

Mitochondrial Genome of the Hermit Crab *Coenobita lila* (Anomura: Paguroidea) and Insights into Gene Rearrangements and Phylogeny of Anomura

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ABSTRACT

The complete mitochondrial genome of *Coenobite lila* was sequenced and annotated. It was 16,396 bp in length and contained 13 protein-coding genes, 2 ribosomal RNA genes, 22 transfer RNA genes and a control region. Mitochondrial genome of *C. lila*, was with negative AT skew and positive GC skew. Ka / Ks of the 13 protein-coding genes indicated purifying selection. The replication-random loss and recombination model was used to explain the mechanism of gene rearrangement of 11 tRNAs and 2 PCGs in *C. lila* relative to pancrustaceans. Phylogenetic analysis using 13 protein-coding genes including 23 species of Anomura, 7 species of Brachyura and 1 outgroup showed that *C. lila* was in Coenobitidae family. The gene order of *C. lila* mitogenome underwent a large rearrangement.

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All authors contributed to the study concept and design. Conceptualization: DZZ, BPT, and GD. Methodology: GW. Formal analysis and investigation: JY, YZ, and YHM. Writing and editing: THY and XLS and DZZ. All authors read and approved the final manuscript.

Key words

Coenobita lila, Gene rearrangement, Hermit crab, Mitogenome, Paguroidea, Phylogenetic analysis

INTRODUCTION

Mitochondrial genome is double-stranded closed-loop structure independent of nuclear chromosomes. In contrast to the light strand, the heavy strand of the mitochondrial genome has more G and less C (Simon *et al.*, 1994). There is no intron sequence in mitochondrial genome with overlapped coding genes. The mitochondrial genome of metazoan is usually 14-20kb in length, which is mainly divided into four parts, including 13 PCGs

(protein-coding genes), 22 tRNAs, 2 rRNAs and a control region (Boore, 1999). Mitochondrial genome has the characteristics of simple structure, maternal inheritance, rapid variation and gene rearrangement, which provides useful information for phylogenetic analysis (Fritsch *et al.*, 2006). Several models has been proposed to explain mitochondrial gene rearrangement, including replication-random loss, replication-non-random loss, recombination and tRNA mismatch mode (Lunt and Hyman, 1997; Moritz and Brown, 1987). Nowadays, complete mitochondrial genomes are increasingly used in population genetics, species identification, molecular evolution and phylogenetic research (Nie *et al.*, 2022; Sun *et al.*, 2022; Reding *et al.*, 2021).

Paguroidea is one of the most abundant species groups in Anomura with more than 72 genera and 1,100 species. Due to the high morphological and ecological diversity, the classification and phylogenetic relationship of Paguroidea have been controversial for a long time (Lemaitre and McLaughlin, 2009). *Coenobita lila* was

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found to be a new species by morphological difference analysis and molecular data identification (Colin *et al.*, 2023). It is widely distributed in the coastal waters of Singapore, Indonesia and Malaysia, and usually inhabits 100 meters from the coast, hiding between grasses or rocks, edge of rocks, mangroves or estuaries.

Preliminary studies focused on the morphological characteristics of *C. lila*, but a few focused on its molecular, biological characteristics and phylogenetic status. Besides, the classification of Paguroidea where *C. lila* is located has always been ambiguous (Tan *et al.*, 2018; Li *et al.*, 2020). Therefore, the mitochondrial genome of *C. lila* was sequenced, and the basic structure and phylogenetic tree of mitochondrial genome were deeply analysed in this study to explore the evolution of mitochondrial genome.

MATERIALS AND METHODS

Sample collection, DNA extraction and sequencing

A sample of *C. lila* was collected from sand flat and stored at -80 °C. Total DNA was extracted from the muscles using SQ Tissue DNA kit (Omega). The quality of the separated DNA was detected by 1% agarose gel electrophoresis, and sequenced by next-generation sequencing paired reads (Illumina Novaseq™; Shanghai Origine Bio-pharmTechnology Co. Ltd. China).

