

The complete mitochondrial genome of sand anemone, *Paracondylactis hertwigi* (Wassilieff, 1908)

Seung-Joon Lee^a , Sang-Hwa Lee^b , Hyo-Jin Yu^a , In-Young Cho^c  and Sung-Jin Hwang^a 

^aDepartment of Life Science, Woosuk University, Jincheon, South Korea; ^bInvertebrate Diversity Institute (InDI), Cheongju, South Korea;

^cNational Marine Biodiversity Institute of Korea, Seocheon, South Korea

ABSTRACT

This study reports the complete mitochondrial genome of *Paracondylactis hertwigi* (Actiniidae) for the first time. The mitogenome is 19,880 bp in length and contains 17 annotated genes, including 13 protein-coding genes, one nonconventional mitochondrial protein gene (ORF), two ribosomal RNA genes, and two transfer RNA genes. The gene content, order, and genome length are consistent with those of other sea anemones. Notably, the *COX1* and *ND5* genes each consist of two exons separated by an intron, with *ND1* and *ND3* genes encoded within the *ND5* intron, confirming the conservation of this unique mitochondrial genomic structure in Actiniaria. Phylogenetic analysis revealed that *Paracondylactis* is paraphyletic, with *P. sinensis* clustering outside the genus alongside species of the family Phymanthidae. These results align with previous findings of paraphyly within Actiniidae and support the hypothesis that the family is polyphyletic within the superfamily Actinioidea, reflecting limitations in morphology-based classifications. Further studies integrating morphological and molecular phylogenetic approaches are needed to clarify the taxonomic relationships within the genus *Paracondylactis*. Additionally, the mitogenomic data of *P. hertwigi* may serve as a valuable resource for the genetic management and conservation of tidal flat organisms in Korea, which are increasingly threatened by coastal development and climate change.

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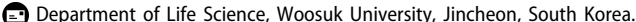
Paracondylactis hertwigi; sea anemone; Actiniidae; complete mitogenome; phylogenetic analysis

Introduction

Hexacorallia, a subclass of Cnidaria that includes Actiniaria (sea anemones), Antipatharia (black corals), and Scleractinia (hard corals), constitutes a diverse taxonomic group with approximately 3,600 described species worldwide (WoRMS editorial board 2025). However, mitochondrial genome sequences are available for only 271 species, representing approximately 7.5% of the known diversity (NCBI 2025). The genus *Paracondylactis*, belonging to the family Actiniidae, comprises three valid species: *Paracondylactis hertwigi* (Wassilieff 1908); *P. sinensis* Carlgren 1934; and *P. singaporensis* (England 1987). These three species inhabit sandy mudflats along intertidal coasts in tropical to temperate regions of the Indo-Pacific, including Singapore, China, Korea, and Japan (Carlgren 1934; Song 1984; England 1987; Fautin et al. 2015; Fautin and Tan 2016; Hwang 2025; Rodríguez et al. 2025). In Korean waters, *P. hertwigi* was first described in 1984, and more recently, *P. sinensis* was newly recorded in 2025. These two species predominantly inhabit the intertidal sandy mudflats of the Yellow Sea and the South Sea of Korea (Song 1984; Hwang 2025).

The tidal flats along the southwest coast of Korea constitute one of the five largest tidal flat systems in the world, as

recognized by the Ramsar Convention on Wetlands (Ramsar Convention Secretariat 2006, 2008, 2009, 2010, 2011, 2014, 2018). In recognition of their global ecological and conservation significance, four tidal flat regions along Korea's western and southern coasts were inscribed as UNESCO World Heritage Sites in 2021 (UNESCO 2021). Despite their ecological importance, the tidal flats of the Yellow and South Seas of Korea have undergone extensive land conversion through reclamation projects aimed at national land expansion (Walton 2010; Choi 2023). Since 1946, reclamation activities have led to the loss of approximately 1,400 km² of habitat, significantly impacting *Paracondylactis* species and a wide range of marine and coastal fauna, including shorebirds, mollusks, and shellfish (Choi 2014). In addition, recent increases in sea surface temperatures associated with global warming further endanger intertidal habitats (Mossman et al. 2013; Ross and Adam 2013; Park et al. 2024). Therefore, although not currently classified as endangered in Korea, the two *Paracondylactis* species may be at risk, and genetic data on this representative tidal flat organism—the sea anemone—are essential for the effective conservation and management of tidal flat biodiversity. In this study, we report the complete mitochondrial genome of *P. hertwigi*, which had

