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MITOGENOME REPORT

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The complete mitochondrial genome of the ice krill *Euphausia crystallorophias* Holt & Tattersall, 1906 (Euphausiacea, Euphausiidae), from the Ross Sea, Antarctica

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ABSTRACT

The mitogenome of *Euphausia crystallorophias* collected from the Ross Sea Region Marine Protected Area (RSR MPA) is described for the first time. The assembled mitogenome was 17,291 bp in length and consisted of two ribosomal RNAs (rRNAs), 22 transfer RNAs (tRNAs), 13 protein-coding genes (PCGs), and noncoding regions, all of which were identical to those of other euphausiid species. The most common start codon for the 13 PCGs was ATG, and the most common termination codon was TAA. The overall G + C content was 33.2% in the heavy strand. *Euphausia crystallorophias* was sister to *E. superba* in the phylogenetic analysis. The mitogenome of *E. crystallorophias* provided significant DNA molecular data for further identification and phylogenetic analysis within the euphausiids.

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KEYWORDS
Antarctic; crystal krill; euphausiid; ice krill; marine protected area (MPA); mitochondrial genome

Introduction

In the Southern Ocean, *Euphausia crystallorophias* Holt & Tattersall, 1906 (ice krill), and *Euphausia superba* Dana, 1850 (Antarctic krill), are prominent zooplankton, providing the main food resource for higher predators such as fish and whales (Belcher et al. 2017; Cavan et al. 2019; Vereshchaka et al. 2019; Kang et al. 2020). Although these two species have similar habitus, ice krill are smaller than Antarctic krill (Sala et al. 2002) and were adapted to much lower water temperatures (Sala et al. 2002; Piñones et al. 2016). Furthermore, geographically, ice krill are known to prefer neritic habitats and are among the most abundant zooplankton on the Antarctic continental shelf, whereas Antarctic krill are dominant in shelf breaks and at deep bottom depths (Guglielmo et al. 2009; La et al. 2015; Schmidt and Atkinson 2016; Davis et al. 2017; Kang et al. 2020). However, both krill species have been commonly observed in the northern part of the Ross Sea, sharing a distribution area (Daly and Zimmerman 2004; Azzali et al. 2006; Taki et al. 2008).

The Ross Sea, which is the sampling region for ice krill material in this study, generates substantial plankton and krill blooms and is the most productive area in the Southern Ocean (Arrigo et al. 2008; Smith et al. 2014). Approximately, 28% of the total primary production in the Southern Ocean is produced in the Ross Sea (Arrigo et al. 2008; Ballard et al. 2012). High-trophic level organisms such as seals, penguins, and whales are abundantly supported by these blooms (Ainley 2010; Ballard et al. 2012; Kang et al. 2020). Furthermore, scientific research and monitoring are required to achieve the objectives of the Ross Sea Region Marine Protected Area (RSR MPA), which was designated as the largest MPA in December 2017 (CCAMLR 2016).

In this situation, mitochondrial markers such as COX1 are quite attractive for identifying cryptic species in most animals (Raupach et al. 2015). Various molecular analyses based on COX1 can be applied for identification, classification, or phylogenetic and population analyses (Figueroa et al. 2020). The present study was performed to support the management of the RSR MPA by providing complete mitochondrial genome information on the keystone species *E. crystallorophias*. This information could be combined with the previously reported complete mitochondrial genome of Antarctic krill in the Southern Ocean (Shen et al. 2010; Zhao et al. 2017) to improve our understanding and identification of euphausiids.

Materials and methods

Material of *E. crystallorophias* was collected from the Ross Sea (74°26′55″S, 171°51′46″E) in the RSR MPA, Antarctica. The collected material was fixed in 99% ethanol and transferred to the laboratory. The voucher specimen of *E. crystallorophias*