Sequence assembly, gene annotation and analysis

GetOrganelles (<http://github.com/Kinggerm/GetOrganelle>) was used to splice the read sequence for multiple iterations to obtain the preliminary assembly results. Clean data without sequencing adapters were adjusted with Pilon v1.23 and de novo assembled by the NOVOPlasty 2.7.2 software. Finally, the mitochondrial genome sequence was obtained based on the reference genome mitochondrial scaffold start position and direction. In total, 37 genes were annotated using MITOS WebServer (<http://mitos.bioinf.uni-leipzig.de/index.py>) and the codon usage of PCGs was computed using the MEGA 7.0 software (Kumar *et al.*, 2016; Bernt *et al.*, 2013). We used OGDRAW (<https://chlorobox.mpimp-golm.mpg.de/OGDraw.html>) to draw the genome map. The skewness of nucleotide composition was analysed according to the following formulas: AT skew $[(A-T)/(A+T)]$ and GC skew $[(G-C)/(G+C)]$ (Perna and Kocher, 1995). The Ka / Ks values of each pair of homologous genes were calculated using KaKs_Calculator 2.0 through ParaAT and Mafft (Wang *et al.*, 2010; Rozewicki *et al.*, 2019).

Phylogenetic analysis and gene rearrangement

The phylogenetic relationship was reconstructed using 13 PCGs of 31 species (23 Anomura species, 7

Brachyura species and 1 outgroup) with *Pteronarcys princeps* as outgroup. Gblocks was used to multiple sequence alignment (Gerard and Jose, 2007). Maximum likelihood (ML) analysis was performed using RAxML 8.2.12, and the best amino acid substitution model selected by Prottest 3.4.2 (Posada, 2011). Bootstrap analysis (1000 replicates) was used to evaluate the relative support level for ML analysis (Sitnikova, 1996). Gene rearrangement was analysed with replication-random loss and recombination models.

RESULTS AND DISCUSSION

Genome composition and structure

The complete mitochondrial genome of *C. lila* was 16,396 bp in length (Fig. 1). Mitochondrial data was deposited in GenBank with the accession No. OP645220. It comprised 13 PCGs, 22 tRNAs, 2 rRNAs and a control region (Table 1). The overall nucleotide composition was A (26.6%), T (36.5%), G (21.7%) and C (15.2%). The GC content was 36.9 %, which was similar to that of *C. brevimanus* (35.0%) and other hermit crabs (Zhang *et al.*, 2021; Hickerson and Cunningham, 2000). Additionally, the AT-skew was appreciably negative (-0.157), reflecting a higher occurrence of Ts to As, and its GC-skew (0.176) was positive indicating a higher content of Gs than Cs.

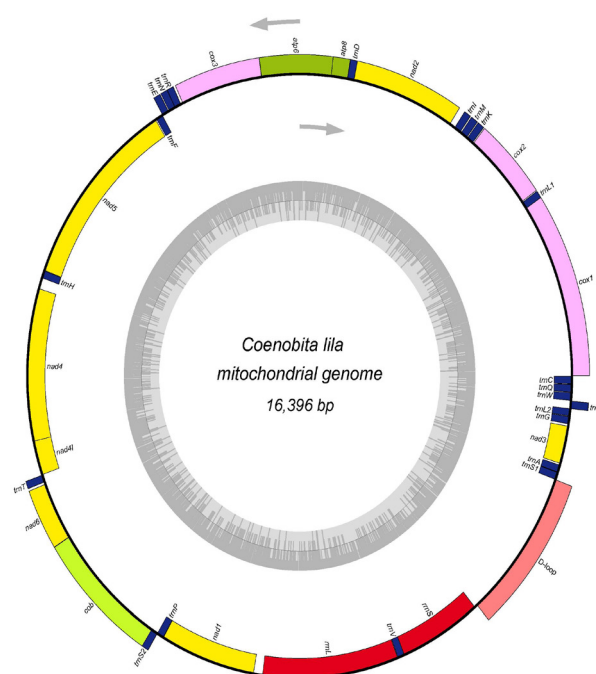


Fig. 1. Gene map of the mitogenome of *Coenobita lila*.

Table I. The mitochondrial genome features of *Coenobita lila*.

