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Full Length Research Paper

Complete mitochondrial genome of the ornate rock lobster *Panulirus ornatus* (Crustacea: Decapoda)

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The ornate rock lobster *Panulirus ornatus* is an important commercial lobster in the world. In this study, we successfully amplified and sequenced the complete mitochondrial genome of *P. ornatus*. The DNA of *P. ornatus* is 15680 bp, containing 13 protein-coding genes (PCGs), two ribosomal RNA genes, 22 transfer RNA genes, and 1 AT-rich non-coding region. The sequence arrangement of *P. ornatus* mitochondrial genome and the structures of 32 mitochondrial genes were analyzed. Phylogenetic analyses, using 13 protein-coding genes of the mitochondrial genome with Bayesian inference (BI) and maximum likelihood (ML) methods were performed. ML analysis showed that Pleocyemata could be separated into five groups: Caridea, Palinura, Astacidea, Anomura and Brachyura, while BI analysis showed that Achelata and Astacidea could be presented as a sister group. Both the results of BI and ML supported that *P. ornatus* and *Panulirus stimpsoni* group together to form a monophyletic clade presented as the sister group to *Panulirus japonicus*.

Key words: *Panulirus ornatus*, mitochondrial genome, decapoda, phylogenetics.

INTRODUCTION

Decapoda, an order of crustaceans, comprise two families, Dendrobranchiata (540 species) and Pleocyemata (13795 species) (DeGrave et al., 2009). Members of Decapoda show a high diversity and heterogeneity in morphological features, ecological adaptability, and life history (DeGrave et al., 2009; Schram, 2001). The now reported sizes of the mitochondrial genomes of Decapoda are 14113 to 18372 bp (Shen et al., 2009). The typical mitochondrial genome contains one control region or non-coding fragment and 37 genes encoding 13 protein subunits, two ribosomal RNAs (rRNAs), and 22 transfer RNAs (tRNAs). Mitochondrial genomes have been widely used in molecular phylogenetic analysis (Yang et al., 2008; Cunha et al., 2009; Wei et al., 2012), population genetic analysis (Valles-Jimenez et al., 2006; Johansson et al., 2012), and identification of DNA barcoding and molecular markers (Hebert et al., 2003a, b; Lise and Raphael, 2008; Williams et al., 2001).

The ornate rock lobster *Panulirus ornatus*, a member species of family Palinuroidea, infraorder Achelata, is one of the most important commercial lobster species in China distributing in the East and South China Seas. *P. ornatus* is the largest tropical lobster with the body weight up to over 6.5 kg (Murugan et al., 2005). Due to its great economic value and important evolutionary status, more and more studies have been focused on its breeding (MacFarlane and Moore, 1986; Zakaria and Kassim, 1999), growth (Dennis et al., 1997; Skewes et al., 1997) and larval rearing (Bourne et al., 2004; Payne et al., 2007). Some mitochondrial genes of *P. ornatus*, such as cox1, cob, and D-loop, have been identified (Diniz et al., 2005). However, the knowledge of *P. ornatus* genetics background is still limited. In this study, we sequenced the complete mitochondrial genome of *P. ornatus* and determined its genomic structure, gene order, base composition and control region features.

Based on these, the phylogenetic status of *P. ornatus*, as well as some other species form Decapoda, was analyzed using Bayesian inference (BI) and maximum

Table 1. Primers for amplifying the mitochondrial genome of *P. ornatus*.

Primer name	Sequence (5'-3')	Amplified length (bp)
L1-F	CGATGATTTTTCTCTACTAATCATAAAGACA	3453
L1-R	CTTCTCGTGTTACGTCTCGTCATCA	
L2-F	GGCCATGACCTTTAACAGGATCG	6194
L2-R	CGTGTTAGGGTGGCGTTGCTTAC	
L3-F	GTCGTTTTGAGGAGCAACAGTTATTACTA	3363
L3-R	TACATATTGCCCGTCGCTTTCA	
L4-F	CCAGTACACCTACTATGTTACGACTTATCTCA	3055
L4-R	TGAAGTATAAGGTACCAATGTCTTTATGA	

likelihood (ML) methods.

MATERIALS AND METHODS

Genomic DNA extraction

Live *P. ornatus* were collected from Hainan Island of China. DNA was purified form muscle tissues using a tissue DNA Kit (Qiagen, USA) and preserved at -20°C.

