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Complete mitochondrial genome characterisation of *Ratha longimana* (H. Milne Edwards, 1834) from the western Atlantic Ocean, with a phylogeny of the Xanthidae (Decapoda: Brachyura)

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ABSTRACT

The longhand rubble crab *Ratha longimana* inhabits coral reefs and rocky shores in the subtropical and tropical western Atlantic Ocean. This species was long considered to be the only chlorodielline species present in the area, but has since been transferred to the genus *Ratha* Lasley, Lai & Thoma, 2013 and is now thought to belong to an undescribed subfamily within Xanthidae MacLeay, 1838. Here we provide a complete mitochondrial assemblage and characterisation of this species. The assembled mitochondrial genome (hereafter mitogenome) of *R. longimana* is 15,819 bp in length and contains 13 protein coding genes (PCGs), 22 transfer RNA (tRNA) genes, and two ribosomal RNA (rRNA) genes. The 22 tRNA genes range from 62 to 69 bp in length. A mitochondrial gene order (MGO) analysis revealed a transposition of the tRNA genes Val (V) and 12S rRNA (rrnS) when compared to the ancestral brachyuran gene order, which is in line with earlier studies on xanthoid mitogenomes. Mitogenome data for xanthid crabs (as well as the superfamily Xanthoidea MacLeay, 1838) are currently scarce considering the species richness of the family, limiting the options for phylogenomic studies. This is partially remedied here by providing a new genomic resource for *R. longimana*.

KEY WORDS: Chlorodiellinae, Crustacea, gene order, mitochondrial assemblage

INTRODUCTION

The xanthid species *Ratha longimana* (H. Milne Edwards, 1834), commonly referred to as the longhand rubble crab, inhabits coral reef and rocky shore habitats in the tropical and subtropical western Atlantic Ocean. This species has been recorded from southern Florida, throughout the Caribbean, to the north coast of Brazil (Lasley *et al.*, 2013), and occurs at shallow depths as well as to 154 m in the Lesser Antilles (Poupin, 2018). This crab was originally described as *Chlorodius longimanus*, but Lasley *et al.* (2013) placed the species in *Ratha* Lasley, Lai & Thoma, 2013, based on morphological and molecular data. A multimarker approach on the subfamily Chlorodiellinae revealed its polyphyletic nature and showed that *Ratha* likely needs to be excluded from the subfamily. Its position in Xanthidae MacLeay, 1838 was nevertheless unclear and the species was therefore considered as *incertae subfamiliae* (Lasley *et al.*, 2015). Mendoza *et al.* (2022) consider *Ratha longimana* a member of a yet undescribed xanthid subfamily (provisionally termed subfamily X1). The exclusion of *Ratha* from Chlorodiellinae Ng & Holthuis, 2007 was not followed by Poore & Ahyong (2023), who retained it as a member of this subfamily.

Xanthoid crabs are important ecological components of marine ecosystems. They occupy various ecological niches as symbionts, primary and secondary consumers, and serve as a food source for many other marine taxa (Mendoza *et al.*, 2022). The superfamily Xanthoidea MacLeay, 1838 is considered monophyletic and to date has 764 extant species in seven families: Antrocarcinidae Ng & Chia, 1994 (4 species), Garthiellidae Mendoza & Manuel-Santos, 2012 (3 species), Linnaeoxanthidae Števčić, 2005 (2 species), Nanocassiopidae Števčić, 2013 (12 species), Panopeidae Ortmann, 1893 (68 species), Pseudorhombilidae Alcock, 1900 (64 species), and Xanthidae McLeay, 1838 (611 species) (DecaNet, 2024). The Xanthidae is by far the largest family of the seven xanthoid families, and one of the

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five largest decapod families (De Grave *et al.*, 2023). The family comprises 13 subfamilies (Ng *et al.*, 2008; DecaNet, 2024). The number of recognized families and subfamilies in the Xanthoidea, however, are subject of ongoing taxonomic revisions and drastic restructuring of the existing xanthid subfamily classification is impending (Mendoza *et al.*, 2022).