CONTACT Sung-Jin Hwang  buteo2@woosuk.ac.kr, buteo2@gmail.com 

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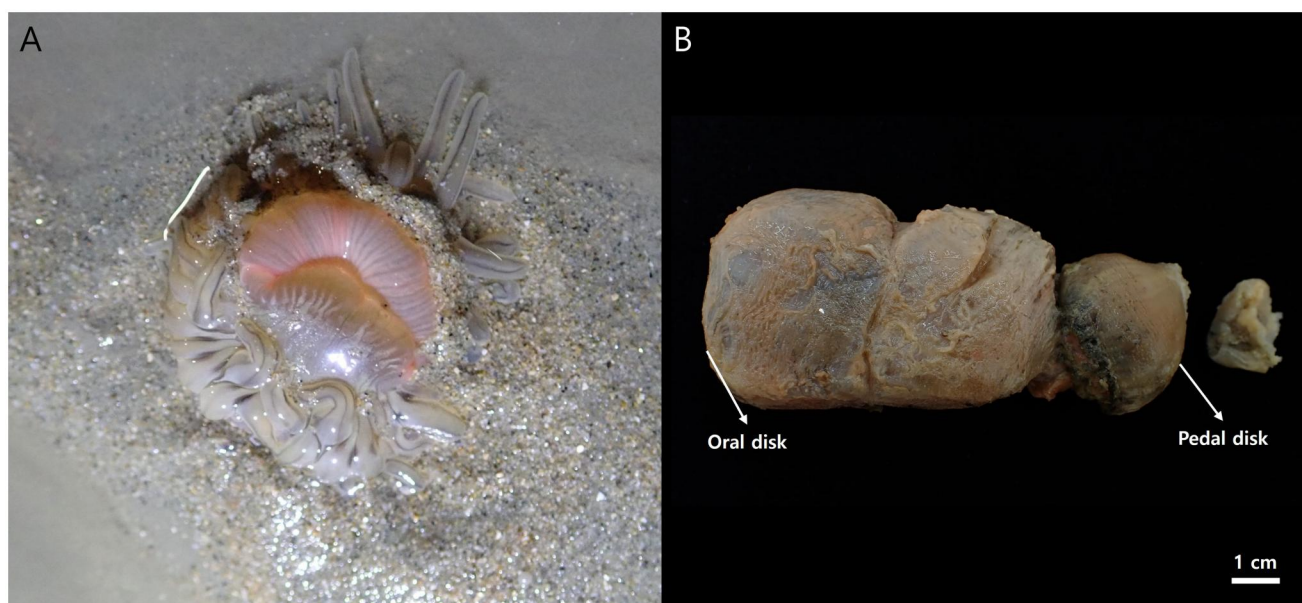


Figure 1. *Paracondylactis hertwigi* (A) A living sea anemone inhabiting the intertidal sandy mudflat at Wangsan Beach, Incheon, Korea. (B) Voucher specimen used in this study. Tentacles are fixed in a retracted state within the oral disk of the specimen and are not visible in the photograph. Photographs of the habitat and voucher specimen were taken by Seung-Chan Jeong (Researcher, Korea National Park Research Institute) and Hyo-Jin Yu (co-author), respectively; copyright permissions were obtained.

not been previously analyzed, excluding *P. sinensis*, whose mitochondrial genome has already been sequenced (Li et al. 2023).

Materials and methods

A single specimen of *Paracondylactis hertwigi* was collected from the intertidal zone of Wangsan Beach, Incheon, Korea (37°27'21" N, 126°22'01" E; Figure 1), and deposited in the Cnidaria Bioresources Bank of Korea at Woosuk University, Jincheon (voucher number: MBCL21CnAnE263; contact: Prof. Sung-Jin Hwang, buteo2@woosuk.ac.kr). Species identification was confirmed based on detailed morphological characteristics of the cnidae, following the diagnostic criteria described by Song (1984).