Genes	Position		Length (bp)	Amino acid	Start/Stop condon	Anticodon	Intergenic region	Strand
	From	To						
<i>cox1</i>	1	1539	1539	512	ATG/TAA		-	H
<i>trnL1</i>	1535	1598	64			CTA	-5	H
<i>cox2</i>	1606	2295	690	229	ATG/TAG		7	H
<i>trnK</i>	2304	2368	65			AAA	8	H
<i>trnM</i>	2376	2443	68			ATG	7	H
<i>trnI</i>	2454	2519	66			ATC	10	H
<i>nad2</i>	2574	3587	1014	337	ATT/TAA		54	H
<i>trnD</i>	3574	3638	65			GAC	-14	H
<i>atp8</i>	3639	3797	159	52	ATT/TAG		0	H
<i>atp6</i>	3794	4465	672	223	ATA/TAA		-4	H
<i>cox3</i>	4465	5256	792	263	ATG/TAG		-1	H
<i>trnR</i>	5276	5338	63			CGA	19	H
<i>trnN</i>	5338	5402	65			AAC	-1	H
<i>trnE</i>	5410	5475	66			GAA	7	H
<i>trnF</i>	5478	5543	66			TTC	2	L
<i>nad5</i>	5553	7266	1714	571	ATT/T		9	L
<i>trnH</i>	7270	7335	66			CAC	3	L
<i>nad4</i>	7432	8772	1341	446	ATG/TAA		96	L
<i>nad4l</i>	8766	9068	303	100	ATG/TAA		-7	L
<i>trnT</i>	9071	9135	65			ACA	2	H
<i>nad6</i>	9155	9665	510	169	ATA/TGA		19	H
<i>cob</i>	9666	10799	1134	377	ATA/TGA		0	H
<i>trnS2</i>	10798	10862	65			TCA	-2	H
<i>trnP</i>	10862	10928	67			CCA	-1	L
<i>nad1</i>	10930	11853	924	307	ATA/TAG		1	L
<i>16S</i>	11939	13258	1320				85	L
<i>trnV</i>	13262	13328	67			GTA	3	L
<i>12S</i>	13326	14120	795				-3	L
<i>trnS1</i>	15481	15546	66			AGA	1360	L
<i>trnA</i>	15549	15613	65			GCA	2	L
<i>nad3</i>	15628	15960	333	110	ATT/TAA		14	L
<i>trnG</i>	15979	16044	66			GGA	18	L
<i>trnL2</i>	16048	16112	65			TTA	3	L
<i>trnY</i>	16112	16178	67			TAC	-1	H
<i>trnW</i>	16183	16251	69			TGA	4	L
<i>trnQ</i>	16256	16323	68			CAA	4	L
<i>trnC</i>	16327	16394	68			TGC	3	L

PCGs and codon usage

The total length of PCGs in mitogenome of *C. lila* was 11,113 bp. Eight PCGs (*nad6*, *cob*, *cox1*, *cox2*, *nad2*, *atp8*, *atp6* and *cox3*) were encoded on the H-strand, while the remaining five PCGs (*nad3*, *nad1*, *nad4l*, *nad4* and *nad5*) were encoded on the L-strand (Table I). The start codons were similar to invertebrate mitochondrial genomes (Xu *et al.*, 2016), and five PCGs (*cox1*, *cox2*, *cox3*, *nad4* and *nad4l*) started from the ATG, four PCGs (*nad2*, *atp8*, *nad5* and *nad3*) started from the ATT and four PCGs (*atp6*, *nad6*, *cob*, and *nad1*) started from the ATA. Six PCGs (*cox1*, *nad2*, *atp6*, *nad4*, *nad4l* and *nad3*) were terminated with TAA, four PCGs (*cox2*, *atp8*, *cox3* and *nad1*) with TAG, two (*cob* and *nad6*) with TGA and one (*nad5*) with a incomplete termination codon T (Table I). The existence of incomplete termination codons was a common phenomenon in mitochondrial genes (Gong *et al.*, 2017; Hamasaki *et al.*, 2017). One explanation for this phenomenon was that the TAA end was produced by post-transcriptional polyadenylation (Honarmand and Shoubridge, 2020).