Our aim was to assemble the mitogenome of *Ratha longimana* in order to increase the amount of genetic information available for the species. Moreover, we conducted a mitochondrial gene order (MGO) analysis, comparing the MGO of *R. longimana* with the ancestral Brachyura MGO, and we provide a phylogeny of Xanthoidea based on all the currently available mitogenomes for this superfamily to facilitate future research on the classification of *R. longimana* as well as subfamilial classification in Xanthidae.

MATERIAL AND METHODS

Sampling

Five specimens of *R. longimana* were collected from Piscadera Bay, Curaçao (in front of CARMABI research station; 12°7′18.1704″N, 68°58′10.66″W) on 14 March 2022, and preserved in 80% ethanol. Tissue from one specimen was used for *cox1* barcoding (partial, Folmer *et al.*, 1994), a second collected specimen was sent to BGI (BGI Tech Solutions, Hong Kong) for DNA extraction following standard manufacturer's protocol and sequenced in a DNBseq system (MGI, Hong Kong) using a short-insert library in a 2 × 150 cycle. A total of 119,311,942 pairs of (PE) reads were generated and used in the subsequent analyses. The specimen used for Sanger sequencing and the remaining three specimens are vouchered at the University of Groningen, Groningen, The Netherlands.

Mitochondrial genome assembly and annotation

The mitogenome was *de novo* assembled using NOVOPlasty 4.3.1 (Dierckxsens *et al.*, 2017) on the Hábrók high performance computing cluster of the University of Groningen. The assemblies used a seed of the *cox1* gene of the barcoded *R. longimana* specimen from Curaçao. The assembled mitogenome was annotated using MITOS (Bernt *et al.*, 2013) on the Galaxy server, and subsequently start and stop codon corrections were done manually in Geneious Prime 2023.1.2 using *Atergatis floridus* as a reference mitogenome (GenBank accession numbers are provided in Table 1).

Mitochondrial gene order

The mitochondrial gene order (MGO) of *R. longimana* was compared to that of the brachyuran ground-pattern MGO, the most common gene order within Brachyura (Wang *et al.*, 2018).

Phylogenetic analysis

A concatenated dataset consisting of 13 protein coding genes (PCGs) and two ribosomal RNA genes (rRNA; rrnS: 12S ribosomal RNA and rrnL: 16S ribosomal RNA) were used in the phylogenetic analyses. These genes were aligned separately using MAFFT v.7.407 (Katoh & Standley, 2013), and PartitionFinder 2 was applied to detect the best partition scheme, as well as the best-fit substitute models for the respective partitions (Supplementary material Table S2). All available Xanthoidea mitogenomes on GenBank were included in this analysis, and the three panopeid species, *Eurypanopeus depressus* (Smith, 1869), *Panopeus herbstii* H. Milne Edwards, 1834, and *Rhithropanopeus harrisii* (Gould,1841) were used as outgroups (Table 1). Maximum likelihood (ML) and Bayesian Inference (BI) approaches were used for the phylogenetic analyses. ML was inferred in IQ-TREE v.1.6.8 (Nguyen *et al.*, 2015) with 20,000 ultrafast bootstraps. MrBayes v.3.2.7 (Ronquist *et al.*, 2012) was used for the BI analysis. Two independent Markov Chain Monte Carlo (MCMC) runs were performed, each with four chains for 1 million generations and sampled every 1,000 iterations. The average standard deviation of split frequencies was 0.03. The trees were visualised in FigTree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

RESULTS

Mitochondrial genome

The assembled mitogenome of *Ratha longimana* is 15,819 bp in length and contains 13 protein coding genes, 22 transfer RNA (tRNA) genes, and two ribosomal RNA (rRNA) genes. The 22 tRNA genes range 62–69 bp in length. The nucleotide composition of the entire mitochondrial genome of *R. longimana* revealed an overall A+T bias (71.9%; base composition: A = 33.6%, T = 38.3%, C = 17.6%, and G = 10.4%). The assembled mitogenome is visualised in Figure 1, while details on the arrangement and annotation of the mitogenome can be found in Supplementary material Table S3.

