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Article *in* Journal of Zoological Systematics and Evolutionary Research · May 2021

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Received: 19 August 2020 | Revised: 25 March 2021 | Accepted: 27 March 2021

DOI: 10.1111/jzs.12478

JOURNAL OF ZOOLOGICAL SYSTEMATICS AND EVOLUTIONARY RESEARCH

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SHORT COMMUNICATION

Descriptive study of the mitogenome of the diamondback squid (*Thysanoteuthis rhombus* Troschel, 1857) and the evolution of mitogenome arrangement in oceanic squids

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Funding information
National Natural Science Foundation of China, Grant/Award Number: 31672257; Fundamental Research Funds for the Central Universities, Grant/Award Number: 201822022

Abstract

The diamondback squid, *Thysanoteuthis rhombus*, is the only currently accepted species within the family Thysanoteuthidae. In this study, the mitogenome of *T. rhombus* was sequenced using the Illumina NovaSeq 6000 platform. Features of the mitogenome were detected, and phylogenetic relationships among the Cephalopoda were reconstructed. Our results indicated that the mitogenome of *T. rhombus* had six duplicated genes and long non-coding regions. The gene arrangement of *T. rhombus* was consistent with that of species belonging to Ommastrephidae. Moreover, the most gene rearrangement patterns were found in Oegopsida and Octopoda, whereas only one pattern was detected in Sepioidea. The mitogenome of Myopsida was highly rearranged among the four taxa. The phylogenetic relationship of *T. rhombus* + (((*Dosidicus gigas* + *Sthenoteuthis oualaniensis*) + *Ommastrephes bartramii*) + (*Illex argentines* + *Todarodes pacificus*)) was highly supported by both mitochondrial gene rearrangement analyses and all the phylogenetic analyses. Our study indicated that both gene sequences and arrangements may provide more information on the phylogeny and evolution of diverse mitogenomes in Cephalopoda and contribute to resolving contentious interclass relationships in the future.

KEYWORDS
gene duplication, gene rearrangement, mitochondrial genome, Oegopsida, phylogeny

摘要

菱鳍鱿鱼 (***Thysanoteuthis rhombus***) 是目前菱鳍鱿科唯一的物种。本研究利用Illumina NovaSeq 6000平台对菱形鱿鱼的线粒体全基因 组进行了测序, 并重建了头足纲的系统发育关系。结果表明, 菱鳍鱿鱼的线粒体全基因组有6个重复的基因和长非编码区。菱鳍鱿鱼的基 因排列与柔鱼科物种的基因排列一致。此外, 基因重排模式在开眼目和八腕目最多, 而在乌贼目中仅发现一种模式。在四大类群中, 闭眼亚目的线粒体基因组高度重排。线粒体基因重排分析和所有的系统发育分析都高度支持了***T. rhombus*** +((***Dosidicus gigas*** + ***Sthenoteuthis oualaniensis***) + ***Ommastrephes bartramii***)) 的系统发育关系。我们的研究表明, 无论是基因序列还是排列方式, 都 可以为头足类不同线粒体基因组的系统发育和进化提供更多的信息, 有助于解决未来有争议的类间关系。

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1 | INTRODUCTION

The diamondback squid, *Thysanoteuthis rhombus* Troschel, 1857, is a large oegopsid (open-eyed) squid that is distributed worldwide in tropical and subtropical waters (Kitaura et al., 1998; Nigmatullin et al., 1995). As the only currently accepted species within the family Thysanoteuthidae Keferstein, 1866 (Cephalopoda Cuvier, 1797: Oegopsida d'Orbigny, 1845) (Allcock et al., 2015; Roper & Jereb, 2010; Sajikumar et al., 2020), *T. rhombus* has been included in a few phylogenetic studies (Carlini et al., 2000; Lindgren, 2010; Sanchez et al., 2016; Takumiya et al., 2005). In addition, Lindgren et al. (2012) suggested that a clade containing Thysanoteuthidae and Ommastrephidae Steenstrup, 1857, was placed as a sister taxon to the rest of the oegopsids, but this clade had low support values. Subsequently, Sanchez et al. (2016) retrieved a different phylogeny of Enoploteuthidae Pfeffer, 19 00 + (Ommastrephidae + (Thysanoteuthidae + Architeuthidae Pfeffer, 1900)); however, the support values were still weak. Hence, the phylogenetic status of Thysanoteuthidae remains largely unknown and the relationships within Oegopsida are unresolved, mainly because of the limited resolution of gene markers or the number of taxa.