Totally, 13 PCGs of the mitogenome totally encoded 3696 amino acids. The number of codons varied from 52 (*atp8*) to 571 (*nad5*) (Table I). The most frequently used amino acids were Leu (15.8%) and Ile (11.0%), and the least common amino acids were Cys (1.1%), Trp (1.6%), and Met (2.2%). The RSCU (relative synonymous codon usage) value of the 13 PCGs for the third positions was shown in Figure 2. The usage of the two most frequent amino acids (Ile and Leu) were ATT and TTA, biased toward in A and T, while Cys, Trp and Met with low frequency were rich in G and T. The AT content of 13 PCGs was 61.2 %, and the AT skewness and GC skewness were -0.219 and 0.014, indicating that the species preferred T to A and G to C (Table II).

Transfer RNAs and ribosomal RNAs

The *C. lila* mitogenome contained 22 tRNAs genes, and the length of tRNA genes ranged from 63 (*trn-Arg*) to 69 bp (*trn-Trp*) with the total length 1452 bp (Tables I, II). Similar to the AT skew and GC skew of PCGs, its AT skew was negative (-0.014) and GC skew was positive (0.119), respectively (Table II). The two rRNA genes were identified on the L-strand in *C. lila* mitogenome, with the *12S rRNA* located between *D-loop* and *trn-Val*, and the *16S rRNA* located between *trn-Val* and *nad1*. The length of *12S rRNA* was 795 bp and the *16S rRNA* was 1320 bp. The AT-skew and GC-skew of rRNAs were 0.110 and -0.039, indicating that more As and Cs than Ts and Gs in rRNAs (Table II).

Table II. Composition and skewness of *Coenobita lila* mitogenome.

	Length (bp)	A (%)	T (%)	G (%)	C (%)	A+T (%)	AT- skew	GC- skew
Mitog- enome	16396	26.6	36.5	21.7	15.2	63.1	-0.157	0.176
<i>cox1</i>	1539	20.7	40.5	23.9	14.9	61.2	-0.323	0.229
<i>cox2</i>	690	21.7	39.7	24.5	14.1	61.5	-0.292	0.271
<i>atp8</i>	159	28.9	39.0	22.0	10.1	67.9	-0.148	0.373
<i>atp6</i>	672	20.1	41.8	21.0	17.1	61.9	-0.351	0.102
<i>cox3</i>	792	20.2	40.3	22.9	16.7	60.5	-0.332	0.157
<i>nad3</i>	333	29.7	30.6	14.4	25.2	60.4	-0.015	-0.272
<i>nad1</i>	924	26.8	32.1	16.9	24.1	59.0	-0.089	-0.177
<i>nad5</i>	1714	31.0	30.5	14.3	24.2	61.5	0.008	-0.258
<i>nad4</i>	1341	29.0	30.4	16.3	24.3	59.4	-0.024	-0.199
<i>nad4l</i>	303	26.7	32.3	15.5	25.4	59.1	-0.095	-0.242
<i>nad6</i>	498	20.1	44.4	22.9	12.7	64.5	-0.377	0.288
<i>cob</i>	1134	19.4	41.3	22.0	17.4	60.7	-0.360	0.117
<i>nad2</i>	1014	17.5	46.3	21.4	14.9	63.7	-0.452	0.179
tRNAs	1452	32.4	33.3	19.2	15.1	65.8	-0.014	0.119
rRNAs	2115	37.9	30.4	15.3	16.5	68.2	0.110	-0.039
PCGs	11113	23.9	37.3	19.7	19.1	61.2	-0.219	0.014

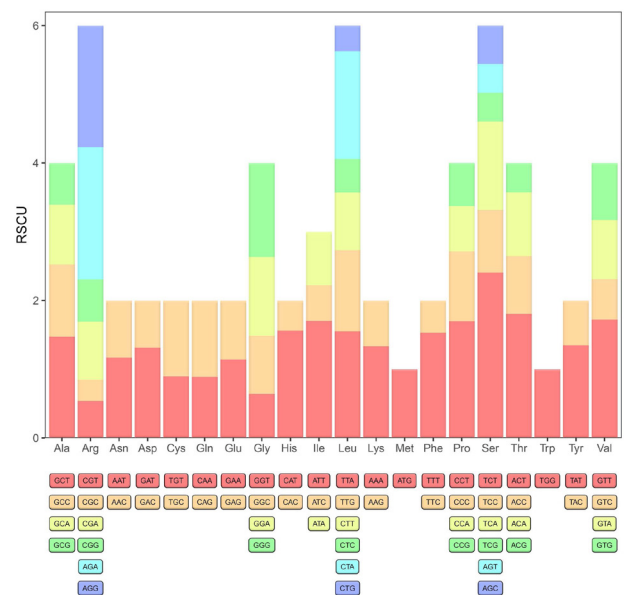


Fig. 2. Relative synonymous codon usage in *Coenobita lila* mitogenome.

