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MITOGENOME REPORT

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Complete mitochondrial genome of the European common barnacle *Perforatus perforatus* Bruguière, 1789 (balanomorpha: balanidae)

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ABSTRACT

This study is the first to sequence the complete mitochondrial genome (mitogenome) of *Perforatus perforatus* Bruguière, 1789 (Balanomorpha: Balanidae). The 15,536-bp long *P. perforatus* mitogenome contained a typical set of animal mitochondrial genes, along with one control region. The *P. perforatus* mitogenome had an inverted gene block (*trnP-ND4L-ND4-trnH-ND5-trnF*) between *trnS*(gct) and *trnT*. This inverted gene block had been detected six species in three subfamilies of the Balanidae family (Balaninae, Acastinae and Megabalaninae), but our results show that it is also present in Concavinae, in which *P. perforatus* is included. The phylogenetic tree based on the concatenated sequences of the 13 protein-coding genes and two rRNA genes showed that *P. perforatus* is closely associated with *Acasta sulcate* and *Balanus trigonus* within Balanidae.

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Mitochondrial genome; balanidae; concavinae; *Perforatus perforatus*; gene inversion

Introduction

As international trade and human movement increase, the emergence of invasive organisms is also increasing. Marine invasive species can disrupt the ecosystem in the given areas by affecting the ecological succession (Gallardo et al. 2016) and ecological pyramid (Giakoumi et al. 2019; Kim et al. 2020). Particularly, invasive barnacle species disrupt local marine ecosystems by competing for space and resources with the native species (Carlton and Newman 2009). Moreover, they can cause economic damage to marine infrastructure facilities when population size increases (Foster and Willan 1979; Kim et al. 2019). The European common barnacle, *Perforatus perforatus*, was frequently observed in European waters, but was first discovered in the ports of Guryongpo, Yangpo, and Gampo in 2006 (Kim and Hong 2010), and is now frequently found in certain ports and bays in the East and South Seas of Korea (Choi et al. 2013; Kim et al. 2020). Currently, 52 species of barnacles have been reported in Korea (National Institute of Biological Resources 2022), but only 11 species have had their mitochondrial genomes (mitogenomes) reported. In this study, we present the first complete mitogenome of *P. perforatus*, covering both the species and its subfamily, Concavinae. Additionally, we conducted a phylogenetic analysis within Balanoidea, a barnacle superfamily. The complete mitogenome sequence of the species will be useful for the understanding of evolutionary characteristics of the species and families in the superfamily Balanoidea and subsequent population-level studies to illustrate expansion characteristics of the species.

Materials and methods

In 2021, an individual of *P. perforatus* was collected from Mulchi-port, Yangyanggun, Gangwondo Province, Korea (Figure 1; 38°9′23″ N, 128°36′32″ E) and was subsequently identified by one of our authors (Hyun Kyong Kim) using several diagnostic characters: parietes conical; dull purple or pinkish; radii white and narrow; scutum triangular; occludent margin straight; articular ridge distinct; and tergum with distinct growth lines and spur longer than wide (Kim 2019). DNA was extracted from a portion of the whole specimen using the DNeasy Blood & Tissue Kit (Qiagen, Germany). The voucher specimen and leftover DNA were deposited at Honam National Institute of Biological Resources in Korea under the voucher number HNIBRIV1595 (http://en.hnibr.re.kr/; contact: Hyun Kyong Kim, hkkim@hnibr.re.kr). Library was prepared using the TruSeq Nano DNA Kit (Illumina, USA) and sequencing was performed on the HiSeq 2500 platform (Illumina, USA), generating 51,828,270 reads. The *de novo* assembly was achieved with SPAdes 3.13.0 (Bankevich et al.

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Figure 1. Image of *Perforatus perforatus* collected from Mulchi-port, Yangyanggun, Gangwondo Province, Korea (38°9′20″ N, 128°36′35″ E). The photo was taken by Hyun Kyong Kim with a digital camera (model 5D mark IV; canon, Tokyo, Japan), and produced with helicon focus software (scale bar: 5 mm).

2012), under the condition of '-cov-cutoff auto' and produced a contig of 15,536 bp with the sequencing depth of 282,505 (Figure S1). Circularity of the mitogenome was further validated with MitoZ v3.4. (Meng et al. 2019), a tool designed for mitochondrial DNA analysis.

Gene annotation was conducted *via* the MITOS Web Server (Bernt et al. 2013). For improved annotation, mitogenome sequences of all species in the Balanidae family registered in GenBank were downloaded and aligned together with *P. perforatus*. Annotation of *P. perforatus* was performed by following the procedure recommended in Cameron (2014). The circular representation of the mitochondrial genome was created using GenomeVx, an online tool for mitochondrial visualization (Conant and Wolfe 2008). For the phylogenetic analysis, 15 species registered as of February 2023 were selected using NCBI blastn with the *P. perforatus* mitogenome as the query, employing the following settings: TaxID limited to the superfamily Balanoidea (TaxID 2899671), sequence length ranging from 14,000 to 17,000, sequence similarity threshold set above 80%, and number of sequences limited to one per species.