Genomic DNA was extracted from the tentacle and column tissues of the voucher specimen using the E.Z.N.A. Mollusc DNA Kit (Omega Bio-tek Inc., Norcross, USA). To enrich mitochondrial DNA (mtDNA) prior to sequencing, the REPLI-g Mitochondrial DNA Kit (Qiagen, Hilden, Germany) was employed to amplify the mtDNA of *P. hertwigi*. The amplified mtDNA was then sequenced by the National Instrumentation Center for Environmental Management (NICEM, Seoul, Korea) using the Illumina NextSeq 1000 platform (Illumina Inc., San Diego, USA) with 150-bp paired-end reads.

The resulting short-read sequences were assembled de novo using NOVOPlasty v.3.3.4 (Dierckxsens et al. 2017) and further analyzed with Geneious Prime (Biomatters Ltd., Auckland, New Zealand). The complete circular mitochondrial genome of *P. hertwigi* was assembled using partial *COX1* sequences as the starting point for the gene map. Circularity was confirmed by identifying overlapping sequences between the initial and terminal contigs and by comparison with mitochondrial genome sequences from other Actiniidae

species. Annotation of the 13 protein-coding genes (PCGs) was performed by identifying open reading frames (ORFs) and comparing them with previously reported Actiniidae mitogenomes using the MITOS2 pipeline on the Galaxy web-server (<https://usegalaxy.org>). Exon-intron structures of the *COX1* and *ND5* genes, which exhibit cis-splicing, were visualized using the PMGmap tool (<http://47.96.249.172:16086/home/>) (Figures S2 and S3). The two ribosomal RNA genes (*rrnS* and *rrnL*) and two transfer RNA genes (*trnM* and *trnW*) were identified through sequence comparison with homologous genes from other Actiniidae mitochondrial genomes.

Phylogenetic analysis was conducted using mitochondrial genome sequences from 22 previously published species of the order Actiniaria, along with *Paracondylactis hertwigi* sequenced in this study. A single species from the order Corallimorpharia was included as an outgroup. Nucleotide sequences of the 13 protein-coding genes (PCGs), excluding stop codons, were concatenated for all 24 species and aligned using MAFFT v.7 (Katoh and Standley 2013). The phylogenetic tree was reconstructed using the maximum likelihood (ML) approach implemented in raxmlGUI 2.0 (Edler et al. 2021), applying the GTR+G+I substitution model. Node support was assessed through 10,000 bootstrap replicates.

Results

The complete mitochondrial genome of *P. hertwigi* is 19,880 bp contains 17 annotated genes, including 13 protein-coding genes (PCGs), an Open Reading Frame (ORF), two ribosomal RNA genes (*rrnS* and *rrnL*), and two transfer RNA genes (*trnM* and *trnW*) with average read mapping depth of $67.76 \times$ (Figure 2, Figure S1). The mitochondrial genome of *P. hertwigi* is consistent with those of other sea anemones within the order Actiniaria in terms of gene number, genome