Gene order of mitogenome

The gene order of *C. lila* mitogenome underwent

a large rearrangement compared with its ancestor (pancontinental crustaceans) (Boore *et al.* 1998) (Fig. 3). In summary, six gene clusters dramatically differed from the typical order, involving eleven tRNAs (*L1*, *L2*, *G*, *A*, *S1*, *P*, *I*, *Q*, *M*, *W* and *Y*), and two PCGs (*nad2* and *nad3*). The gene *cox1-cox2-K-D-atp8-atp6-cox3-R-N-E-F-nad5-H-nad4-nad4I-T-nad6-cob-S2-nad1-16S-V-12S-C* were not rearrangement, which was the same as that of the ancestral crustaceans. In these six gene clusters, the *I-Q-M-nad2* cluster was split into two parts, with *Q* being transferred to the end of the linear mitochondrial genome. Another (*I*, *M* and *nad2*) was transferred downstream of *K*. The *W-C-Y* cluster order became the *Y-W-C* order, and *L1* moved between *cox1* and *cox2*. When a single *P* moved downstream from *T* to *S2*, the *G-nad3-A-S1* cluster moved from the *cox3* of the heavy strand to the *CR* downstream of the heavy strand. A single *L2* moved to the position between the *S1-A-nad3-G* cluster and the *Y-W-Q-C* cluster downstream of *CR* forming a large-scale rearrangement region.

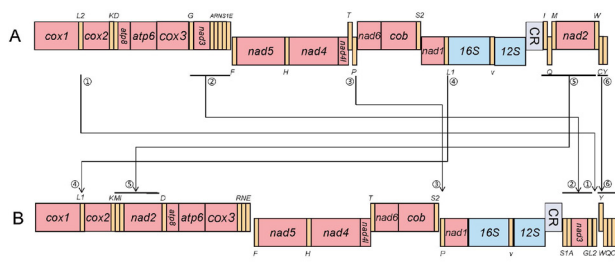


Fig. 3. Gene rearrangements in *Coenobita lila* mitogenome. A, The ancestral gene arrangement of crustaceans. B, The gene order in the *Coenobita lila* mitogenome.

Here, we used replication-random loss and recombination models to explain the mitochondrial genome rearrangement of *C. lila*. First, one gene cluster underwent a complete copy to form one dimer block (*I-Q-M*). Continuous copies were followed by random loss of duplicate genes, *I-Q-M-I-Q-M* (underline represents the deleted gene), and then a new gene block (*Q-M-I*) was formed. Tandem repeats followed by random loss have been widely used to explain this type of translocation of mitochondrial genes (Gong *et al.*, 2019; Shi *et al.*, 2015; Chai *et al.*, 2017). Therefore, we determined that the repeat-random loss model was the most likely explanation for the rearrangement of this gene block. Subsequently, the *M-I-nad2* block moved to the junction of *K* and *D*. In the second step, seven genes or gene blocks were translocated. *L1* was moved to the junction of *cox1* and *cox2*, *L2* was moved to the middle of *nad2* and *W*, and then *Y* was moved to the downstream of *L2*. The gene cluster *G-nad3-A* and gene *S1*

moved to between *CR* and *Q* and changed to *S1-A-nad3-G*. At the same time, *P* moved to the middle of *S2* and *nad1*, and *Q* moved to the middle of *W* and *C*. Moreover, restructuring events seemed to explain these translocations and the final gene arrangement of mitochondrial genome in *C. lila*.