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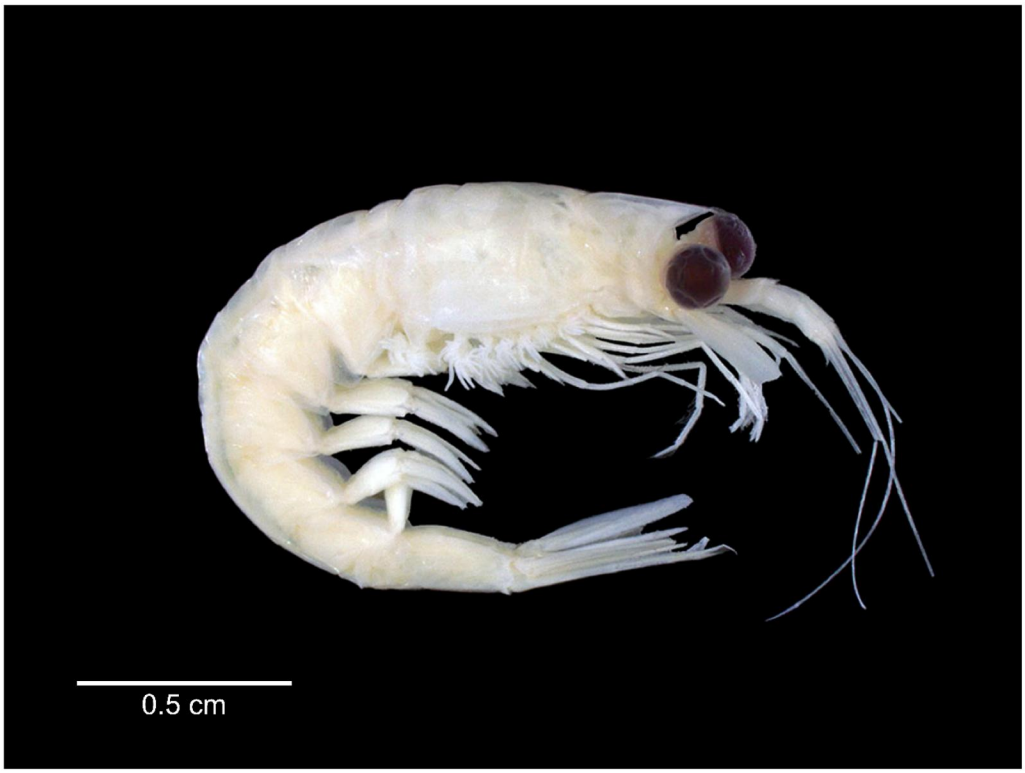

Figure 1. Photograph of *Euphausia crystallorophias* Holt & Tattersall, 1906 from the Ross Sea, Antarctica. This photo was taken by Sung Hoon Kim at the Korea Polar Research Institute (KOPRI).

Table 1. Species list, classification, and GenBank accession numbers for 19 eumalacostracan species used for phylogenetic analyses in this study.

Species	Classification	GenBank accession no.
Aparapotamon huizeense	Eucarida, Decapoda, Potamidae	NC_069577
Arisubathynella cheongmiensis	Syncarida, Bathynellacea, Parabathynellidae	KY310670
Atyopsis moluccensis	Eucarida, Decapoda, Atyidae	NC_070241
Bathynella cf. *rufa*	Syncarida, Bathynellidae, Bathynellidae	KY310671
Charcotia amundseni	Peracarida, Amphipoda, Lysianassidae	NC_062583
Curtonida isos	Eucarida, Decapoda, Munididae	NC_039112
Epipenaeon fissurae	Peracarida, Isopoda, Bopyridae	NC_070272
Euphausia crystallorophias	**Eucarida, Euphausiacea, Euphaussidae**	**OR478165**
Euphausia pacifica	Eucarida, Euphausiacea, Euphaussidae	NC_016184
Euphausia superba	Eucarida, Euphausiacea, Euphaussidae	NC_040987
Fenneropenaeus penicillatus	Eucarida, Decapoda, Penaeidae	NC_026885
Gammarus lacustris	Peracarida, Amphipoda, Gammaridae	NC_044469
Gyge ovalis	Peracarida, Isopoda, Bopyridae	NC_037467
Lophogaster typicus	Peracarida, Mysidacea, Lophogastridae	NC_065836
Lysmata boggessi	Eucarida, Decapoda, Lysmatidae	NC_064049
Pseudeuphausia sinica	Eucarida, Euphausiacea, Euphausiidae	NC_045269
Pseudohelice subquadrate	Eucarida, Decapoda, Varunidae	NC_042685
Spelaeomysis bottazzii	Peracarida, Mysidacea, Lepidomysidae	NC_065837
Xeruca formosensis	Eucarida, Decapoda, Ocypodidae	NC_070434

Table 2. Mitochondrial genome organization of *Euphausia crystallorophias*.