Two Chthamaloidea species (*Eochionelasmus coreana* and *E. ohtai*) were used as the outgroups. We aligned each protein-coding gene (PCG) using RevTrans 2.0 (Wernersson and Pedersen 2003) and each rRNA using MAFFT 7.245 (Katoh and Standley 2013). Poorly aligned and highly divergent sequences were eliminated using Gblocks 0.91b (Castresana 2000) and then all sequences were concatenated. Phylogenetic analysis was performed *via* the maximum likelihood (ML) method with 1,000 bootstrap replications (Felsenstein 1985) using CIPRES Portal 3.1 (Miller et al. 2010), based on the TVM + I + G model, which was determined using the jModelTest (Posada 2008). To ensure the robustness of our phylogenetic results against potential saturation effects, we performed a saturation test for each gene using DAMBE software (Table S1; Xia and Lemey 2009).

Results

The complete *P. perforatus* mitogenome was 15,536-bp long, encoding 13 PCGs, two rRNA genes, and 22 tRNA genes, along with a control region (Figure 2). The start codons for 12 PCGs are ATN, whereas *ND4L* started with GTG. TAA was the most common stop codon, whereas TAG was present in *CYTB* only, and incomplete T codons were present in four PCGs (*COX3*, *ND3*, *ND4*, and *ND4L*). The *ND1* gene, five tRNA genes (*trnK*, *trnQ*, *trnC*, *trnL*(tag), and *trnV*), and two rRNA genes (*rrnL* and *rrnS*) were located on the light strand, whereas the remaining 29 genes (12 PCGs and 17 tRNA genes) were located on the heavy strand. The A/T content was 70.0% in both PCGs and tRNA genes, 75.6% in *rrnL* gene, 68.8% in *rrnS* genes, 80.5% in the control region, and 71.1% in the whole genome (Table S2). *P. perforatus* exhibits an inverted gene block (*trnP-ND4L-ND4-trnH-ND5-trnF*) between *trnS*(gct) and *trnT*, identically to all species in Megabalaninae, Acastinae, and only *Balanus trigonus* in Balaninae, within the Balanidae family.

A non-monophyletic Balanidae was notably observed (Figure 3). Pyrgomatidae, which are represented by two species (*Pyrgopsella youngi* and *Nobia grandis*) interrupted the monophyly of Balanidae, forming Pyrgomatidae and the subfamily Archaeobalaninae in Balanidae the sister group, with relatively higher nodal support (Bootstrap Support (BS) = 88%). *P. perforatus*, representing the Concavinae, was identified as a sister group to the *Acasta sulcate* and *Balanus trigonus*, but nodal support for the sister relationship was lower (BS = 45%).

Discussion and conclusion

We assembled and annotated the mitogenome sequence of *P. perforatus* for the first time. A non-monophyletic Balanidae detected in this study has also been found in previous studies using mitogenome sequences (Bae et al. 2021; Ji et al. 2021; Mao et al. 2021, 2024). Moreover, phylogenetic analysis using several nuclear gene fragments, along with mitochondrial *COX1* gene has also shown non-monophyletic Balanidae (Pérez-Losada et al. 2014). Thus, our research and previous studies suggest the necessity for further investigation into taxonomic classifications and further scrutinized phylogenetic analysis using a diverse type of molecular markers for Balanidae and allied groups.

