






The complete mitochondrial genome and phylogenetic analysis of hydrozoan jellyfish *Eirene ceylonensis* (Cnidaria, Hydrozoa, Eirenidae) in the coastal sea of Qinhuangdao, China

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ABSTRACT

Eirene ceylonensis, a hydrozoan jellyfish species with a complex polymorphic life cycle, is widely distributed in the Chinese coastal sea. In this study, we conducted sequencing and analysis of the first complete mitochondrial genome of *E. ceylonensis*, obtained from the coastal sea of Qinhuangdao, China. The linear mitochondrial genome is 14,997 bp in length with the overall AT content being 72.8%, encoding 13 protein-coding genes (PCGs), two transfer RNA (tRNA) genes (*tRNA-Met* and *tRNA-Trp*) and two ribosomal RNA (rRNA) genes (*rrnS* and *rrnL*). Phylogenetic analysis of 13 PCGs suggests that the *E. ceylonensis* is closely related to *Laomedea flexuosa*. The availability of the complete mitochondrial genome of *E. ceylonensis* will be useful for studying the evolutionary relationships of hydrozoan jellyfish species.

ARTICLE HISTORY

Received 14 September 2023
Accepted 29 November 2023

KEYWORDS

Eirene ceylonensis; hydrozoa; mitogenome; phylogenetic analysis

1. Introduction



Jellyfish disasters occurred frequently in the coastal water of Qinhuangdao in the Bohai Sea, which is known for its high diversity of jellyfish species (Yuan et al. 2021). The hydrozoan jellyfish are a diverse group of aquatic animals with various morphologies and life cycles, and hydrozoan is an ideal model for studying germ cell development due to their simplicity of organization and manipulation, as well as their transparency (Amiel et al. 2010). *Eirene ceylonensis* Browne 1905, once named as the *Irene ceylonensis*, was first collected from the Galle Bay in the Gulf of Manaar (Browne 1905). It is a typical marine hydrozoan species in the family Eirenidae (Cnidaria: Hydrozoa: Leptothecata), has a worldwide distribution and is also widely found in the Chinese coastal seas (Zhang 1979). In recent years, *E. ceylonensis* has become a dominant species in many areas of the Bohai Sea, including the southwest part (Liu et al. 2023), Qinhuangdao coastal waters (Xu et al. 2022), and the Yellow River estuary and its adjacent area (Li et al. 2018). *Eirene ceylonensis* has a complex polymorphic life cycle that includes both the medusa and polyp phases, with the medusa phase having an umbrella diameter of only about 15–25 mm (Xu et al. 2014). And the morphology of the jellyfish varies greatly in different periods, so these characteristics may hinder accurate identification of


the jellyfish species. Therefore, we conducted mitogenome sequencing of *E. ceylonensis*. The first complete mitogenome of *Eirene* species will be useful for species identification, phylogenetic studies, and biogeographical research of hydrozoan jellyfish.

2. Materials and methods

2.1. Sample collection

A total of five *E. ceylonensis* specimens were collected from the coastal sea of Qinhuangdao (39.916°N, 119.620°E) in the Bohai Sea, China, using the plankton net on 13 August 2022. Firstly, the specimens (voucher CMY22Q801–CMY22Q805) underwent microscopic examination for identification purpose prior to genome sequencing. These specimens have the same physiological structure characteristics, except for the umbrella diameter. For example, the voucher CMY22Q801 (Figure 1), which flat and thin umbrella is about 10 mm in diameter with 48 tentacles, and four linear gonads extending from the base of the peduncle to near the margin of the umbrella. These characteristics are basically consistent with the hydrozoan jellyfish *E. ceylonensis* (Browne 1905). Then, the voucher CMY22Q801 was frozen using liquid nitrogen for the DNA extraction. The remaining specimens were stored in

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 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/23802359.2023.2290845>.

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absolute ethanol and deposited at Hebei Normal University of Science and Technology (<https://www.hevttc.edu.cn/>, contact person: Yang Chen, email: cy4043@hevttc.edu.cn).