	Position		Size		Codons			
Gene/region	Start	Finish	No. nt	No. aa[a]	Initiation	Termination	Intergenic sequence	Direction
COX1	1	1,539	1,539	512	ACG	TAG	13	Forward
trnL1	1553	1617	65				0	Forward
COX2	1618	2305	688	229	ATA	T	0	Forward
trnK	2306	2374	69				16	Forward
trnD	2391	2458	68				0	Forward
ATP8	2459	2617	159	52	ATC	TAA	–4	Forward
ATP6	2614	3285	672	223	ATA	TAA	–1	Forward
COX3	3285	4077	793	264	ATG	T	0	Forward
trnG	4078	4144	67				0	Forward
NAD3	4145	4498	354	117	ATT	TAG	–2	Forward
trnA	4497	4562	66				0	Forward
trnR	4563	4628	66				0	Forward
trnN	4629	4693	65				0	Forward

(*continued*)

Table 2. Continued.

	Position		Size		Codons			
Gene/region	Start	Finish	No. nt	No. aa[a]	Initiation	Termination	Intergenic sequence	Direction
trnS1	4694	4760	67				1	Forward
trnE	4762	4830	69				80	Forward
trnF	4911	4977	67				–1	Reverse
NAD5	4977	6707	1,731	576	GTG	TAA	0	Reverse
trnH	6708	6772	65				0	Reverse
NAD4	6773	8110	1,338	445	ATG	TAA	–7	Reverse
NAD4L	8104	8403	300	99	ATG	TAA	2	Reverse
trnT	8406	8471	66				1	Forward
trnP	8473	8539	67				3	Reverse
NAD6	8543	9064	522	173	ATT	TAA	–1	Forward
CYTB	9064	10200	1,137	378	ATG	TAG	28	Forward
trnS2	10229	10300	72				17	Forward
NAD1	10318	11256	939	312	ATA	TAG	16	Reverse
trnL2	11273	11338	66				0	Reverse
rrnL	11339	12664	1,326				0	Reverse
trnV	12665	12736	72				0	Reverse
rrnS	12737	13350	614				0	Reverse
NCR	13351	15858	2,508				0	Forward
trnI	15859	15923	65				–3	Forward
trnQ	15921	15989	69				–1	Reverse
trnM	15989	16056	68				0	Forward
NAD2	16057	17058	1,002	333	ATT	TAA	–2	Forward
trnC	17057	17124	68				11	Reverse
trnY	17136	17201	66				15	Reverse
trnW	17217	17286	70				5	Forward

nt: nucleotides; aa: amino acids.
[a]Stop codons were not included.