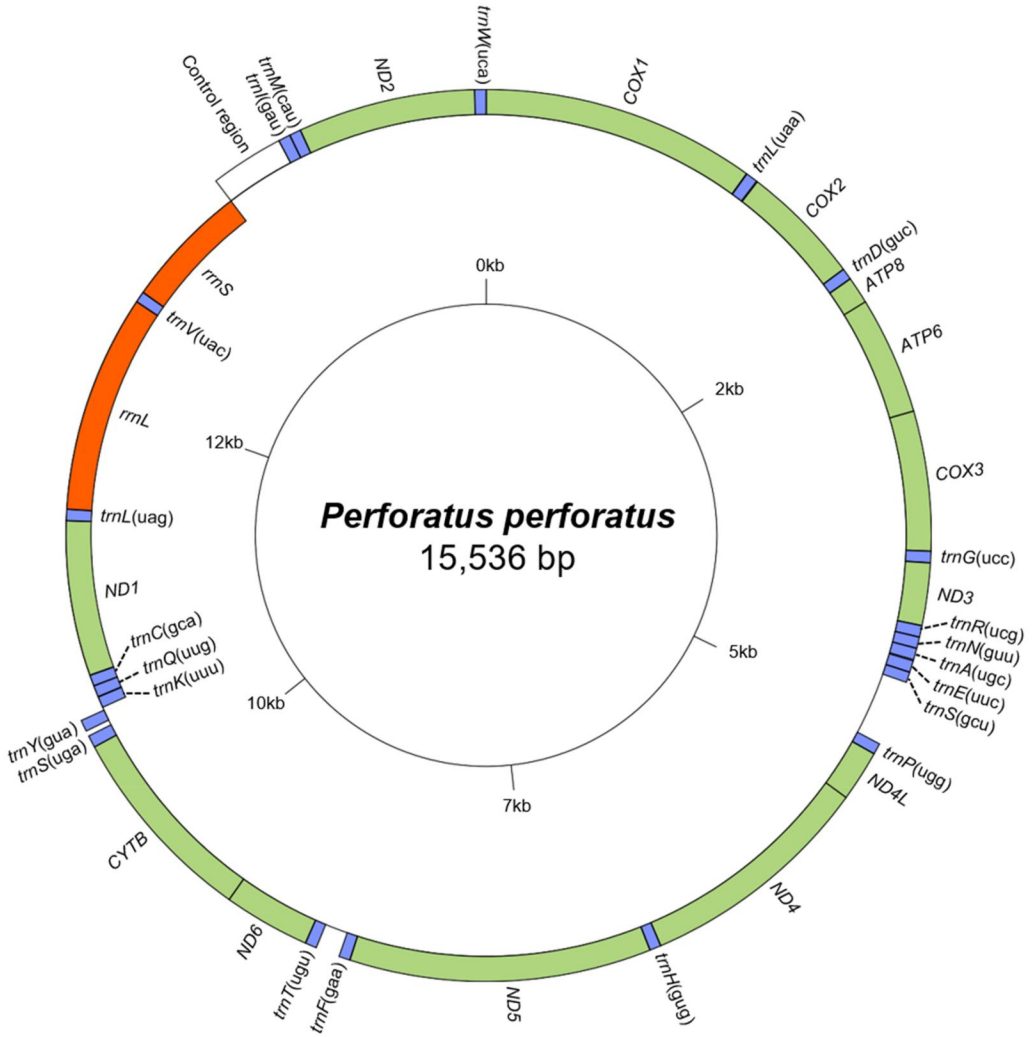

Figure 2. Mitochondrial genome map of *perforatus perforatus* obtained by the GenomeVx tool. tRNAs are abbreviated by the one-letter code of the corresponding amino acid with the anticodon within the parenthesis. Gene names located on the outside of the large circle are encoded on the heavy strand (5′-3′ direction) excluding control region, while gene names located inside are encoded on the light strand (3′-5′ direction). Color codes: green for PCGs, blue for tRNAs, orange for rRNAs, and white for control region.

Our findings highlight the presence of an inverted gene block also in the subfamily Concavinae, along with six species belonging to three subfamilies in the family Balanidae to which current *P. perforatus* is included. Recently, Zhang et al. (2023) scrutinized mitogenome arrangement in Balanomorpha including Balanidae to which Concavinae is included and found a diverse type of gene rearrangement within Balanomorpha. However, phylogenetic tree did not exclusively reflect these types of rearrangement (Zhang et al. 2023). Thus, further extensive mitogenome data could be required to improve our understanding on the genomic rearrangements and evolutionary relationships.

Current mitogenome sequence can be used for subsequent mitogenome-based molecular phylogenetic study along with available public data. Moreover, the sequences can be used for the tracing the origin of invasive species (Farrington et al. 2015), population genetics (Jeong et al. 2021), and the development of environmental DNA detection markers (Jerde et al. 2011).

Ethics statement

This study did not involve human participants or animals. This research does not involve experiments that require ethical review. This species is not endangered or collected in nature reserves, so it did not need any specific permissions.

Authors' contributions

Conceptualization, JSJ, HKK, and IK; field work, HKK; analysis and interpretation of the data, JSJ, H-SH and JSP; writing—original draft preparation, JSJ, HKK, H-SH and IK; writing—review and editing, JSP, H-SH and IK; supervision, IK; project administration, JSJ. All authors approved the final version to be published and agree to be accountable for all aspects of the work.

Disclosure statement

The authors report there are no competing interests to declare.

