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To cite this article: Mei Yang , Tianyue Peng , Liqiang Liu , Zhen Zhang , Xinzheng Li , Lixing Wang & Lin Ma (2026) The complete mitogenome data and phylogenetic positioning of the deep-sea penaeoid shrimps *Cerataspis monstrosa* (Penaeoidea, Aristeidae), Mitochondrial DNA Part B, 11:2, 301-305, DOI: [10.1080/23802359.2026.2619270](https://doi.org/10.1080/23802359.2026.2619270)

To link to this article: <https://doi.org/10.1080/23802359.2026.2619270>



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Published online: 28 Jan 2026.



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The complete mitogenome data and phylogenetic positioning of the deep-sea penaeoid shrimps *Cerataspis monstrosa* (Penaeoidea, Aristeidae)

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ABSTRACT

The deep-sea penaeoid shrimp *Cerataspis monstrosa* performs a vertical ontogenetic migration, with its early larval stages are typically found in surface waters, while adults inhabit the deep-sea. In this study, we present the complete mitogenome of *C. monstrosa*, which is 15,911 bp in length and comprises 13 protein-coding genes, 2 rRNA genes, 22 tRNA genes, and a control region. Phylogenetic analysis indicates that *C. monstrosa* has closest genetic relationship with *Aristeus virilis* and is clustered within the Aristeidae family. The mitogenome of *C. monstrosa* provides valuable molecular data for further research into the evolution of penaeoid shrimps.

ARTICLE HISTORY

Received 1 July 2025

Accepted 15 January 2026

KEYWORDS

Cerataspis monstrosa; deep-sea; mitogenome; Penaeoidea; phylogeny

Introduction

Cerataspis monstrosa Gray, 1828, first identified in the gut contents of a dolphin in 1828, is remarkable for its heavy armor, robust body, and distinctive horn-like ornamentation. For a long time, this species was placed within a new genus of primitive crustacean Leptostraca. Until 2012, based on phylogenetic analyses of five nuclear and mitochondrial gene sequences, Bracken-Grissom et al. (2012) confirmed that *C. monstrosa* is an early developmental stage of the globally distributed deep-water aristeid shrimp, *Plesiopenaeus armatus* (Spence Bate 1881). Generally, under Linnaean nomenclature, the earliest validly published name has priority and any later names are treated as synonyms. If the larval name was published before the adult name, the larval name must be retained. Therefore, *C. monstrosa* is retained. The WoRMS (World Register of Marine Species) also accepts this name (<https://marinespecies.org/aphia.php?p=tax-details&id=589796>).

The Aristeidae is a predominantly deep-water shrimp family, contains nearly 30 species (Tavares and Serejo 2007). Given aristeids often high abundance in the water column, these shrimps are pivotal in oceanic food webs, with many species acting as active predators while others serving as prey for predatory fishes. Mitochondria are essential organelles in eukaryotic cells that serve as the primary site of oxidative phosphorylation and are involved in various cellular processes, such as cell differentiation and apoptosis (Martijn et al. 2018). Furthermore, mitochondrial genome

(mitogenome) contain abundance genetic information. As a popular and crucial molecular marker, the mitogenome playing important role in species classification and phylogenetics at various taxonomic levels.

At present, there were only three complete aristeid mitogenome sequences are available in GenBank (accessed on: 25 December 2025). In this study, we determined the mitogenome of *C. monstrosa*. This research will enrich the taxon sampling of mitogenomes in Aristeidae family and offering valuable data for further research on the biodiversity of deep-sea crustaceans.

Materials and methods

The specimen of *C. monstrosa* (Figure 1) was obtained from a seamount in the western Pacific (17°15' N, 134°43' E, depth 2391 m) in July 2024 using the remotely operated vehicle (ROV). The sample has been deposited at the Guangzhou Marine Geological Survey, China Geological Survey, Guangzhou, China, with the voucher number: GMGS-SR-S01-HSL2024PH (contact: Tianyue Peng, E-mail: pengtianyue@mail.cgs.gov.cn).

Genomic DNA was extracted using a DNeasy Tissue Kit (Qiagen) following the manufacturer's protocols. After DNA isolation, 1 µg of purified DNA was fragmented to ~500 bp using the Covaris M220 system. Short-insert libraries were then constructed using TruSeq™ Nano DNA Sample Prep Kit

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 Supplemental data for this article can be accessed online at <https://doi.org/10.1080/23802359.2026.2619270>.