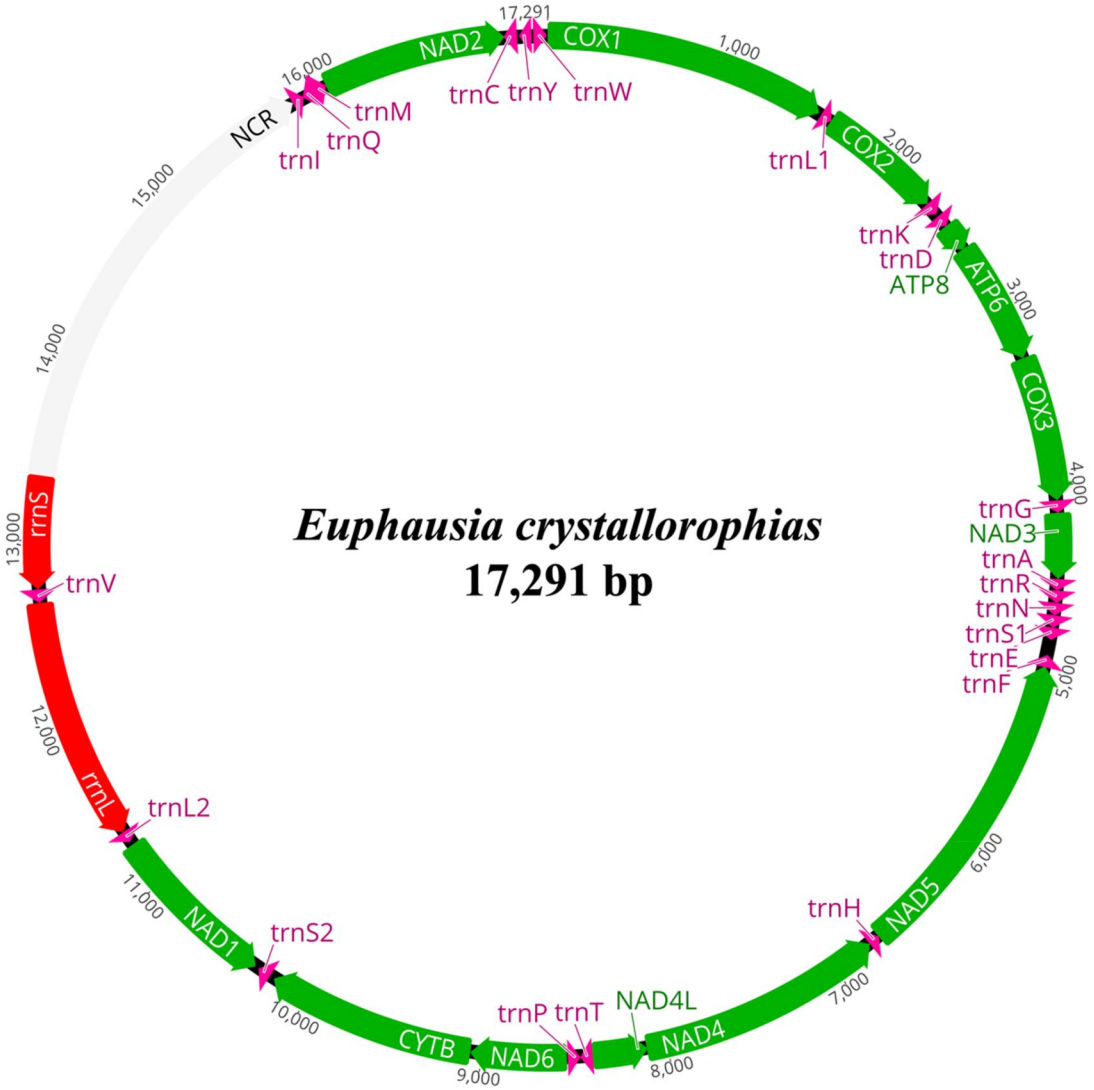

Figure 2. Mitochondrial genome map of *Euphausia crystallorophias* (GenBank accession number: OR478165).