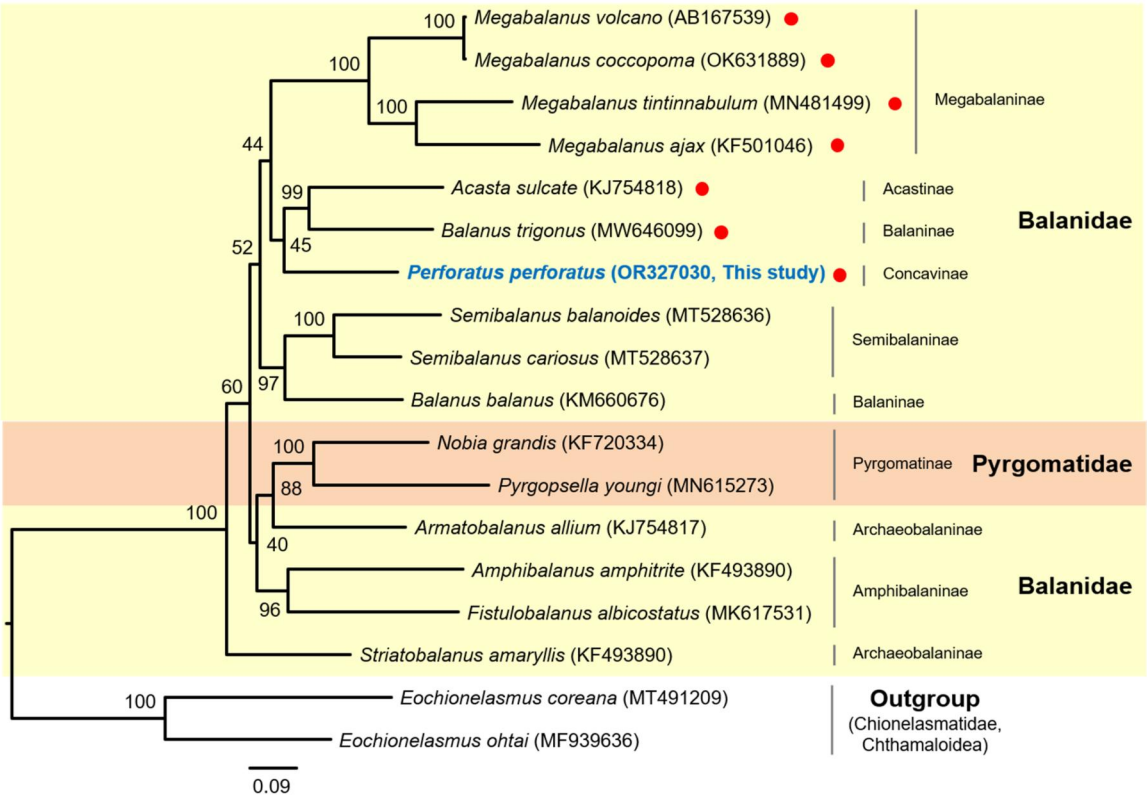

Figure 3. The phylogenetic tree of two families in balanoidea (Balanidae and pyrgomatidae) within balanoidea. The tree was obtained using concatenated nucleotide sequences of 13 protein-coding genes and two rRNAs using the maximum likelihood method. The numbers at each node indicate the bootstrap values. The scale bar indicates the number of substitutions per site. Two chionelasmatidae species (*Eochionelasmus coreana* and *E. ohtai*) in chthamaloidea were used as outgroups. Red dots indicate the species with an inverted sequence block (*trnP-ND4L-ND4-trnH-ND5-trnF*) between *trnS*(gct) and *trnT*. The following sequences were used: *Acasta sulcate* KJ754818 (Unpublished); *Balanus trigonus* MW646099 (Liu et al. 2021); P*erforatus perforatus* OR327030 (This study); *Megabalanus tintinnabulum* MN481499 (Feng et al. 2019); *Megabalanus ajax* KF501046 (Shen et al. 2016); *Megabalanus volcano* AB167539 (Unpublished); *Megabalanus coccopoma* OK631889 (Zhang et al. 2023); *Semibalanus cariosus* MT528637 (Nunez et al. 2021); *Semibalanus balanoides* MT528636 (Nunez et al. 2021); *Balanus balanus* KM660676 (Shen et al. 2016); *Pyrgopsella youngi* MN615273 (Unpublished); *Nobia grandis* KF720334 (Shen et al. 2016); *Armatobalanus allium* KJ754817 (Unpublished); *Amphibalanus amphitrite* KF493890 (Shen et al. 2015); *Fistulobalanus albicostatus* MK617531 (Song et al. 2020); *Striatobalanus amaryllis* KF493890 (Tsang et al. 2015); *Eochionelasmus coreana* MT491209 (Lee et al. 2021); and *Eochionelasmus ohtai* MF939636 (Kim et al. 2017).

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Data availability statement

The genome sequence data that support the findings of this study are openly available in the GenBank of the National Center for Biotechnology Information at https://www.ncbi.nlm.nih.gov, under the accession number OR327030. The associated BioProject, SRA, and BioSample numbers: PRJNA1057449, SRR27587530, and SAMN39129815, respectively.

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