Polymerase chain reaction (PCR) amplification and sequencing

The complete mitochondrial genome of *P. ornatus* was artificially separated into four regions. Four fragments, corresponding to the four regions with overlapping tail ends were obtained by PCR amplification. Four pairs of mismatched PCR primers (Table 1), covering the complete genome of *P. ornatus*, were designed by referring to the mitochondrial genomes from *Panulirus japonicus* (GenBank accession No. NC_004251) and *Scylla serrata* (GenBank accession No. NC_012565). Long-PCR reactions were carried out in 25 μL reaction mixtures containing 2.5 μL of 10× buffer, 0.5 μL of 10 mM dNTP, 1.0 μL of 5 pM primer-F, 1.0 μl of 5 pM primer-R, 0.5 μL of DNA template, 1.0 μL of LA Taq enzyme and 18.5 μL of dd H_2O. Amplifications were performed with initial denaturation at 94°C for 5 min, followed by 30 cycles of denaturation at 94°C for 20 s, annealing at 58°C for 45 s, extension at 72°C for 5 min, and a final extension at 72°C for 10 min. The PCR reaction products were cloned into PMD-19T vector (Takara, Dalian, China) and sequenced on the ABI 3730 platform.

Sequence analysis and gene prediction

The sequenced four fragments was assembled using SeqMan tool of DNAstar. The open reading frame (ORF) was determined using ORF finder and basic local alignment search tools (BLAST) of National center for biotechnology information (NCBI). The two ribosomal RNAs were predicted using DOGMA (Wyman et al., 2004) and BLAST. The parameter settings of the DOGMA were as follows: genome type was set to mitochondrial, percent identity cutoff for protein-coding genes (PCGs) was set to 40, genetic code for BLASTX was set to invertebrate mitochondrial, and other parameters were set to default values. The 22 tRNA coding genes were identified by BLAST and tRNAScan-SE software (http://lowelab.ucsc.edu/tRNAscan-SE/), with parameter settings as follows: search mode was set to tRNAscan only and source to be as mit/chloroplast. The two rRNA genes were determined by BLAST, together with their conservative positions in the genome and adjacent genes. The mitochondrial structure chart of *P. ornatus* was drawn by OGDRAW v1.1 (http://ogdraw.mpimp-golm.mpg.de/).

Phylogenetic analysis

The mitochondrial genome sequences of 30 species of Decapoda and two species (*Lysiosquillina maculata* and *Squilla empusa*) of Stomatopoda (as outgroups) were obtained from GenBank. Multiple alignments of the amino acid sequence were deduced using Clustal X (Larkin et al., 2007), and a conservative region was obtained using Gblocks (Castresana, 2000) after contrast, thereby yielding 3348 determined amino acid sites for analysis. All the PCGs of each species were re-arranged into the same gene order (*cox1*, *cox2*, *atp8*, *atp6*, *cox3*, *nad3*, *nad6*, *cob*, *nad2*, *nad5*, *nad4*, *nad4L* and *nad1*). The phylogenetic trees were constructed using the ML method (Guindon and Gascuel, 2003) and the BI method (Huelsenbeck and Ronquist, 2001). The phylogenetic tree of maximum likelihood method was constructed by the PhyML 3.0 software (Guindon and Gascuel, 2003). The best model for analysis was determined as MtRev + I + G + F by Protest version 2.4, and the parameter of PhyML 3.0 (Guindon and Gascuel, 2003) were set to aamodelpr = fixed (mtREV) and rates = invgamma. In the Bayesian method, the analysis was carried out using Mrbayes3 software (http://mrbayes.csit.fsu.edu/index.php) and the best-scoring MtRev matrix and invgamma model were adopted for the analysis. A Markov chain was selected for running 1000000 generations (the tree construction frequency was 1000 generations), which ensured sufficient time for achieving convergence. After about 100000 generations, the log-likelihood value in each tree construction became stable. The first 100 trees were removed, collegiality was carried out on the remaining 900 trees according to the principle of ">50%", and Bayesian prior probability was estimated.