Mitochondrial gene order

The MGO analysis revealed the transposition of the tRNA genes Val (V) and 12S rRNA (rrnS), when compared to that of the brachyuran basic mitochondrial gene order (Fig. 2).

Phylogenetic analysis

The BI and ML analyses generated phylogenetic trees with similar overall topologies, the three species of Panopeidae were used as outgroups (Fig. 3, Supplementary material S1). *Ratha longimana* is placed basal to the main clade containing the majority of xanthid species. The subfamilies Cymoinae Alcock, 1898 and Polydectinae Dana, 1851 are not included in this main clade, but instead cluster together with full support.

DISCUSSION

The nucleotide composition of the entire mitochondrial genome was A+T biased (71.9%), which is in line with that of other brachyurans (e.g. Ki *et al.*, 2009; Wang *et al.*, 2018; Duan *et al.*, 2022; Bravo *et al.*, 2023). An A+T bias is the norm not only in the mitochondrial genomes of most crustaceans and a G+C bias is considered a rare occurrence (but see Tan *et al.*, 2019).

Wang *et al.* (2021) reported that 16 brachyuran families share the ancestral brachyuran MGO, including Xanthidae. Our results nevertheless show that *Ratha longima* has one transposition (tRNA-Val and 12S) compared to the ancestral brachyuran MGO. This result is in agreement with the results of Jennings *et al.* (2021) and Duan *et al.* (2022), who found the same MGO (termed

Table 1. List of species of Xanthoidea included in this study and their GenBank accession numbers. Subfamilial classification is added based on DecaNet (2024), as well as the newly proposed classification by Mendoza *et al.* (2022).

Family	Species	Subfamily (based on WoRMS to DecaNet, 2024)	Subfamily as proposed by Mendoza *et al.* (2022)	GenBank accession number	Reference
Panopeidae	*Eurypanopeus depressus* (Smith, 1869)	-	-	MN399962	Jennings *et al.*, 2021
Panopeidae	*Panopeus herbstii* H. Milne Edwards, 1834	-	-	MT024990	Jennings *et al.*, 2021
Panopeidae	*Rhithropanopeus harrisii* (Gould, 1841)	-	-	MW446897	McDonald *et al.*, unpublished data
Xanthidae	*Actaeodes hirsutissimus* (Rüppell, 1830)	Actaeinae	Subfamily X5	OP672436	Gries *et al.*, 2024
Xanthidae	*Atergatis floridus* (Linnaeus, 1767)	Zosiminae	Zosiminae	MG792341	Karagozlu *et al.*, 2018a
Xanthidae	*Atergatis integerrimus* (Lamarck, 1818)	Zosiminae	Zosiminae	MG792342	Karagozlu *et al.*, 2018b
Xanthidae	*Chlorodiella nigra* (Forskål, 1775)	Chlorodiellinae	Etisinae	OP672433	Gries *et al.*, 2024
Xanthidae	*Cymo andreossyi* (Audouin, 1826)	Cymoinae	Cymoinae	OP672426	Gries *et al.*, 2024
Xanthidae	*Cymo quadrilobatus* Miers, 1884	Cymoinae	Cymoinae	OP672425	Gries *et al.*, 2024
Xanthidae	*Etisus anaglyptus* H. Milne Edwards, 1834	Etisinae	Etisinae	MG751773	Karagozlu *et al.*, 2018c
Xanthidae	*Etisus dentatus* (Herbst, 1785)	Etisinae	Etisinae	MW122295	Liu & Shen, 2021
Xanthidae	*Etisus laevimanus* Randall, 1840	Etisinae	-	NC086869	Lee *et al.*, unpublished data
Xanthidae	*Leptodius exaratus* (H. Milne Edwards, 1834)	Xanthinae	? Etisinae (based on *Leptodius* spp.)	MF198250	Liu *et al.*, unpublished data
Xanthidae	*Leptodius sanguineus* (H. Milne Edwards, 1834)	Xanthinae	Etisinae	KT896744	Sung *et al.*, 2016
Xanthidae	*Lybia plumosa* Barnard, 1947	Polydectinae	Polydectinae	OP672427	Gries *et al.*, 2024
Xanthidae	*Lybia tessellata* (Latreille in Milbert, 1812)	Polydectinae	Polydectinae	OP672424	Gries *et al.*, 2024
Xanthidae	*Macromedaeus distinguendus* (De Haan, 1835)	Xanthinae	? Etisinae (based on *M. crassimanus*)	MW118602	Wang *et al.*, 2021
Xanthidae	*Polydectus cupulifer* (Latreille in Milbert, 1812)	Polydectinae	Polydectinae	OP672418	Gries *et al.*, 2024
Xanthidae	*Pseudoliomera* sp.	Actaeinae	Subfamily X7	OP672432	Gries *et al.*, 2024
Xanthidae	*Ratha longimana* (H. Milne Edwards, 1834)	Chlorodiellinae	Subfamily X1	PP546287	Herein
Xanthidae	*Zosimus aeneus* (Linnaeus, 1758)	Zosiminae	Zosiminae	OP672435	Gries *et al.*, 2024