Ka/ Ks ratio

The ratio of Ka/ Ks represents the ratio between non-synonymous mutations (Ka) and synonymous mutations (Ks) of the two protein-coding genes, which determines whether there is selective pressure on the protein-coding gene (Hurst, 2002). In the study, the calculated Ka/ Ks values of the 13 PCGs of the Anomura were all less than 1 (Fig. 4), suggesting the presence of purification selection. The ratio of *atp8* was the largest, ranging from 0.056 to 0.920, indicating that *atp8* faced the least pressure. This was consistent with the results of *C. clypeatus* (Colin *et al.*, 2022). On the contrary, the evolutionary selection pressure on *atp6* was different from that on *atp8*, where the evolutionary pressure was high.

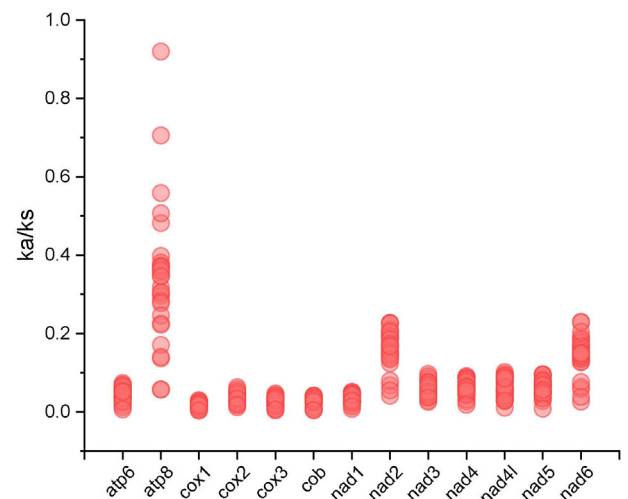


Fig. 4. Ka/ Ks ratios of 13 PCGs.

Phylogenetic analysis and gene rearrangement patterns

In order to analyse the phylogenetic status of *C. lila* in Anomura, we constructed a phylogenetic tree (ML) based on 13 PCGs of 30 species with *P. princeps* as the outgroup (Table III, Fig. 5). The results showed that all 23 species of Anomura and 7 species of Brachyura were clustered together separately. And 9 superfamily were monophyletic groups except for the Paguroidea. Paguroidea was paraphyletic with Paguroidea group and Coenobitidae + Diogenidae group, which was consistent with the previous research (Tan *et al.*, 2018; Li *et al.*, 2020). And *C. lila* was clustered in Coenobitidae family.

Table III. List of 31 mitogenome data in this paper.

Species	Length(bp)	Accession No.
Superfamily: Paguroidea		
Family: Diogenidae		
<i>Dardanus arrosor</i>	16,592	NC_060631
<i>Dardanus aspersus</i>	16,916	MW715812
<i>Clibanarius infraspinus</i>	16,504	NC_025776
Family: Coenobitidae		
<i>Birgus latro</i>	16,411	NC_045091
<i>Coenobita rugosus</i>	16,433	MN030161
<i>Coenobita lila</i>	16,396	OP645220
<i>Coenobita variabilis</i>	16,421	KY352236
<i>Coenobita brevismanus</i>	16,393	MN030160
Superfamily: Hippoidea		
Family: Albuneidae		
<i>Stemonopa insignis</i>	15,596	KY352240
Superfamily: Galatheaidea		
Family: Porcellanidae		
<i>Petrolisthes haswelli</i>	15,348	NC_025572
Family: Galatheididae		
<i>Munida gregaria</i>	16,326	NC_030255
Family: Munidopsidae		
<i>Munidopsis lauensis</i>	17,483	MH717895
<i>Munidopsis verrilli</i>	17,636	MH717896
Superfamily: Paguroidea		
Family: Paguridae		
<i>Pagurus longicarpus</i>	15,630	AF150756
<i>Pagurus similis</i>	17,100	NC_057304
<i>Pagurus nigrofascia</i>	15,423	NC_042412
Superfamily: Lithodoidea		
Family: Lithodidae		
<i>Paralithodes brevipes</i>	16,303	NC_021458
<i>Paralithodes platypus</i>	16,883	NC_042240
<i>Paralithodes camtschaticus</i>	16,720	NC_020029
Superfamily: Lomoidea		
Family: Lomidae		
<i>Lomis hirta</i>	17,239	KY352239
Superfamily: Chirostyloidea		
Family: Kiwaidae		
<i>Kiwa tyleri</i>	16,865	NC_034927
Family: Chirostylidae		
<i>Gastroptychus rogeri</i>	16,504	KY352238
<i>Gastroptychus investigatoris</i>	16,423	KY352237
Superfamily: Xanthoidea		
Family: Oziidae		
<i>Epixanthus frontalis</i>	15,993	MF457404
Superfamily: Pilumnoidea		
Family: Pilumnidae		
<i>Pilumnus vespertilio</i>	16,222	MF457402

Table continued on next column.....