RESULTS AND DISCUSSION

Genome features

The structural organization of the complete mitochondrial

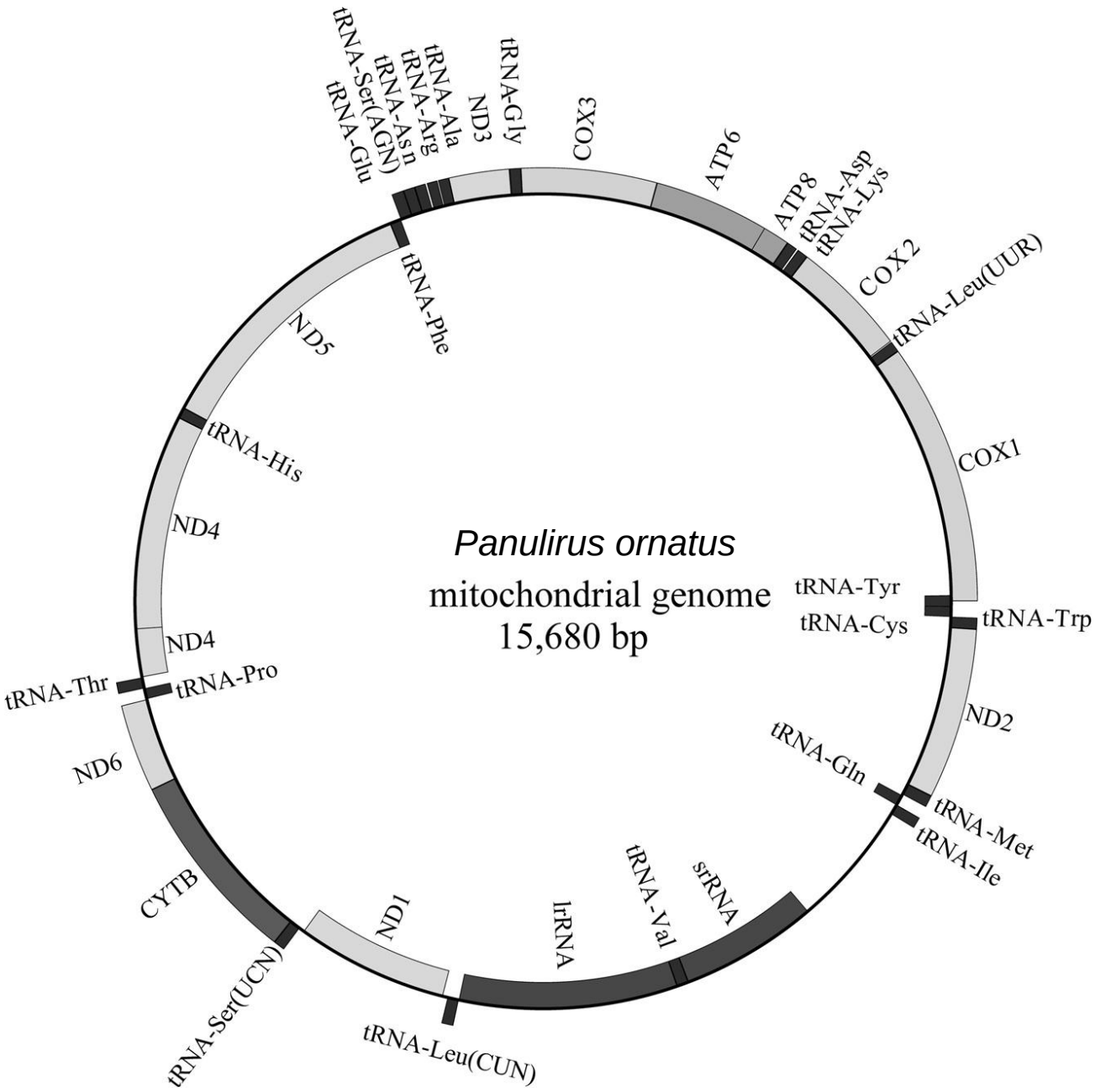

Figure 1. Mitochondrial genome structure chart of *P. ornatus* drawn by OGDRAW. The outer and inner boxes represent the positive and negative strands of the mitochondrial DNA, respectively.

geneome of *P. ornatus* is shown in Figure 1. The double-stranded cyclic mitochondrial genome of *P. ornatus* is 15680 bp in length (GenBank accession no. HM446347) which is between the shortest (15182 bp, *Shinkala crosnleri*) and longest (18197 bp, *Geothelphusa dehaani*) mitochondrial genomes from Decapoda. It is slightly shorter than that of *P. japonicus* (15717 bp) and slightly longer than that of *Panulirus stimpsoni* (15677 bp). Like other species of Decapoda, it has 13 protein-coding genes, two ribosomal RNAs and 22 transfer RNAs coded. The positive strand codes 23 genes (nine protein-coding genes and 14 tRNA genes) and the negative strand codes 14 genes (four protein-coding genes, eight tRNA genes and two rRNA genes) (Table 2 and Figure 1). The A + T content of the complete *P. ornatus* genome is66.72% (A = 34.30%, T = 32.42%, C = 20.08%, G = 13.2%), which is higher than that of either *P. japonicus* (64.5%) or *P. stimpsoni* (65.6%) and lower than the average of Decapoda (68.93, 62.3 to 74.9%). The A + T content of the protein-coding genes is 65.19% (A =

Table 2. Mitochondrial gene profile of *P. ornatus* (15680 bp).