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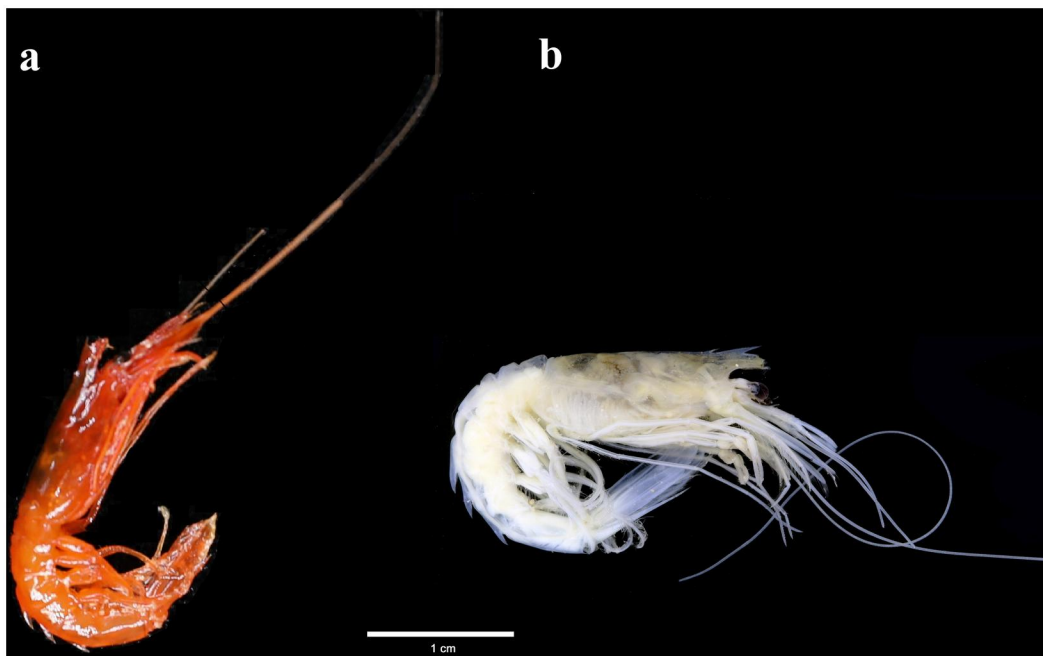


Figure 1. Photographs of *Cerataspis monstrosa* collected from the western Pacific: a. fresh specimen; b. specimen was deposited in 95% ethanol. The photographs were taken by Lin Gong and Qi Kou.

(Illumina) and sequenced on an Illumina NovaSeq 6000 platform with 150 bp paired-end reads. Prior to assembly, raw reads were filtered by Trimmomatic 0.39 (Bolger et al. 2014), yielded a total of 23,953,764 clean reads. Subsequently, the mitogenome of *C. monstrosa* was assembled using MitoZ v2.3 (Meng et al. 2019a) and annotated with the MITOS2 webserver (Donath et al. 2019). Gene predictions were further confirmed by comparing nucleotide or amino acid sequences with those of published aristeid shrimps using BLAST searches in GenBank. To visualize the assembly and annotation results, a circular mitogenome map was constructed using Proksee (<https://proksee.ca/>) (Grant et al. 2023).

To determine the evolutionary position of *C. monstrosa*, a phylogenetic tree was conducted based on the 13 mitochondrial protein-coding genes (PCGs) of *C. monstrosa* and other 20 penaeoid shrimps from five families, including Aristeidae, Benthescymidae, Penaeidae, Sicyoniidae and Solenoceridae. Additionally, two Squillidae species, *Oratosquilla oratoria* De Haan, 1844 and *Oratosquillina perpensa* Kemp, 1911 and one stomatopod species, *Squilla empusa* Say, 1818, were included in the analyses as outgroups. The nucleotide sequences of the 13 PCGs were aligned using MAFFT (Katoh et al. 2019) with default parameters and then concatenated into a single dataset. The optimal partitioning schemes and evolutionary models for the combined mitochondrial dataset were determined by PartitionFinder 2 (Table S1) (Lanfear et al. 2017). Phylogenetic relationships were inferred using the maximum likelihood (ML) method in IQ-TREE (Nguyen et al. 2015). The node reliability was assessed with 5000 ultrafast bootstrap replicates.