Recently, complete mitogenomes have been proven to be an important source of information for phylogenetic analyses and comparative or evolutionary genomic research at higher levels because of their fast evolution rates, small genome sizes, low sequence recombination, and maternal inheritance (Boore, 2006; Sun et al., 2016; Tang et al., 2019; Zarowiecki et al., 2007). Studies using mitogenomes have also been conducted within Cephalopoda, based not only on amino acid and nucleic acid sequences (Cheng et al., 2012, 2013; Tang et al., 2019; Yokobori et al., 2004), but also on gene order rearrangements within the genomes (Akasaki et al., 2006; Allcock et al., 2011; Kawashima et al., 2013; Stöger & Schrödl, 2013; Strugnell et al., 2017). Since the number of cephalopods that have been analyzed thus far has been limited (Akasaki et al., 2006), it is crucial to obtain additional mitochondrial genomic information to infer both the relationships within and among several clades that could not be resolved to understand the evolution of the mitochondrial genome.

In this study, we sequenced the mitogenome of the diamondback squid, *T. rhombus* using next-generation sequencing (NGS). The aim of the present study was to use both mitochondrial sequence data and gene arrangement to resolve the phylogenetic status of *T. rhombus* and phylogenetic relationships among coleoid cephalopods. In addition, we also discussed the potential phylogenetic association between gene rearrangement events in the mitogenomes and the evolution of biological characteristics within Cephalopoda.

2 | MATERIALS AND METHODS

2.1 | Sample collection and genomics DNA extraction

One specimen of *T. rhombus* (176.6 mm dorsal mantle length, immature female, Figure 1) collected from the South China Sea (latitude 23°17′N and longitude 117°37′E) in June 2019 was included in our analysis. Our study did not require ethical approval as the squid specimen was collected by local fishermen. Approximately 50 mg of muscle tissue was taken from the mantle of the squid and stored in 100% ethyl alcohol for molecular analysis. Total DNA was extracted using the E.Z.N.A.TM Mollusk DNA Kit (OMEGA Bio-Tek Company). The remaining body of the specimen in this study was stored in 10% formalin for 1 week, transferred to 95% alcohol, and then deposited as a voucher specimen (OUC-201906140101) at the Fisheries College, Ocean University of China.

2.2 | Library preparation, mitogenome sequencing, and assembly

The mitogenome of *T. rhombus* was sequenced by Novogene Company (Beijing, China) on the Illumina NovaSeq 6000 platform. The raw data were deposited into the Sequence Read Archive (SRA) database (https://www.ncbi.nlm.nih.gov/sra/) with the accession SRR13556517. A total of 65,067,334 high-quality reads (9.1 Gb) were obtained and assembled de novo using NOVOPlasty software (Dierckxsens et al., 2017). In the seed extension algorithm achieved via NOVOPlasty, the *cox1* gene fragment (654 bp, MW513724) of this specimen was used as a seed sequence. The assembled mitogenome was manually checked for overlapping segments at the beginning and end of the sequence to establish a circular mtDNA. To ensure the accuracy of the mitogenome, we used PCR and Sanger sequencing methods to verify partial fragments that had not been assembled well using next-generation sequencing in earlier attempts (Sanger et al., 1977). The primers were designed with Primer Premier v5.0 software (Lalitha, 2000). The primer sequences, lengths, positions, annealing temperatures, and GC content are shown in Table S1.