Gene	Strand	Position	Size (bp)	Start codon	Stop codon	Intergenic nucleotide
cox1	+	1-1534	1534	ACG	T*	
tRNA$^{Leu(UUR)}$	+	1535-1599	65			0
cox2	+	1604-2291	688	ATG	T*	4
tRNA^{Lys}	+	2292-2356	65			0
tRNA^{Asp}	+	2370-2432	63			13
atp8	+	2433-2591	159	ATG	TAA	0
atp6	+	2585-3262	678	ATG	TAA	-7
cox3	+	3262-4053	792	ATG	TAA	-1
tRNA^{Gly}	+	4053-4118	66			-1
nad3	+	4119-4470	352	ATC	T*	0
tRNA^{Ala}	+	4471-4533	63			0
tRNA^{Arg}	+	4535-4598	64			-7
tRNA^{Asn}	+	4604-4669	66			5
tRNA$^{Ser(AGN)}$	+	4670-4737	68			0
tRNA^{Glu}	+	4739-4810	72			1
tRNA^{Phe}	-	4818-4884	67			7
nad5	-	4884-6613	1730	ATG	TA*	-1
tRNA^{His}	-	6614-6678	65			0
nad4	-	6679-8017	1339	ATG	T*	0
nad4L	-	8011-8313	303	ATG	TAA	-7
tRNA^{Thr}	+	8316-8382	67			2
tRNA^{Pro}	-	8383-8450	68			0
nad6	+	8453-8968	516	ATT	TAA	2
cob	+	8969-10105	1137	ATG	TGA	0
tRNA$^{Ser(UCN)}$	+	10104-10171	68			-2
nad1	-	10202-11146	945	ATT	TAA	30
tRNA$^{Leu(CUN)}$	-	11181-11249	69			34
lrRNA	-	11250-12593	1344			0
tRNA^{Val}	-	12594-12664	71			0
srRNA	-	12665-13520	856			0
Noncoding region	+	13521-14274	754			0
tRNA^{Ile}	+	14275-14340	66			0
tRNA^{Gln}	-	14338-14406	69			-3
tRNA^{Met}	+	14416-14481	66			9
nad2	+	14482-15483	1002	ATG	TAA	0
tRNA^{Trp}	+	15482-15550	68			-2
tRNA^{Cys}	-	15550-15615	66			-1
tRNA^{Tyr}	-	15616-15680	65			0

The negative value means that the adjacent genes are overlapped. *Tthe complete stop codon is formed by polyadenylation after transcription.

33.73%, T = 31.46%, G = 13.84%, C = 20.97%), which is also higher than that of *P. japonicus* or *P. stimpsoni* and lower than the average level of Decapoda (67.07%). The length of the non-coding portion of the *P. ornatus* genome is 852 bp, distributed in 18 intergenic regions. The largest region with a size of 754 bp and an A + T content as high as 72.28%, located between srRNA and tRNA^{Ile}, shows a basic feature of the control region, and the position is consistent with those from other crustaceans (Miller and Austin, 2006; Shen et al., 2007). The sizes of the control regions of Decapoda vary considerably, and range from 327 bp (*S. crosnleri*) to 1435 bp (*S. crosnleri*) with high A + T contents, averaging about 79.76%.

Gene arrangement

Through contrasting with 32 mitochondrial gene arrangements from Decapoda and Stomatopoda, we

found that the mitochondrial genome of *P. ornatus* shares the exact same gene arrangement with other species, including *Drosophila yakuba* (insect) and *Daphnia magna* (crustacean) (Boore and Brown, 1998; Kilpert and Podsiadlowski, 2006; Miller et al., 2004; Place et al., 2005). This arrangement is as follows: cox1-L_2-cox2-K-D-atp8-atp6-cox3-G-nad3–A–R–N–S_1–E–F–nad5–H–nad4–nad4L–T–P–nad6–cob–S_2–nad1–L_1–lrRNA–V–srRNA–nCR–I–Q–M–nad2–W–C–Y. Among the compared species, the same gene arrangement profile was also found in 10 other species, including five species from Penaeoidea (*Fenneropenaeus chinensis, Litopenaeus vannamei, Litopenaeus stylirostris, Penaeus monodon*, *M. japonicus*), three species from Caridea (*M. lanchesteri, M. rosenbergii, H. rubra*), and two species from Achelata (*P. japonicas, P. stimpsoni*). In Decapoda, the gene rearrangement of the mitochondrial genome occurs in Dendrobranchiata and Pleocyemata. In Penaeoidea, the $tRNA^{Pro}$ gene translocation occurs in *F. californiensis*. In Caridea, $tRNA^{Thr}$ and $tRNA^{Pro}$ inversion (Shen et al., 2009) occurs in *E. carinicauda*. One or a plurality of gene translocation, duplication, inversion, or rearrangement (Yamauchi et al., 2002; Miller et al., 2005; Place et al., 2005; Segawa and Aotsuka, 2005; Sun et al., 2005) occur in Astacidea, Anomura, and all 14 species of Brachyura.