'XanGo') for the six xanthoid species used in their studies. The different MGO rearrangements within Eubrachyura highlight the potential use of MGO patterns in studies on higher level classifications in Brachyura (Jennings *et al.*, 2021; Duan *et al.*, 2022).

Our phylogenetic reconstruction (Fig. 3, Supplementary material S1) only contains 18 xanthid species and three panopeid species. The observed clustering of the subfamilies Cymoinae and Polydectinae is, however, in agreement with Mendoza *et al.* (2022), and the clustering of the remaining species aligns well with the proposed new subfamilial classification. *Ratha longimana* clusters separately in the phylogenetic trees (Fig. 3, Supplementary material Fig. S1), which is in line with earlier studies (Lasley *et al.*, 2013; Mendoza *et al.*, 2022). In a study on American mud crabs, Thoma *et al.* (2014) retrieved *R. longimana* in a highly supported clade representing species of Xanthidae *sensu stricto*. Mendoza *et al.* (2022), however, retrieved two clades with western Atlantic (and some tropical eastern Pacific) species: 'Paraxanthinae' and subfamily X1, containing *Ratha longimana*.

While the family Xanthidae is most diverse in tropical West and Indo-West Pacific waters, species of this family are also a common component of tropical and subtropical assemblages in the western Atlantic (Serène, 1984). Mitogenome data for the species-rich Xanthidae crabs (as well as for the superfamily Xanthoidea) are currently scarce considering the species richness of the family, limiting the options for meaningful phylomitogenomic studies. To improve our understanding of the phylogenetic position of *R. longimana,* target taxa for obtaining (mito) genomic data include western Atlantic and eastern Pacific species in the subfamilies X1 and 'Paraxanthinae' (Thoma *et al.*, 2014; Mendoza *et al.*, 2022).

Mitochondrial genomes offer high species-level characterization, low sequencing costs, and an ease of data handling. Phylomitogenomic studies have has so far substantially contributed to our understanding of phylogenetic relationships in brachyuran crabs and beyond (e.g. Wang *et al.*, 2018; Chen *et al.*, 2019; Duan *et al.*, 2022). Moreover, mitogenomic data can provide insights into evolutionary pressures shaping the diversity and abundance