Results

The complete mitogenome of *C. monstrosa* contains 15,911 bp in length and the average coverage depth was 1280× (Figure S1). The mitogenome comprises the typical

set of 13 PCGs, 2 ribosomal RNA genes (*rrnS* and *rrnL*) and 22 transfer RNA genes (GenBank accession number: PV765900). Twenty-three genes are encoded on the heavy (H) strand, while the remaining fourteen genes are encoded on the light (L) strand (Figure 2). The overall base nucleotide composition of the mitogenome is A = 31.64%, T = 31.82%, C = 22.52%, and G = 14.92%, resulting in A + T content of 63.46%. The combined length of 13 PCGs was 11,139 bp, accounting for 70.01% of the entire mitogenome. The largest non-coding region (993 bp) is located between *rrnS* and *trnI* and is identified as the putative control region (CR) due to its location and high A + T content (76.13%). The two ribosomal RNA genes, *rrnS* and *rrnL*, are located on the L strand, with lengths of 847 bp and 1322 bp, respectively. The lengths of 22 tRNA genes range from 65 to 72 bp, and all tRNA genes are able to fold into classic clover leaf structures.

Phylogenetic analysis revealed that *C. monstrosa* clustered within the family Aristeidae and had the closest relationship with *Aristeus virilis* Spence Bate, 1881 (Figure 3). The families Aristeidae and Benthescymidae form a sister group, which subsequently clustering with Solenoceridae. Furthermore, the resulting phylogenetic tree indicates that Penaeidae is polyphyletic, with Sicyoniidae nested within it. This finding is consistent with the results of previous studies (Ma et al. 2009; Robalino et al. 2016).

Discussion and conclusion

C. monstrosa exhibits a characteristic ontogenetic vertical migration, with early larval occurring in surface waters, while more advanced larval and adults inhabit the deep-sea (Dall 2001; Tavares and Serejo 2007; Wicksten and Kuhn 2015; Lira et al. 2017). The correlation between the larval and adult forms provides novel perspectives into the life history of penaeoid shrimps. In the present study, we conduct the first