Protein-coding genes

The mitochondrial genome of *P. ornatus* contains 13 protein-coding genes in total. Nine genes (*atp6*, *atp8*, *cox1*, *cox2*, *cox3*, *cob*, *nad2*, *nad3* and *nad6*) are coded on the positive strand, and the remaining four (*nad1*, *nad4*, *nad4L*, and *nad5*) are coded on the negative strand. The transcription direction of the protein-coding genes is consistent with that of Pancrustacea. Three pairs of coding genes (*atp8* and *atp6*, *atp6* and *cox1*, and *nad1* and *nad4L*, with 7-, 1-, and 7-base repeats, respectively) overlap on the positive strand. 12 of the 13 protein-coding genes of *P. ornatus* have ATS start codon (including ATG: cox2, *atp8*, *atp6*, *cox3*, *nad4*, *nad4L*, *nad2*, and *cob*; ATC: nad3) or ATT start codon (nad6 and nad1), and the start codon of the *cox1* gene is ACG. The stop codon of seven protein-coding genes is TAA (*atp8*, *atp6*, *cox3*, *nad1*, *nad2*, *nad4L* and *nad6*), and the stop codon of the *cob* gene is TGA. The five remaining genes lack a complete TAA or TGA stop codon (TA-:nad5, T-:cox1, cox 2, nad3, and nad 4) (Table 2). These genes obtain a stop codon by adenylation at the tail of T during mRNA processing. The types of start and stop codons of *P. ornatus* mitochondrial coding genes are common, found in other crustaceans (Ivey and Santos, 2007).

Transfer RNA genes

The mitochondrial genome of *P. ornatus* encodes 22 tRNAs with the lengths from 62 to 72 bp (Table 2). Similar to that of *P. japonicus*, *P. stimpsoni*, *F. chinensis*, *L. vannamei*, and some other crustaceans, each tRNA can be folded to form a clover-like secondary structure, with the exception of $tRNA^{Ser(AGN)}$, which lacks the dynein heavy chain (DHC) arm (Figure 2) (Wilson et al., 2000; Yamauchi et al., 2002; Miller et al., 2004; Tjensvoll et al., 2005; Miller and Austin, 2006; Shen et al., 2007; Liu and Cui, 2010).

Ribosomal RNA

Two rRNA genes, the long rRNA (*lrRNA*) gene and the short rRNA (*srRNA*) gene, were found in *P. ornatus* mitochondrial genome. The *lrRNA* gene, with a size of 1344 bp and an A + T content of 72.2%, lies between $tRNA^{Leu\ (CUN)}$ and $tRNA^{Val}$. The *srRNA* gene, with a size of 856 bp and an A + T content of 68.8%, lies between the $tRNA^{Val}$ and the control region (D-loop). The two rRNA genes are localized on the negative strand, and their directions are basically consistent with those of most crustaceans (Miller and Austin, 2006). So far, in Decapoda, only five species (*Cherax destructor, Eriocheir hepuensis, Eriocheir japonica, Eriocheir sinensis,* and *Geothelphusa dehaani*) are known to have different positions and directions of these two rRNA genes.

Phylogenetic relationship of decapoda

13 coding genes of the mitochondrial genome were used for constructing the phylogenetic trees. The results of analysis using BI and ML methods (Figures 3 and 4), showed that Decapoda could be separated into Dendrobranchiata and Pleocyemata, and were consistent with the classification system of Martin and Davis (2001), and the results of Ki et al. (2009), Miller and Austin (2006) and Shen et al. (2007, 2009), but not with that of Liu and Cui (2010). Both the results of BI and ML supported that *P. ornatus* and *P. stimpsoni* grouped together to form a monophyletic clade presenting as the sister group to P. japonicus, which was consistent with that of Margaret et al. (2001). ML analysis showed that the suborder Pleocyemata could be separated into five groups: Achelata, Anomura, Astacidea, Brachyura, and Caridea, which was consistent with that of Qian et al. (2011). BI analysis showed that Achelata and Astacideacould be presented as a sister group, which was consistent with the results from Alexandre (2006), Ivey and Santos (2007) and Shen et al. (2007, 2009).