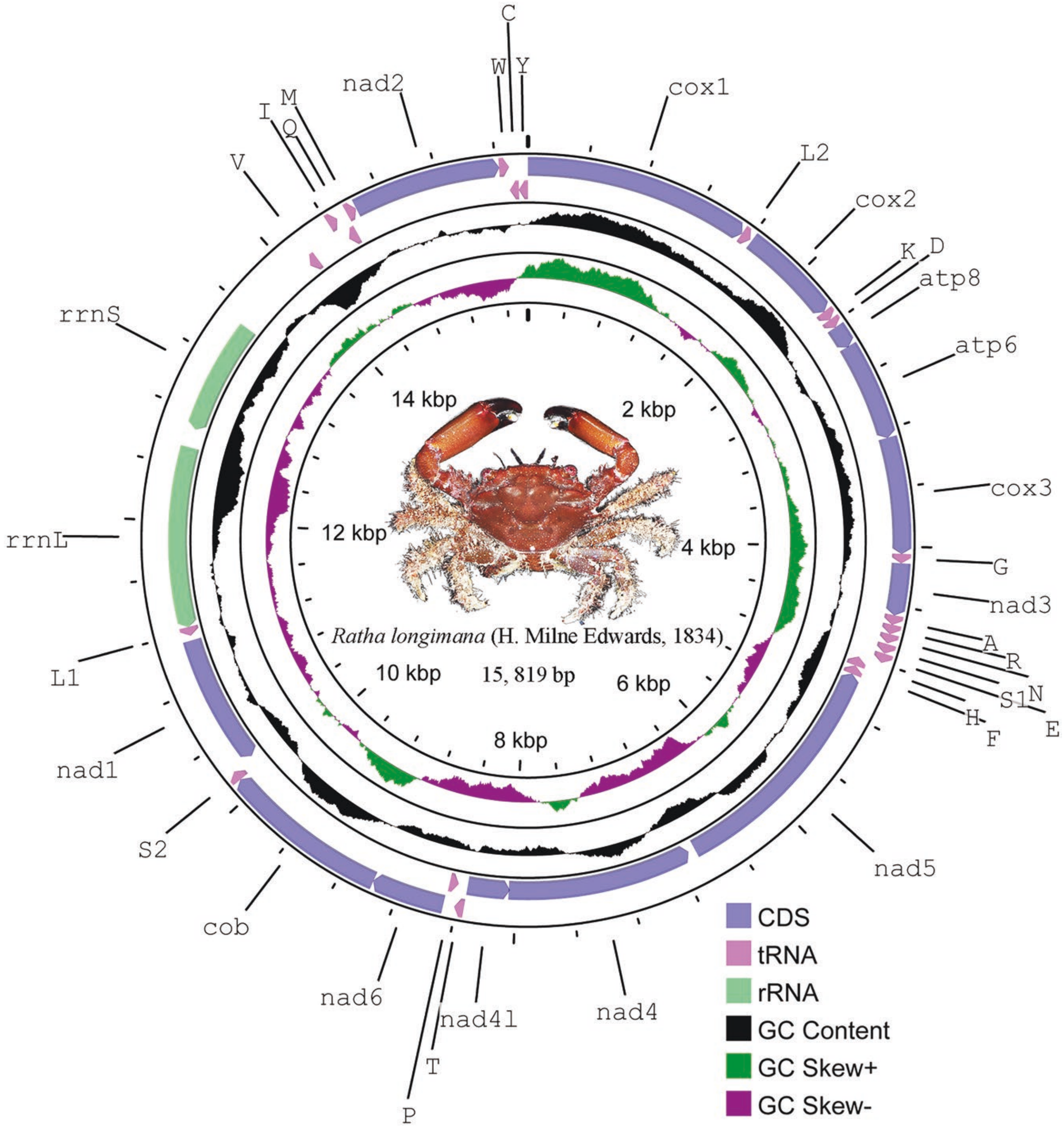

Figure 1. Visualisation of the assembled mitochondrial genome of *Ratha longimana*. Photo by Gustav Paulay/Arthur Anker.