2.2. Methods

Total DNA was extracted from the muscle tissue of *E. ceylonensis* voucher CMY22Q801 using a DNeasy Blood & Tissue Kit (QIAGEN, Germany) according to the manufacturer's instructions. The whole genome was sequenced using an Illumina HiSeq 2500 platform (paired-end 150 bp reads) at Novogene Co., Ltd. (Beijing, China). The sequencing results (about 16.86 M raw paired reads) were assembled into the

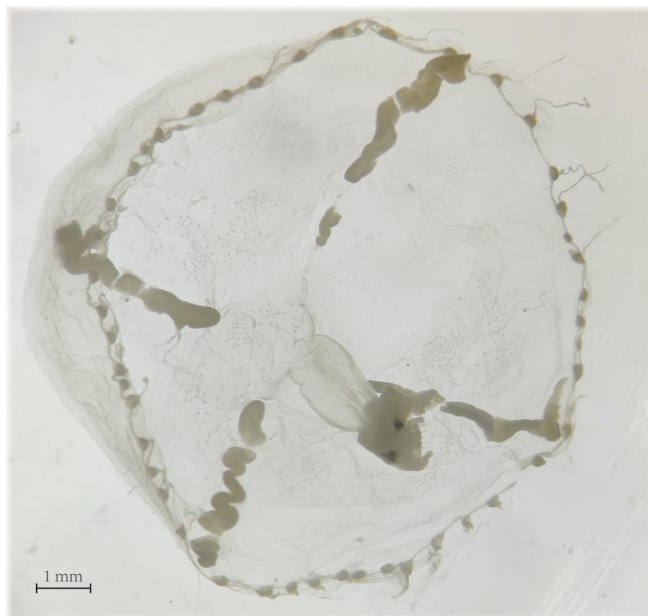


Figure 1. The reference image of *Eirene ceylonensis* voucher CMY22Q801. This reference image was taken by Yang Chen, the first author listed in this study.

mitogenome using GetOrganelle v 1.7.2 (Jin et al. 2020), with SPAdes v 3.13.2 as the assembler (Bankevich et al. 2012). The read coverage depth map (Figure s1), extracted using the Integrative Genomics Viewer (Robinson et al. 2011), is presented in supplementary material. The ORFfinder and MITOS (Bernt et al. 2013) were used to identify the protein-coding genes (PCGs), transfer RNA (tRNA) genes, and ribosomal RNA (rRNA) genes in the mitogenome. The gene map of *E. ceylonensis* mitogenome was generated using the Organellar Genome DRAW (Greiner et al. 2019).

By searching the NT database (www.ncbi.nlm.nih.gov), there were 22 hydrozoan species with complete mitogenome sequences available, including 12 complete mitochondrial genomes with associated publications (Table 1). For phylogenetic analysis, the 23 complete mitochondrial genomes from hydrozoan species were included, including *E. ceylonensis*. To enhance the resolution of the phylogenetic relationship among hydrozoan jellyfish species, two mitogenomes of Scyphozoa species of Cnidaria, *Nemopilema nomurai* (KY454767) (Wang and Sun 2017) and *Aurelia aurita* (DQ787873) (Shao et al. 2006) were used as outgroup. Amino acid sequences of 13 PCGs from the 25 species were individually aligned using MAFFT v7.471 (Katoh and Standley 2013). The alignments were then trimmed using trimal v1.2 (Capella-Gutiérrez et al. 2009) and concatenated using Phyutility (Smith and Dunn 2008). The incongruence length difference (ILD) test was conducted using PAUP4.0 (Swofford 2002) with the same parameters in our previous work (Chen et al. 2021). Finally, a Maximum-likelihood (ML) phylogenetic tree was constructed using IQtree v1.6.12 (Trifinopoulos et al. 2016) with 1000 bootstraps replicates.

3. Results

Through microscopic examination, the voucher CMY22Q801 can be basically determined as *E. ceylonensis* (Figure 1). The complete mitogenome of *E. ceylonensis* is linear in structure

Table 1. The 25 complete mitochondrial genomes of Cnidaria species used for phylogenetic analysis in this study.