2.3 | Gene annotation and sequence analysis

The protein-coding genes (PCGs) were identified using the Open Reading Frame Finder (ORF Finder, https://www.ncbi.nlm.nih.gov/orffinder/) with the invertebrate mitochondrial genetic code. The tRNA genes were annotated with the MITOchondrial genome annotation Server (MITOS) (Bernt, Donath, et al., 2013) and ARWEN (Laslett & Canbäck, 2008) using the invertebrate genetic code and default search mode. All gene names and abbreviations were listed in Table S2. The boundaries of two rRNA genes were confirmed by comparing them with the mitogenome of the closely related species *Ommastrephes bartramii* (Lesueur, 1821) (NC020348, unpublished). The complete mitochondrial genome sequences were submitted to GenBank under accession number MT733875.

The nucleotide composition and base content values of *T. rhombus* were determined using Editseq program in DNASTAR software package (DNASTAR Inc.). The base skew values were calculated according to the formula: AT skew = (A − T)/(A + T) and

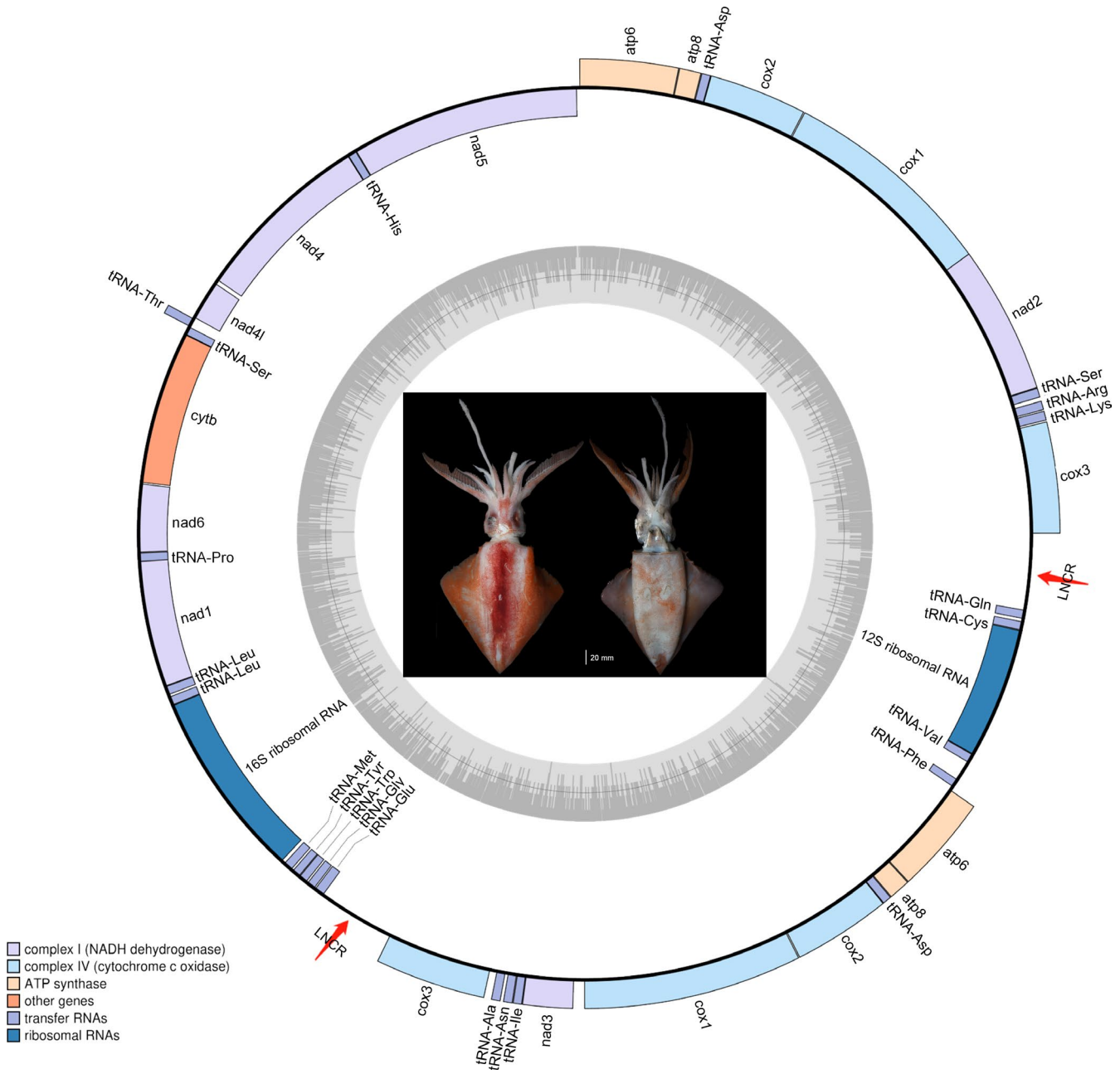

FIGURE 1 Gene map of *Thysanoteuthis rhombus*

GC skew = (G − C)/(G + C) (Perna & Kocher, 1995). The frequencies of codons, amino acids, and the relative synonymous codon usage (RSCU) were calculated using MEGA v7.0 (Kumar et al., 2016). The gene map was drawn using OrganellarGenomeDRAW (OGDRAW) v1.3.1 (Greiner et al., 2019; Lohse et al., 2007, 2013).

2.4 | Phylogenetic analyses

Forty-five coleoid mitogenomes used in the phylogenetic analyses were obtained from GenBank (Table S3). In addition, *Nautilus macromphalus* G. B. Sowerby II, 1849 (NC007980), and *Allonautilus scrobiculatus* (Lightfoot, 1786) (NC026997), two cephalopods in the separate subclass Nautiloidea, were selected as outgroups. Two datasets were used for phylogenetic analyses, that is the nucleotide sequences of 13 PCGs and two rRNA genes (Alignment S1) and the amino acid sequences of 13 PCGs (Alignment S2), which were aligned using MAFFT v7.313 (Katoh & Standley, 2013) in Phylosuite v1.2.1 (Zhang, Gao, et al., 