Figure 2. Mitochondrial gene order of ancestor Brachyura (above) and *Ratha longimana* (below), showing the transposition of the tRNA-A genes Val (V) and 12S rRNA (rrnS).

in species-rich taxa, and has, for example, been used in studies focussing on adaptations to life in the deep sea (Ramos *et al.*, 2023), to terrestriality (Lü *et al.*, 2023), to a symbiotic lifestyle (Xu *et al.*, 2023), as well as in overarching studies on comparative mitochondrial genomics (Gendron *et al.*, 2024). It will thus be possible to shed light on the evolution and diversity of xanthoid

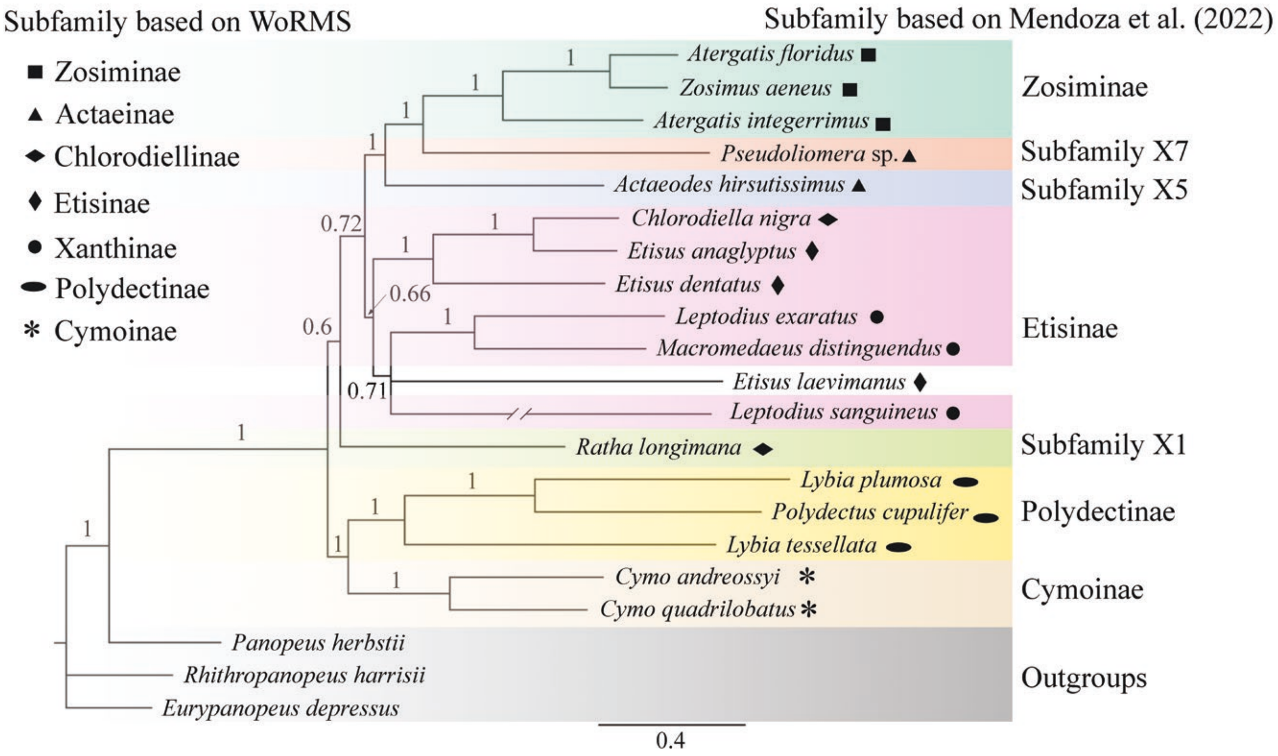

Figure 3. Bayesian phylogenetic tree based on a concatenated dataset of all available Xanthoidea mitogenomes, with three Panopeidae species as outgroups.

crabs and their phylogenetic relationship with other families of Brachyura with the increase in genomic studies of this nature.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Figure. Maximum likelihood phylogenetic tree based on the concatenated dataset of all available Xanthidae mitogenomes.

S2 Table. The best partition scheme for the phylogenetic analyses, and the best-fit substitute models for the respective partitions.

S3 Table. The annotation of the mitochondrial genome of *Ratha longimana*.

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