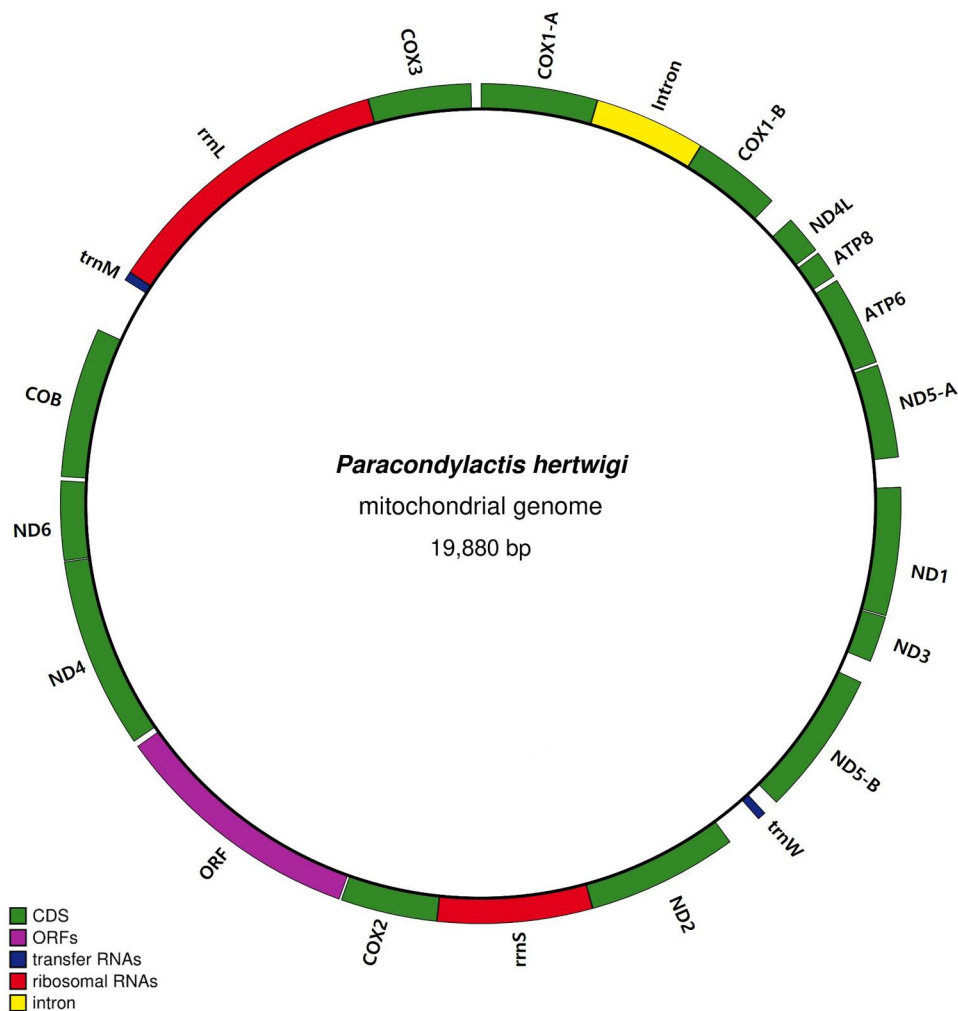


Figure 2. Circular mitochondrial genome map of *Paracondylactis hertwigi* generated using the OGDraw program (<https://chlorobox.mpimp-golm.mpg.de/OGDraw.html>). The mitogenome contains 13 protein-coding genes, an Open Reading Frame (ORF), 2 rRNA genes, and 2 tRNA genes, each represented by different colors.

length, and gene order (Li et al. 2023). All PCGs are encoded on the heavy strand, initiate with the start codon ATG, and terminate with the stop codons TAA or TAG. Among the 13 PCGs, eleven genes (*ATP6*, *ATP8*, *COX1*, *COX2*, *COX3*, *ND1*, *ND3*, *ND4*, *ND4L*, *ND5*, and *ND6*) end with TAA, while two genes (*COB* and *ND2*) terminate with TAG. The nucleotide composition of the mitochondrial genome is 26.8% A, 17.4% C, 21.5% G, and 34.3% T, resulting in a G+C content of 38.9%. Notably, the *COX1* and *ND5* genes are annotated as containing two exons separated by one intron, with the exons joined by cis-splicing to produce a single functional protein. Additionally, the *ND1* and *ND3* genes are located within the intronic region of the *ND5* gene.

Phylogenetic analysis based on mitochondrial genome data from 23 species of Actiniaria and one species of Corallimorpharia as an outgroup revealed that the family Actiniidae clusters with Phymanthidae, Liponematidae, and Stichodactylidae (Figure 3). Within this tree, *P. hertwigi* was strongly supported as being closely related to the clade containing *Anemonia manjano* and *Heteractis aurora*. Interestingly, the two species of the genus *Paracondylactis* did not form a monophyletic group. Notably, *P. sinensis* clustered with *Phymanthus crucifer* (family Phymanthidae),

consistent with the results of previous studies. These results confirm that the phylogenetic reconstruction of these 24 species confirms that the family Actiniidae, which includes the genus *Paracondylactis*, is not monophyletic.