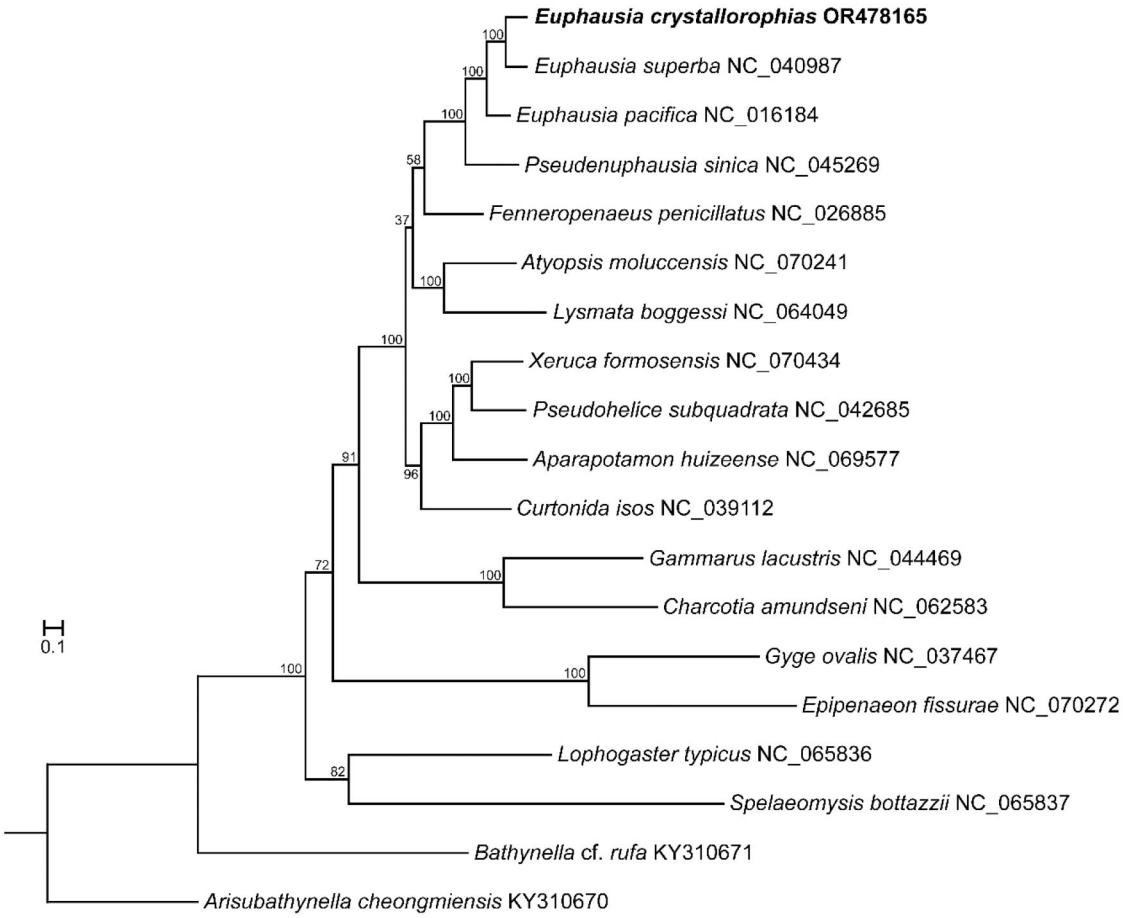

Figure 3. Maximum-likelihood (ML) phylogenetic tree based on the protein-coding genes (PCGs) of *Euphausia crystallorophias* and 18 eumalacostracan species. Numbers on the branches represent ML bootstrap values from 1000 replications. The following sequences with GenBank accession were used: *Euphausia crystallorophias* (this study), *Euphausia superba* NC_040987 (Zhao et al. 2017), *Euphausia pacifica* NC_016184 (Shen et al. 2011), *Pseudeuphausia sinica* NC_045269 (Wang et al. 2019), *Fenneropenaeus penicillatus* NC_026885 (unpublished), *Atyopsis moluccensis* NC_070241 (unpublished), *Lysmata boggessi* NC_064049 (unpublished), *Xeruca formosensis* NC_070434 (unpublished), *Pseudohelice subquadrata* NC_042685 (Kim et al. 2019), *Aparapotamon huizeense* NC_069577 (unpublished), *Curtonida isos* NC_039112 (Tan et al. 2018), *Gammarus lacustris* NC_044469 (Sun et al. 2020), *Charcotia amundseni* NC_062583 (Salabao et al. 2022), *Gyge ovalis* NC_037467 (Yu et al. 2018), *Epipenaeon fissurae* NC_070272 (An et al. 2023), *Lophogaster typicus* NC_065836 (Höpel et al. 2022), *Spelaeomysis bottazzii* NC_065837 (Höpel et al. 2022), *Bathynella* cf. *rufa* KY310671 (unpublished), and *Arisubathynella cheongmiensis* KY310670 (unpublished).

was deposited at the National Institute of Biological Resources (NIBR) (http://www.nibr.go.kr/cmn/main/enMain.do, Hyoung Sul La, hsla@kopri.re.kr) under voucher number NIBRIV0000909363 (Figure 1). Genomic DNA was extracted from the single individual using Nextera DNA Library Preparation Kit (Illumina, San Diego, CA) following the manufacturer's protocol. The concentration of the extracted DNA was checked by using a spectrophotometer (Infinium F-200, NanoDrop) and mitogenome sequences were analyzed by application of the Illumina NovaSeq 6000 sequencing platform (Theragen Bio, Seongnam, South Korea). The raw data were trimmed using NOVOplasty v4.3.1. The coverage depth of mitochondrial genome of *E. crystallorophias* is shown in Supplementary Figure 1. However, certain regions with low coverage depth were confirmed in sequenced data. To enhance the accuracy of sequence in this region, two distinct primer sets were designed centering around this region (Supplementary Table 1). Sanger sequencing was performed using the designed primer sets. As a result, complementary information for regions showing low coverage depth in the sequenced data was obtained, ensuring the accuracy of the sequenced data. The functional elements of mitochondrial genomes were identified and annotated using mitochondrial genome annotation (MITOS) server (Bernt et al. 2013). The start and end of each gene were confirmed by comparing those of other euphausiids.