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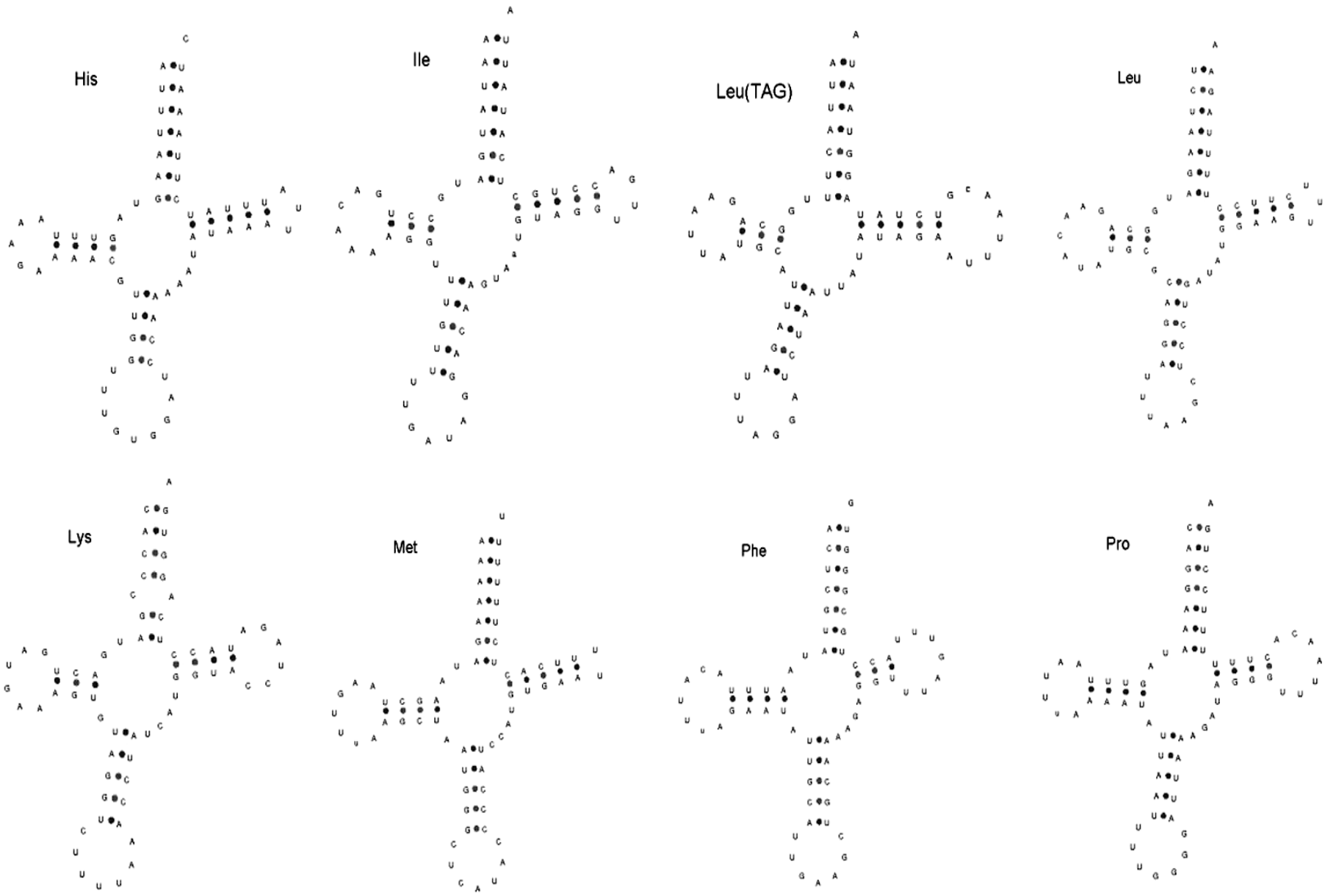

Figure 2. Secondary structure charts of 22 tRNAs from *P. ornatus* mitochondrial genome.