Discussion and conclusions

In this study, the complete mitogenome sequence of *P. hertwigi* was reported for the first time. Previous studies on the mitogenomes of some sea anemones, including already reported species *P. sinensis*, and some black coral belonging to the Hexacorallia have identified two key structural features: the *COX1* and *ND5* genes, each consisting of two exons separated by an intron, with the exons joined through cis-splicing, and the presence of *ND1* and *ND3* genes encoded within the *ND5* intron (Li et al. 2023; Shizuru et al. 2024). Our findings in *P. hertwigi* are consistent with these patterns, further supporting the conservation of this unique mitochondrial genomic structure across these groups.

Phylogenetic analysis of two species within the genus *Paracondylactis*—which currently comprises three valid species—indicates that the genus is paraphyletic rather than monophyletic. Comparative mitogenomic analysis revealed

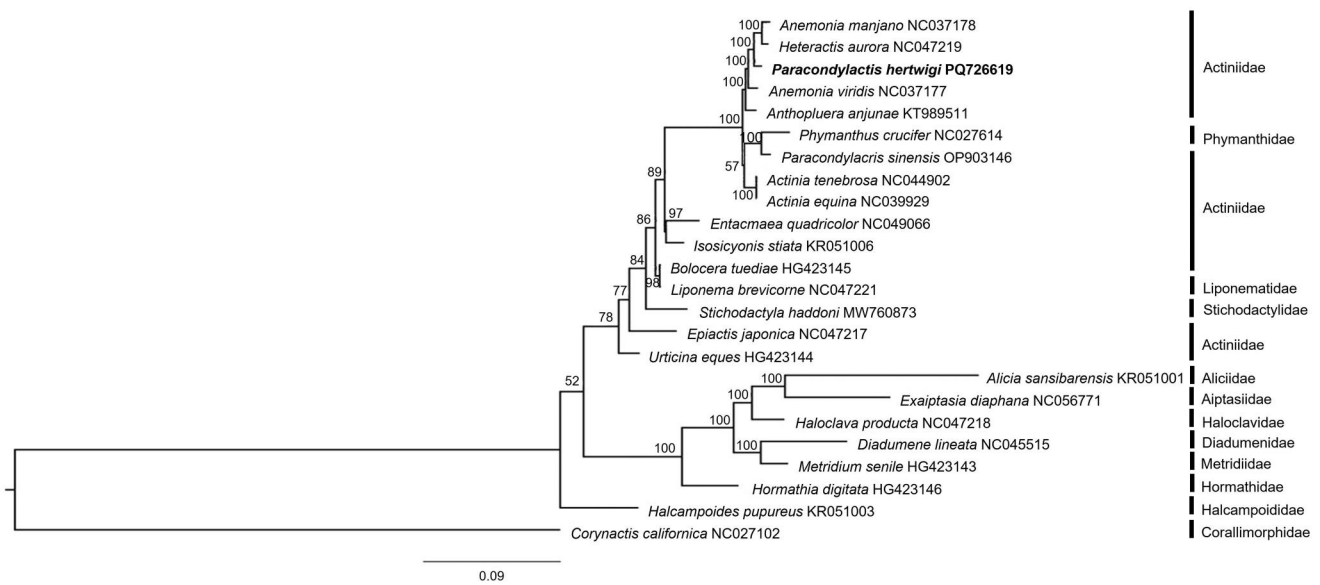


Figure 3. Maximum-likelihood phylogenetic tree based on the concatenated nucleotide sequences of 13 protein-coding genes from 23 Actiniaria species and one Corallimorpharia species (*Corynactis californica*), which was used as an outgroup. GenBank accession numbers are indicated after each species name. The sequence obtained in this study (*Paracondylactis hertwigi*) is highlighted in bold. Sequences used in the analysis are as follows: *Anemonia manjano* NC037178 (Chi et al. 2018), *Heteractis aurora* NC047219 (unpublished), *Paracondylactis hertwigi* PQ726619 (this study), *Anemonia viridis* NC037177 (Chi et al. 2018), *Anthopleura anjunae* KT989511 (Zhang and Zhu 2017), *Phymanthus crucifer* NC027614 (Fook et al. 2016), *Paracondylactis sinensis* OP903146 (Li et al. 2023), *Actinia tenebrosa* NC044902 (Surm et al. 2019), *Actinia equina* NC039929 (Wilding and Weedall 2019), *Entacmaea quadricolor* NC049066 (unpublished), *Isosicyonis stiata* KR051006 (Fook et al. 2016), *Bolocera tuediae* HG423145 (unpublished), *Liponema brevicornis* NC047221 (unpublished), *Stichodactyla haddoni* MW760873 (Johansen et al. 2021), *Epiactis japonica* NC047217 (unpublished), *Urticina eques* HG423144 (Emblem et al. 2014), *Alicia sansibarensis* KR051001 (Fook et al. 2016), *Exaiptasia diaphana* NC056771 (Emblem et al. 2014), *Haloclava producta* NC047218 (unpublished), *Diadumene lineata* NC045515 (unpublished), *Metridium senile* HG423143 (Emblem et al. 2014), *Hormathia digitata* HG423146 (Emblem et al. 2014), *Halcampoides pupureus* KR051003 (Fook et al. 2016), *Corynactis californica* NC027102 (Lin et al. 2014).