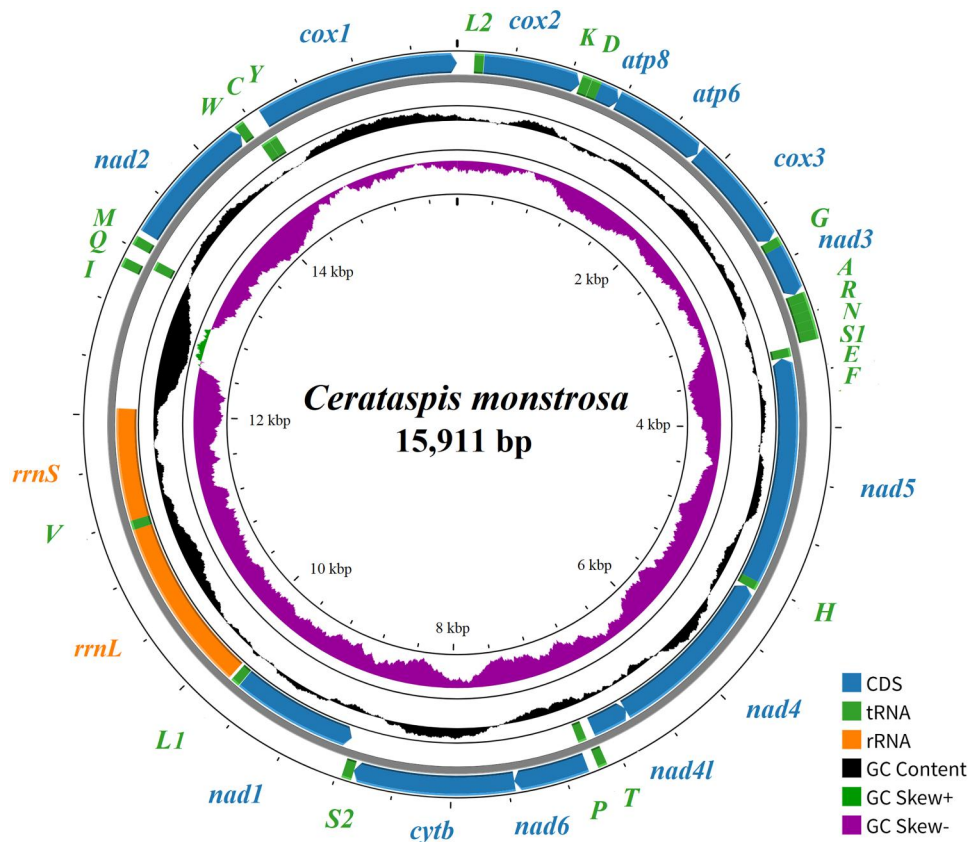


Figure 2. The organization of the mitogenome of *C. monstrosa*. Genes for proteins and rRNAs are shown with standard abbreviations. Genes for tRNAs are represented by a single letter for the corresponding amino acid, with two leucine tRNAs and two serine tRNAs differentiated by numerals.