Species	Length(bp)	Accession No.
Superfamily: Ocypodoidea		
Family: Ocypodidae		
<i>Cranuca inversa</i>	15,677	MF457405
<i>Tubuca capricornis</i>	15,629	MF457401
<i>Tubuca polita</i>	15,672	MF457400
Superfamily: Grapsoidea		
Family: Gecarcinidae		
<i>Cardisoma carnifex</i>	15,597	NC_039105
Family: Grapsidae		
<i>Pachygrapsus marmoratus</i>	15,406	MF457403
Superfamily: Plecoptera		
Family: Pteronarcyidae		
<i>Pteronarcys princeps</i>	16,004	NC_006133

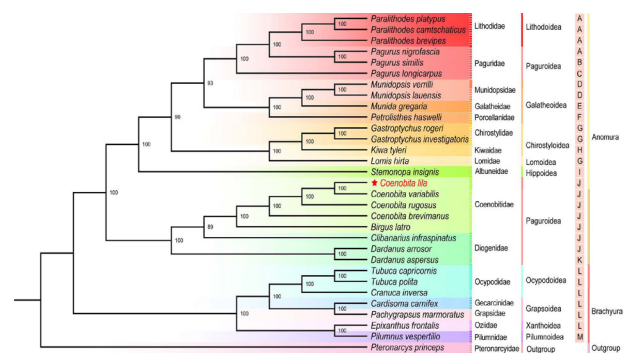


Fig. 5. Phylogenetic tree inferred from the 13 PCGs based on maximum likelihood (ML) analysis.

According to the gene rearrangement of all the 30 species, 13 gene rearrangement patterns (A-M) were defined. Mitochondrial gene rearrangements were mainly divided into three main forms: Shuffling, translocation and inversion. In general, every family of Anomura had its own unique arrangement type, such as Lithodidae (A), Munidopsidae (D), Galatheididae (E), Porcellanidae (F), Chirostylidae and Lomidae (G), Kiwaidae (H), Albuneidae (I), Coenobitidae (J) except for Paguridae (B and C) and Diogenidae (J and K). In all the gene rearrangement patterns of Anomura (A-K), we found that three gene clusters were conserved: *cox2-trnK*, *atp8-atp6-cox3-trnR-trnN*, *trnP-nad1*. Paguroidea was divided into two independent clades in the phylogenetic tree. In addition, these two clades had five different patterns in gene rearrangement patterns. Coenobitidae+Diogenidae group was clustered together, and except for *D. aspersus*, the gene rearrangement patterns of the other seven species were the same, while the gene rearrangement patterns of the three species in Paguridae were different. This indicated that gene rearrangement might be used in the study of systematic evolution of Anomura.

CONCLUSION

This study reported the complete mitochondrial genome of *C. lila*. It was 16,396 bp in length and contained 13 protein-coding genes, 2 ribosomal RNA genes, 22 transfer RNA genes and a control region. Mitochondrial genome of *C. lila* was with negative AT skew and positive GC skew. Ka/Ks of the 13 protein-coding genes indicated purifying selection. The phylogenetic tree provided a certain reference for the reclassification of Paguroidea. Mitochondrial genome characteristics and gene rearrangement patterns might be used in the study of systematic evolution of Anomura.

DECLARATIONS

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IRB approval

The research work was approved by Jiangsu Key Laboratory for Bioresources of Saline Soils, Jiangsu Provincial Key Laboratory of Coastal Wetland Bioresources and Environmental Protection, Jiangsu Synthetic Innovation Center for Coastal Bio-agriculture, Yancheng Teachers University, Yancheng, China.

Data availability statement

The data that support the findings of this study are openly available in NCBI (Accession number: OP645220).

Statement of conflict of interest

The authors have declared no conflicts of interest.

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