For phylogenetic analysis, three euphausiids, including *E. crystallorophias* and 15 eumalacostracan species, were chosen from GenBank (Table 1). Nucleotide sequences of the 13 PCGs of 19 species were aligned individually using MAFFT with default option (Katoh and Standley 2013). The individual nucleotide alignments of 13 PCGs were concatenated using maximum-likelihood (ML) analysis with RAxML 8.2.10 (Stamatakis 2014); program was run through the CIPRES portal (Miller et al. 2010). Each of the 13 PCGs was treated as a separate, unlinked data partition; for RAxML, the GTR GAMMA model for finding the optimal tree, with the shape of the gamma distribution estimated separately for each partition. Bootstrap ML analysis was performed using the rapid bootstrapping option with 1000 iterations.

Results

The assembled *E. crystallorophias* mitogenome (GenBank accession number OR478165) was 17,291 bp in length, with

two ribosomal RNAs (rRNAs), 22 transfer RNAs (tRNAs), 13 protein-coding genes (PCGs), and noncoding regions (NCRs) (Table 2, Figure 2). Two rRNA genes were encoded on the light-strand. Fourteen tRNA genes (trnL1, trnK, trnD, trnG, trnA, trnR, trnN, trnS1, trnE, trnT, and trnS2) encoded on the heavy-strand, while eight tRNA genes (trnE, trnH, trnP, trnL2, and trnV, trnQ, trnC, and trnY) encoded on the light-strand. Among the PCGs, the most common start codon was ATG (COX3, CYTB, ND4, and ND4L), followed by ATT (ND2, ND3, and ND6), ATA (ATP6, ND1, and COX2), ACG (COX1), ATC (ATP8), and GTG (ND5); the most common termination codon was TAA (ATP6, ATP8, ND2, ND4, ND4L, ND5, and ND6), followed by TAG (COX1, CYTB, ND1, and ND3) and the incomplete termination codon T– (COX2 and COX3). Nine genes (ATP6, ATP8, COX1, COX2, COX3, CYTB, NAD3, and NAD6) were encoded on the heavy-strand, whereas the other four genes (NAD1, NAD4, NAD4LM, and NAD5) were encoded on the light-strand. In the phylogenetic tree, *E. crystallorophias* clustered with other euphausiid species such as *E. pacifica*, *E. superba*, and *Pseudeuphausia sinica*. Among them, *E. crystallorophias* was most closely positioned to the *E. superba*. And then, euphausiids, including *E. crystallorophias*, were closely clustered with decapod species.

Discussion and conclusions

To date, three complete mitochondrial genomes (*E. pacifica*, *E. superba*, and *Pseudeuphausia sinica*) for the order Euphausiacea have been deposited in the NCBI genome database (Shen et al. 2010; Shen et al. 2011; Zhao et al. 2017). A phylogenetic analysis based on the complete mitochondrial genomes of *E. crystallorophias*, three other euphausiids, and 15 other eumalacostracan species was conducted to infer a phylogenetic tree with the ML method (Table 1, Figure 3) (Shen et al. 2010; Shen et al. 2011; Zhang et al. 2015; Zhao et al. 2017). The resulting mitochondrial tree depicted the monophyly of euphausiid species, including *E. crystallorophias*, with high bootstrap support (Figure 3). *Euphausia crystallorophias* first clustered with *E. superba*, showing the closest relationship between them, while *E. superba* closely clustered with *E. pacifica* in the previous report (Zhao et al. 2017). However, although *E. superba* has 23 tRNA genes, including extra trnN, *E. crystallorophias* has only 22 tRNA genes (Shen et al. 2010). Euphausiids were clustered with decapods as a sister group. This result well corresponds with the previous studies (Shen et al. 2010; Zhao et al. 2017). Among the eumalacostracan species, Syncarida, including *Arisubathynella cheongmiensis* and *Bathynella* cf. *rufa* were clustered at the base of the tree as a most primitive taxon, whereas peracarids such as isopods (*G. ovalis* and *E. fissurae*) and amphipods (*G. lacustris* and *C. amundseni*) were relatively closely clustered with eucarids.

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Author contributions

HSL and JHK conceived and developed the research concept and design of this study. WS collected the samples. SHK conducted species identification and data analyses, and drafted the manuscript. TK performed bioinformatics data analyses and processing. JHK provided funding. All authors revised and commented on the manuscript. All authors read and approved the final manuscript.

Ethical approval

Specimen collection protocols were approved by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

The genome sequence data that support the findings of this study are openly available in GenBank of NCBI at https://www.ncbi.nlm.nih.gov/ under the accession no. OR478165. The associated BioProject, SRA, and Bio-Sample numbers are PRJNA1014971, SRR27985591, and SAMN37344700, respectively.

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