that the mitochondrial genome of *P. hertwigi* is 19,880 bp in length, whereas that of *P. sinensis* is 20,786 bp, resulting in a total length difference of 906 bp and 2.58% nucleotide differences across a concatenated 11,950 bp sequence of annotated genes. Paraphyletic relationships have also been previously reported within the family Actiniidae, notably in *Anthopleura*, the largest genus in the family (Daly et al. 2017). Furthermore, Actiniidae has been suggested to be polyphyletic with respect to other families in the superfamily Actinioidea, a finding supported by the results of this study and previous research. This apparent polyphyly likely reflects the limitations of traditional morphology-based classifications within the order Actiniaria, as evidenced by multiple phylogenetic studies (Daly et al. 2003; 2010; Rodríguez et al. 2014; Daly et al. 2017). To facilitate a more comprehensive and integrative taxonomic revision of *Paracondylactis*, future studies should include the complete mitochondrial genome of *P. singaporensis*, the only remaining species in the genus yet to be analyzed, using both morphological and molecular data.

Additionally, the mitogenomic data of *P. hertwigi* may serve as a foundational resource for the genetic management and conservation of tidal flat organisms in Korea, which are increasingly threatened by coastal development and climate change.

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Author contributions

CRediT: **Seung-Joon Lee**: Data curation, Writing – original draft; **Sang-Hwa Lee**: Data curation, Writing – original draft; **Hyo-Jin Yu**: Data curation, Visualization; **In-Young Cho**: Funding acquisition, Resources, Writing – original draft; **Sung-Jin Hwang**: Conceptualization, Supervision, Writing – review & editing.

Ethical approval

This research does not involve ethical research. The sample collection area was not protected area. And *P. hertwigi* is widespread in South Korea and is not listed as a threatened or endangered species.

Disclosure statement

No potential conflict of interest was reported by the authors.

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ORCID

Seung-Joon Lee <http://orcid.org/0000-0003-4880-1547>
 Sang-Hwa Lee <http://orcid.org/0000-0002-1828-705X>
 Hyo-Jin Yu <http://orcid.org/0000-0002-4143-1101>
 In-Young Cho <http://orcid.org/0000-0002-0979-7971>
 Sung-Jin Hwang <http://orcid.org/0000-0002-1259-6775>

Data availability statement

The data that supports the findings of this study are openly available in the GenBank of NCBI at <https://www.ncbi.nlm.nih.gov> under the accession PQ726619. The associated BioProject, SRA and Bio-sample numbers are PRJNA1193831, SRR31617080, and SAMN45122048, respectively.

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