Species name	Accession number	Class	Order	Reference
<i>Agalma elegans</i>	OQ957203	Hydrozoa	Siphonophorae	unpublished
<i>Apolemia rubriversa</i>	OQ957214	Hydrozoa	Siphonophorae	unpublished
<i>Aurelia aurita</i>	DQ787873	Scyphozoa	Semaeostomeae	Shao et al. 2006
<i>Bargmannia elongata</i>	OQ957202	Hydrozoa	Siphonophorae	unpublished
<i>Bargmannia lata</i>	OQ957216	Hydrozoa	Siphonophorae	unpublished
<i>Blackfordia virginica</i>	MW376866	Hydrozoa	Leptothecata	Seo et al. 2021b
<i>Cladonema multiramosum</i>	MZ747707	Hydrozoa	Anthoathecata	Fang et al. 2022
<i>Clava multicornis</i>	JN700935	Hydrozoa	Anthoathecata	Kayal et al. 2012
<i>Cubaia aphrodite</i>	JN700942	Hydrozoa	Limnomedusae	Kayal et al. 2012
<i>Eirene ceylonensis</i>	OR149020	Hydrozoa	Leptothecata	This study
<i>Erenna sirena</i>	OQ957209	Hydrozoa	Siphonophorae	unpublished
<i>Eutima japonica</i>	MW066348	Hydrozoa	Leptothecata	Seo et al. 2021a
<i>Halistemma rubrum</i>	OQ957197	Hydrozoa	Siphonophorae	unpublished
<i>Hydra oligactis</i>	EU237491	Hydrozoa	Anthoathecata	Kayal and Lavrov 2008
<i>Hydra sinensis</i>	JX089978	Hydrozoa	Anthoathecata	Pan et al. 2014
<i>Laomedea flexuosa</i>	JN700945	Hydrozoa	Leptothecata	Kayal et al. 2012
<i>Nemalecium lighti</i>	MZ457217	Hydrozoa	Anthoathecata	Macher et al. 2021
<i>Nemopilema nomurai</i>	KY454767	Scyphozoa	Rhizostomeae	Wang and Sun 2017
<i>Resomia ornicephala</i>	OQ957218	Hydrozoa	Siphonophorae	Unpublished
<i>Rhizophysa eysenhardtii</i>	OQ957206	Hydrozoa	Siphonophorae	Unpublished
<i>Spirocodon saltatrix</i>	MT150265	Hydrozoa	Anthoathecata	Seo et al. 2020
<i>Stephalia dilata</i>	OQ957207	Hydrozoa	Siphonophorae	Unpublished
<i>Stephanomia amphitridis</i>	OQ957194	Hydrozoa	Siphonophorae	Unpublished
<i>Turritopsis dohrnii</i>	KT020766	Hydrozoa	Anthoathecata	Lisenkova et al. 2017
<i>Turritopsis lata</i>	MW399220	Hydrozoa	Anthoathecata	Seo et al. 2021c

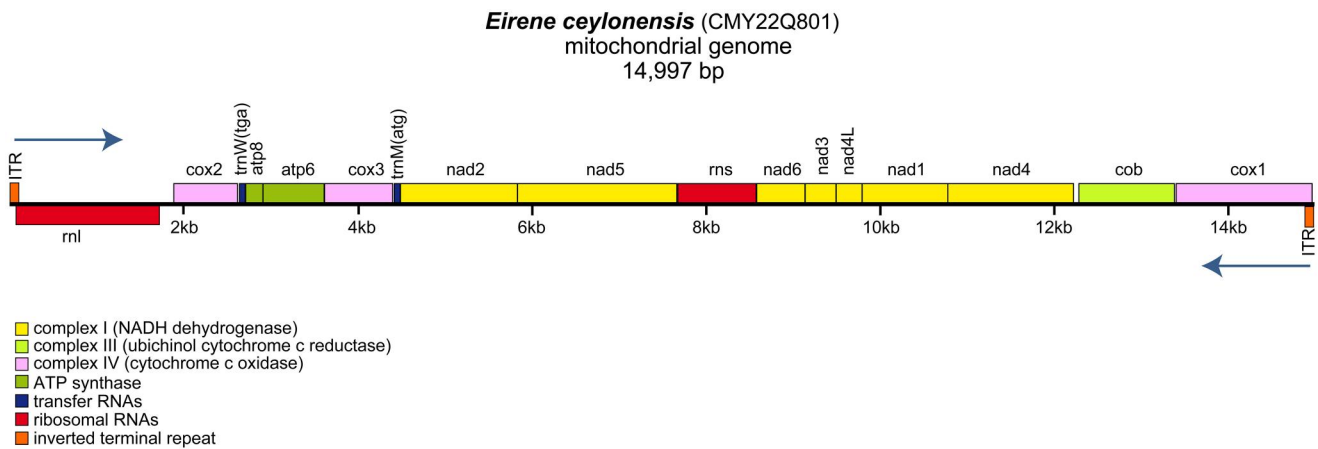


Figure 2. The genome map of *Eirene ceylonensis* (voucher CMY22Q801) mitogenome.