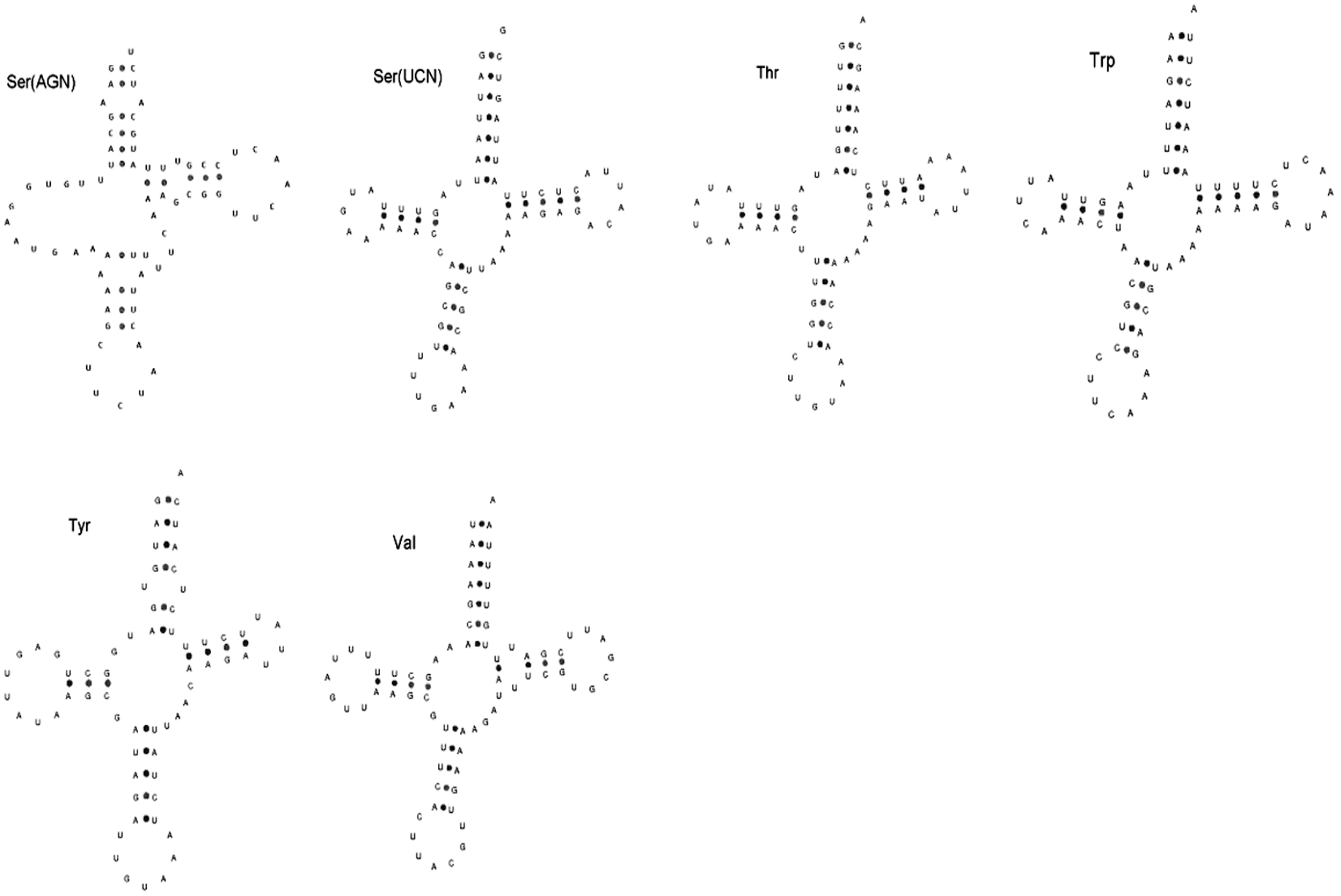

Figure 2. Continued.

