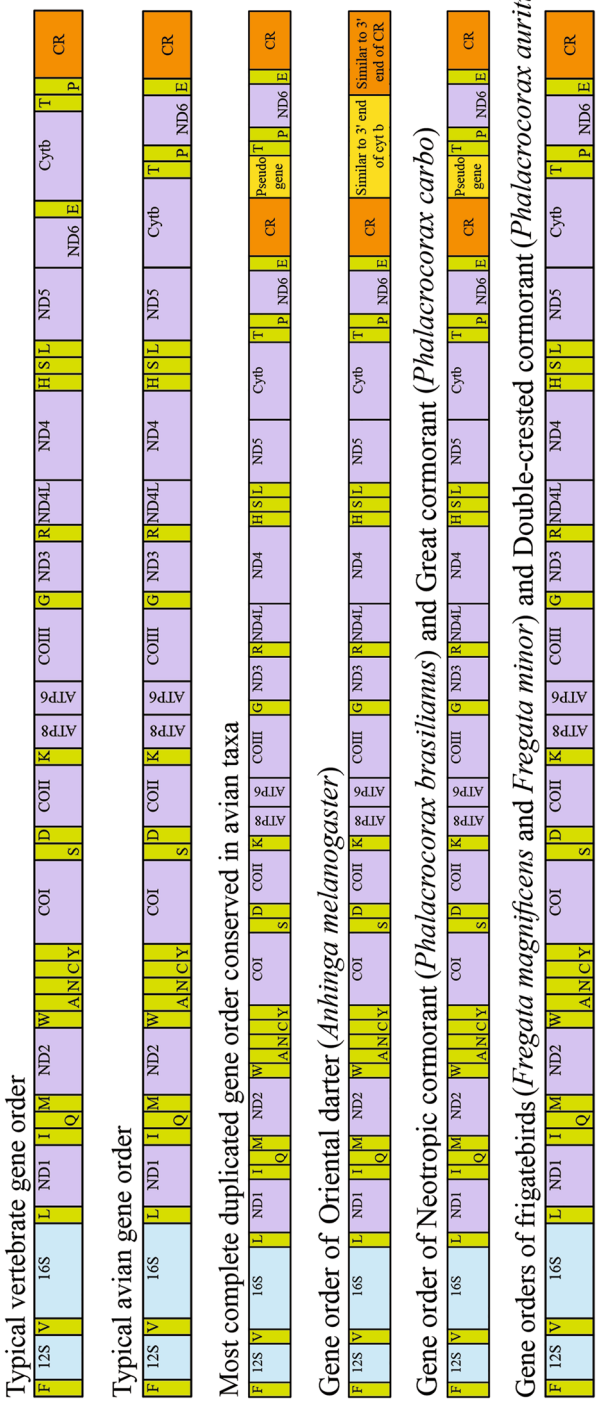

Fig. 3 Gene arrangement scenario of *F. minor* and compared with other Suliformes species

separated all the Suliformes species with high bootstrap support (Fig. 2). The studied species, *F. minor* shows a close relationship with its sister species *F. magnificens*. The members of Fregatidae, Phalacrocoracidae, and Anhingidae (order Suliformes) showed cohesive clustering and branched from Ardeidae species (order Pelecaniformes) with high bootstrap supports. The newly generated complete mitogenome of *F. minor* might be useful for further in-depth phylogenetic relationships with more taxon sampling from different taxonomic groups as well as in population genetics analysis.

The common mitochondrial gene arrangement in birds is unique and derived from the typical vertebrate gene order (Desjardins and Morais 1990). Later on, the fully duplicated region with pseudogenization or loss of selected genes and/or the control region was found in the mitogenome of Gruidae, Suliformes, Pelecaniformes, Procellariiformes, Bucerotiformes, and Psittaciformes species (Abbott et al. 2005; Gibb et al. 2007, 2013; Morris-Pocock et al. 2010; Sammler et al. 2011; Zhou et al. 2014; Lounsberry et al. 2015; Eberhard and Wright 2016; Akiyama et al. 2017; Rodrigues et al. 2017; Zhang et al. 2017; Urantowka et al. 2018). However, limited taxon sampling was considered to reveal gene order scenario of Suliformes (Urantówka et al. 2020). We observed the gene order of the Neotropic Cormorant, *Phalacrocorax brasilianus* and the Great Cormorant, *Phalacrocorax carbo* have the fully duplicated region gene order as described earlier (Urantówka et al. 2020). However, the frigatebirds (*F. magnificens*, and *F. minor*) and the Double-crested cormorant, *Phalacrocorax auritus* have the typical avian gene order. In addition, the duplication of the 3′ end of both Cytb and CR were detected in the Oriental Darter, *Anhinga melanogaster* mitogenome (Fig. 3). Hence, we speculate that the mitochondrial gene arrangements of the order Suliformes) is not congruent with the earlier hypothesis and phylogenetic relationship (Urantówka et al. 2020). However, to confirm the complete mitochondrial gene order perception within the ancestral lineages and all modern taxa, further studies with many avian representatives are necessitated.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10528-021-10156-6.

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Data Availability The data that support the findings of this study are openly available in GenBank of NCBI at https://www.ncbi.nlm.nih.gov, reference accession number MZ681908.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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