2020). Duplicated protein-coding genes (*cox1*, *cox2*, *cox3*, *atp6*, and *atp8*) were detected in oegopsids. Due to the extremely low divergence between duplicated genes within a species, only a single copy of each duplicated gene was included in the datasets. The genes were concatenated using Phylosuite v1.2.1 (Zhang, Gao, et al., 2020), and the poorly aligned sections were

removed using Gblocks v0.91b with its default settings (Castresana, 2000). PartitionFinder v2.1.1 (Lanfear et al., 2017), based on the Akaike information criterion (AICc), was used to estimate the best partition scheme and substitution models for the maximum likelihood (ML) and Bayesian inference (BI) analyses (Table S4). The ML analysis was performed using IQ-TREE v1.6.12 under an edge-linked partition model for 10,000 ultrafast bootstraps replicates (Nguyen et al., 2015). The BI analysis was conducted using MrBayes v3.2.6 (Ronquist et al., 2012) with linked branch lengths for each partition scheme, 3,000,000 generations under the Markov chain Monte Carlo (MCMC) command, sampling every 100 generations, and discarding the first 25% of generations as burn-in. Parameter convergence was checked with Tracer v1.7 (Rambaut et al., 2018), and the effective sample size (ESS) value was more than 200. All phylogenetic results were visualized using FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/figtree).

2.5 | Gene rearrangement analyses

We checked all the mitochondrial gene arrangements analyzed in our study using MITOS web server (Bernt, Donath, et al., 2013) and changed some missing or incorrect annotations in these GenBank files (Figure 2). We reconstructed the gene rearrangement history using tree rearrangement explorer (TreeREx), which is a program that analyzes the evolution of mitogenome rearrangements with heuristical searches based on common intervals; this allows for the inference of tandem duplicate-random loss events (TDRL), transpositions (T), inversions (I), and inversion-transpositions (IT) mapping to the defined phylogenetic tree (Bernt et al., ,2007, 2008).