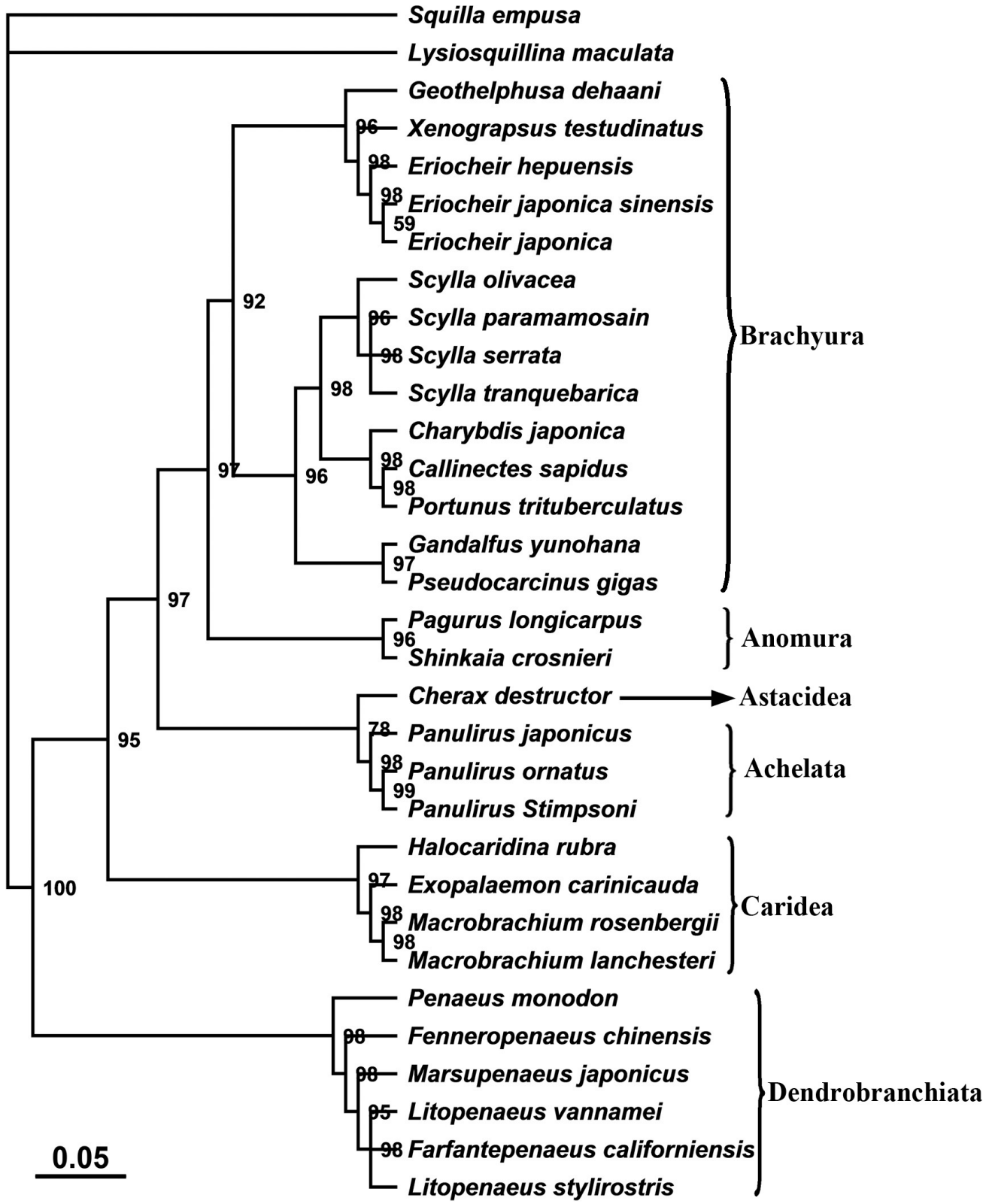

Figure 3. Internal phylogenetic tree (Bayesian method) of Decapoda constructed by amino acid sequences based on 13 protein-coding genes of the mitochondrial genome. The node support rate is Bayesian prior probability. The outgroup is stomatopoda.

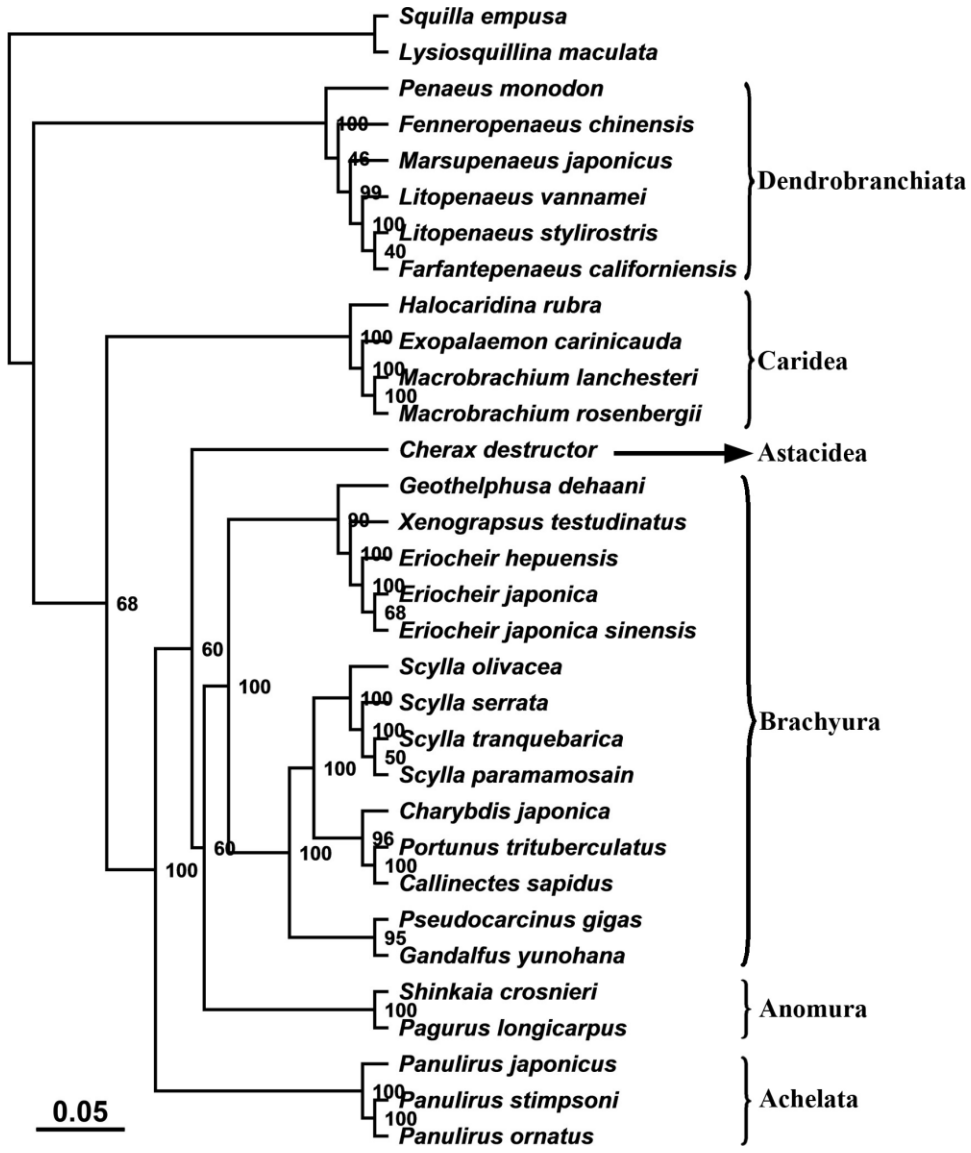

Figure 4. Internal phylogenetics tree (maximum likelihood method, ML) of Decapoda constructed by amino acid sequences based on 13 protein-coding genes of the mitochondrial genome. The node support rate is the bootstrap value of the ML method. The outgroup is stomatopoda.

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