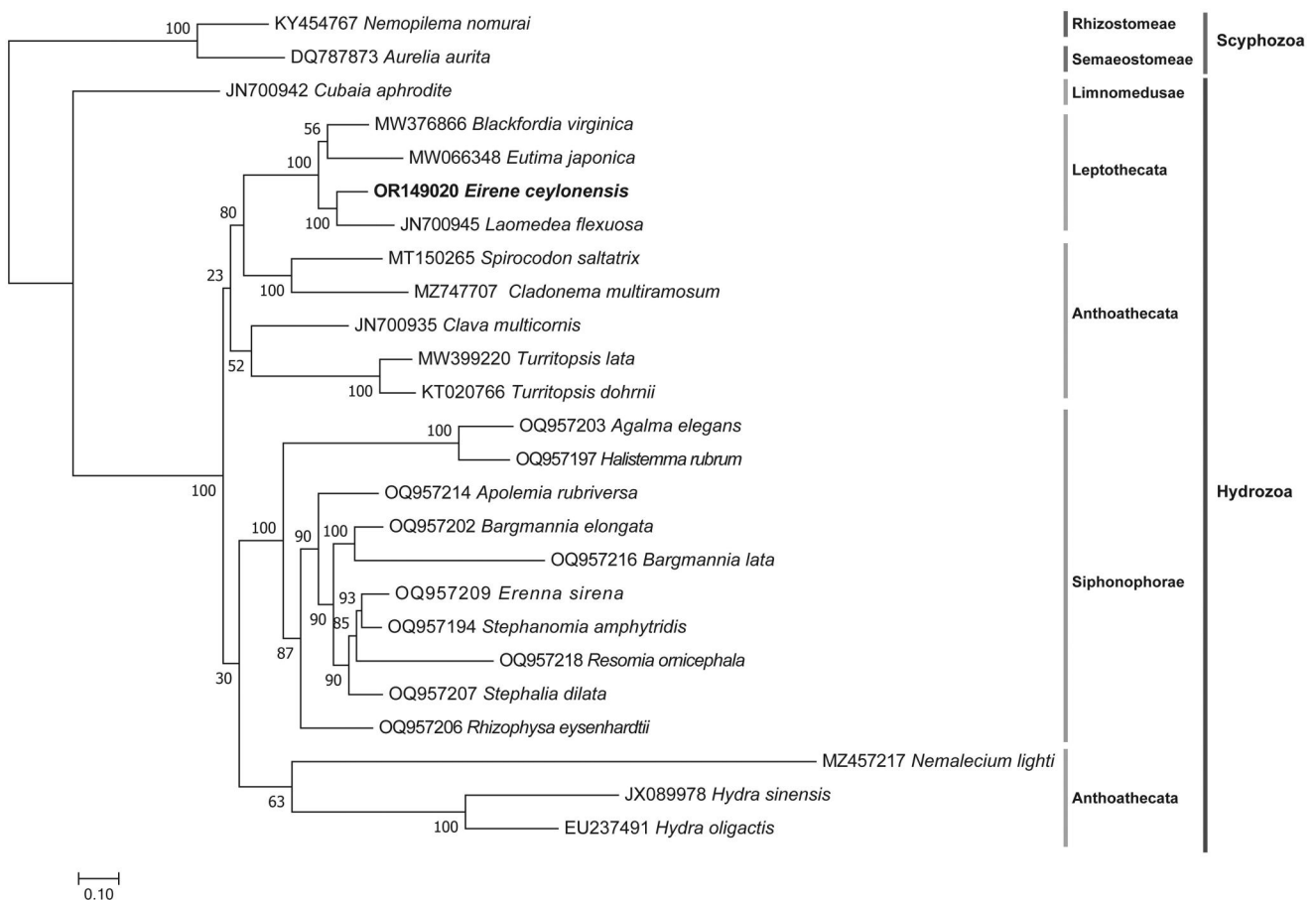


Figure 3. Phylogenetic tree based on maximum likelihood (ML) analysis of amino acid sequence dataset of 13 mitochondrial PCGs in 23 Hydrozoa species and 2 Scyphozoa species.