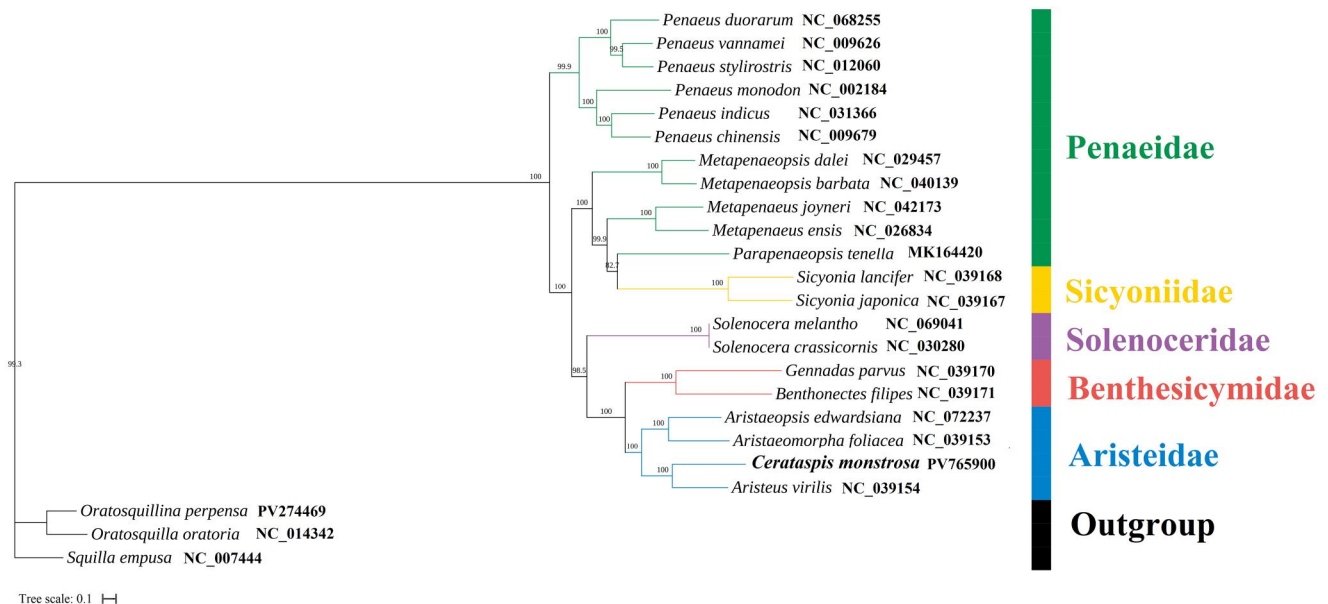


Figure 3. The maximum-likelihood (ML) phylogenetic tree for *C. monstrosa* and the other Penaeoidea species based on the concatenated nucleotide sequences of 13 protein-coding genes. The following sequences were used: *Aristaeopsis edwardsiana* NC_072237 (Liang et al. 2023), *Aristaeomorpha foliacea* NC_039153 (Cheng et al. 2018), *Aristeus virilis* NC_039154 (Cheng et al. 2018), *Benthonectes filipes* NC_039171 (Cheng et al. 2018), *Cerataspis monstrosa* PV765900 (this study), *Fenneropenaeus chinensis* NC_009679 (Shen et al. 2007), *fenneropenaeus indicus* NC_031366 (Katneni et al. 2021), *Gennadas parvus* NC_039170 (Cheng et al. 2018), *Litopenaeus stylirostris* NC_012060 (Peregrino-Uriarte et al. 2009), *Metapenaeopsis barbata* NC_040139 (unpublished), *Metapenaeopsis dalei* NC_029457 (Kim et al. 2016), *Metapenaeus ensis* NC_026834 (unpublished), *Metapenaeus joyneri* NC_042173 (Meng et al. 2019b), *Parapenaeopsis tenella* MK164420 (Meng et al. 2019c), *Penaeus duorarum* NC_068255 (Collins et al. 2022), *Penaeus monodon* NC_002184 (Wilson et al. 2000), *Penaeus vannamei* NC_009626 (unpublished), *Sicyonia japonica* NC_039167 (Cheng et al. 2018), *Sicyonia lancifer* NC_039168 (Cheng et al. 2018), *Solenocera crassicornis* NC_030280 (Yuan et al. 2016), *Solenocera melantho* NC_069041 (unpublished), *Oratosquilla oratoria* NC_014342 (Liu and Cui 2010), *Oratosquillina perpensa* PV274469 (unpublished), *Squilla empusa* NC_007444 (unpublished). Bootstrap support values are indicated at each node.

comprehensive analysis of the complete mitogenome of *C. monstrosa*, filling the gap in mitogenome data for this species.

The phylogenetic relationships of penaeoid shrimps have long been contentious, especially at the family level. Morphology-based phylogenetic analyses indicated that Aristeidae was closely related to Benthescymidae and Solenoceridae, and Sicyoniidae formed a clade with Penaeidae (Burkenroad 1983). And this morphological classification scheme for Penaeoidea was consistent with molecular phylogenetic results derived from nuclear gene data (Ma et al. 2009; Robalino et al. 2016). However, in contrast to the above conclusions, phylogenetic analyses used partial mitochondrial sequences revealed close affinity among Aristeidae, Benthescymidae, and Sicyoniidae, while Solenoceridae nested within Penaeidae (Quan et al. 2004; Voloch et al. 2005). In line with previous morphology and nuclear phylogenetic studies, our phylogenetic reconstruction based on the nucleotide sequences of 13 PCGs supporting the close relationship among Aristeidae, Benthescymidae and Solenoceridae. Additionally, our study reveals that Penaeidae was polyphyletic, with Sicyoniidae nested within it. Based on mitogenomic data of penaeoid shrimps, the work of Cheng et al. (2018) also confirmed the non-monophyly of Penaeidae. And phylogenetic analyses of a concatenated mitochondrial and nuclear gene dataset reaffirmed the paraphyly of the Penaeidae, with the Sicyoniidae nested within the penaeid tribe Trachypenaeini (Hurzaid et al. 2020). In summary, these inconsistent results may stem from the use of different molecular markers. Numerous previous studies have confirmed that mitogenome contains sufficient genetic variation information to resolve systematic relationships among diverse taxa of decapod crustaceans (Shen et al. 2013; Kou et al. 2020). And naturally, mitogenome data could yield a relatively accurate phylogeny. To elucidate the natural evolutionary history of Penaeoidea, more comprehensive taxon samplings and new molecular data are necessary in the future.

Acknowledgements

We sincerely thank Drs. Jixing Sui and Lin Gong (Institute of Oceanology, Chinese Academy of Sciences, Qingdao) for the collection of samples. We also extend our thanks to Dr. Qi Kou (Institute of Oceanology, Chinese Academy of Sciences, Qingdao) for species identification, took the photos of *Cerataspis monstrosa* and helpful comments on the earlier version of the manuscript.

Ethical approval

The sampling and researches conducted on *Cerataspis monstrosa* are compliant with relevant regulations. This study does not involve any human, vertebrate or regulated invertebrates experiments and as such, ethical approval is not required.

Author contributions

CRediT: **Mei Yang**: Data curation, Formal analysis, Writing – original draft; **Tianyue Peng**: Conceptualization, Data curation; **Liqiang Liu**: Data curation, Investigation; **Zhen Zhang**: Data curation, Investigation; **Xinzheng**

Li: Supervision, Writing – review & editing; **Lixing Wang**: Supervision, Writing – review & editing; **Lin Ma**: Supervision, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the China Geological Survey Project (DD20191009, DD20230646 and DD20230301200) and the National Natural Science Foundation of China (NSFC) (41876178).

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. PV765900. The associated Bio-Sample, BioProject, and SRA numbers are SAMN48968890, PRJNA1273949, and SRR33893907, respectively.

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