and 14,997 bp in length (GenBank accession number OR149020), with high AT bias (A: 32.0%; T: 40.8%; C: 12.4%; G: 14.8%). Within the mitogenome of *E. ceylonensis*, 13 protein-coding genes (*cox2*, *atp8*, *atp6*, *cox3*, *nad2*, *nad5*, *nad6*, *nad3*, *nad4L*, *nad1*, *nad4*, *cob*, *cox1*), two tRNAs (*tRNA-Met* and *tRNA-Trp*), and two rRNAs (*rnrS* and *rnrL*) were encoded. Most of these genes were located on the plus strand, except for the *rnrL*, which resided on the minus strand (Figure 2). Moreover, an inverted terminal repeat (ITR) sequence with 105 bp in length was found in the mitogenome of *E. ceylonensis* (Figure s2).

The ILD test ($p=0.01$) indicated that amino acid sequence concatenation of 13 PCGs from 25 species would not affect phylogenetic accuracy (Cunningham 1997). The ML phylogenetic tree revealed that *E. ceylonensis* mitogenome formed a cluster with three other Leptothecata species mitogenomes (Figure 3).

4. Discussion and conclusions

The mitogenome of *E. ceylonensis* exhibits a linear molecular structure with a length of 14,997 bp, which is comparatively

shorter than that of three other Leptothecata species, namely *L. flexuosa* (16,075 bp) (Kayal et al. 2012), *Eutima japonica* (15,315 bp) (Seo et al. 2021a) and *Blackfordia virginica* (15,109 bp) (Seo et al. 2021b). However, the linear molecular structure of the *E. ceylonensis* mitogenome is consistent with the aforementioned Leptothecata species. High AT bias (A + T: 72.8%) is found in the *E. ceylonensis* mitogenome, which is similar to other hydrozoan mitogenomes, such as the *Nemalécium lighti* (A + T: 71.8%) (Macher et al. 2021) and *B. virginica* (A + T: 73.6%) (Seo et al. 2021b). The gene map of the *E. ceylonensis* mitogenome resembles those of *Clytia hemisphaerica*, particularly the ITR structure in the *C. hemisphaerica* mitogenome (GenBank accession number CACVBU010001317) (Leclère et al. 2019). Repeat sequences have been discovered in many hydrozoan mitochondrial genomes with different length, such as the *Hydra oligactis* and *Liriope tetraphylla* (Kayal et al. 2015). However, the function of these ITR structures is still unclear and deserves further exploration. The first reported mitogenome sequence of *E. ceylonensis* in this study will enhance our understanding of the phylogenetic relationship of *Eirene* species. Moreover, it will contribute to future research in phylogenetic analysis, population genetics, and biogeography of the hydrozoans.

Acknowledgement

We would like to thank Dr Xiaobo Yuan for his help in fieldwork and sampling.

Ethical approval

The jellyfish species is not included in the 'List of Protected Animals in China', and the study did not involve endangered or protected species. The approval of sample collection is not required according to the Animal Ethical and Welfare Committee of Hebei Normal University of science and Technology.

Author contribution

YC, conceived and designed the experiments, analyzed the data, prepared figures, and approved the final draft. SD, analyzed the data, prepared figures, and approved the final draft. DS, analyzed the data, prepared figures, and approved the final draft. YW, analyzed the data, prepared figures, reviewed drafts of the paper. JN, analyzed the data, prepared figures, reviewed drafts of the paper. ZL, conceived and designed the experiments, reviewed drafts of the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by Hebei Natural Science Foundation, grant number D2022407010; Science and Technology Project of Hebei Education Department, grant number QN2023194; Doctor Foundation of Hebei Normal University of Science and Technology, grant number 2022YB016; Open Fund Project of Hebei Key Laboratory of Ocean Dynamics, Resources and Environments, grant number HBHY01.

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Data availability statement

The genome sequence data supporting this study's findings are openly available in GenBank of NCBI at <https://www.ncbi.nlm.nih.gov/under> the accession number OR149020. The associated BioProject, Bio-Sample and SRA numbers are PRJNA985931, SAMN35816308, and SRR24984782, respectively.

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