Gene duplication events are present in all oegopsids sequenced so far, which are mainly reflected in the *cox1-3*, *atp6*, *atp8*, and *trnD* genes (Yokobori et al., 2004). Since it is difficult to use TreeREx to assess gene loss and duplication in rearrangements (Yoshizawa et al., 2018), we prepared the following data matrices to estimate of the history of rearrangements according to the methodology described by Kawashima et al. (2013): (a) excluding all the duplicated genes; (b) reserving all the oegopsids and *Bathyteuthis abyssicola* Hoyle, 1885 only and treating the duplicated genes in this order as two different genes labeled "-1" and "-2"; (c) reserving the conserved gene blocks that contain duplicated genes (i.e., the "*nad2-cox1-cox2-trnD-atp8-atp6*" gene block on the right side of the mitochondrial genomes of *Bathyteuthis abyssicola* and *Architeuthis dux* Steenstrup, 1857 and the left side of those of other oegopsids; see Figure 2). Three levels of nodes were inferred from the TreeREx analysis: "consistent," "1-consistent," and "fallback," which represent a successively lower level of certainty.

Moreover, we used qMGR to quantify the rearrangement features of individual genes and their mitogenomes in the whole Coleoidea Bather, 1888. The qMGR is a novel statistical method for calculating the rearrangement frequency (RF) of each gene and the rearrangement score (RS) of each genome by comparing a reference arrangement (a benchmark) (Zhang, Kan, et al., 2020). This software can cope with various rearrangements and is not limited by gene loss and duplications present in the mitogenome to be studied (Zhang, Kan, et al., 2020). The rearrangement features were used as important reference features for rearrangement patterns and evolution in this study. According to previous studies, the gene arrangement of *Vampyroteuthis infernalis* Chun, 1903 and most octopods is hypothesized to represent the ancestral state of the most recent common ancestor of coleoid cephalopods (Guerra et al., 2018; Kawashima et al., 2013; Strugnell et al., 2017). Thus, we selected their gene arrangement as a benchmark for the rearrangement feature analysis in this study.

3 | RESULTS AND DISCUSSION

3.1 | General features of the mitogenome

The mitogenome was found to be 20,545 bp in length (Table S5, Figure 1), which is the largest reported mitogenome length (20,091 bp–20,332 bp) in oegopsids to date (Akasaki et al., 2006; Kawashima et al., 2013; Yokobori et al., 2004). Twenty-one of the forty-three genes were encoded by the plus strand, with the others encoded by the minus strand (Figure 1, Table S5). Six genes (*cox1*, *cox2*, *cox3*, *atp6*, *atp8*, and *trnD*) and one long non-coding region (LNCR) are duplicated. Two LNCRs are of more than 500 bp length, which are almost identical each other (the similarities >98%). The duplication pattern of six genes and LNCRs was identical to those of most oegopsids except for *Watasenia scintillans* (Berry, 1911) and *Architeuthis dux* (Figure 2). Yokobori et al. (2007) and Kawashima et al. (2013) detected six common motifs in the LNCRs of cephalopod mitogenomes (Figure S1). The LNCR of *T. rhombus* shared all 6 motifs like those of other Decapodiformes investigated by previous studies (Kawashima et al., 2013; Yokobori et al., 2007). Motif 1 and Motif 6 are conserved in cephalopod mitogenome LNCRs (Figure S1), which are supposed to have a role in replication/transcription initiation processes (Kawashima et al., 2013; Yokobori et al., 2007).

The A+T content was 66.24% of the whole mitogenome (Table S6). Among the eighteen PCGs of *T. rhombus*, the lowest A+T content was 59.10% and 59.23% in two *cox3* genes, whereas the highest A+T content was 74.36% in two *atp8* genes. The A+T content of the two LNCRs was 74.69% and 74.87%, respectively. The AT skew and GC skew in the plus strands were 0.0630 and −0.2710 in the mitogenome, respectively (Table S6). Most genes showed negative AT and GC skews (Table S6), indicating that there is a skew away from T in favor of A and G in favor of C (Tang et al., 2019).

A total of 4723 amino acids were encoded in the *T. rhombus* mitogenomes, among which the frequently used ones were AUU (isoleucine), UUU (phenylalanine), and UUA (leucine), whereas the codons of CGC (arginine) and CCG (proline) were encoded less (Table S7). This finding was also supported by the fact that amino acids coded by A+T-rich codon families were more frequent than amino acids coded by G+C-rich codon families (Sun et al., 2016). In addition, within synonymous codons, we found that they ended with A

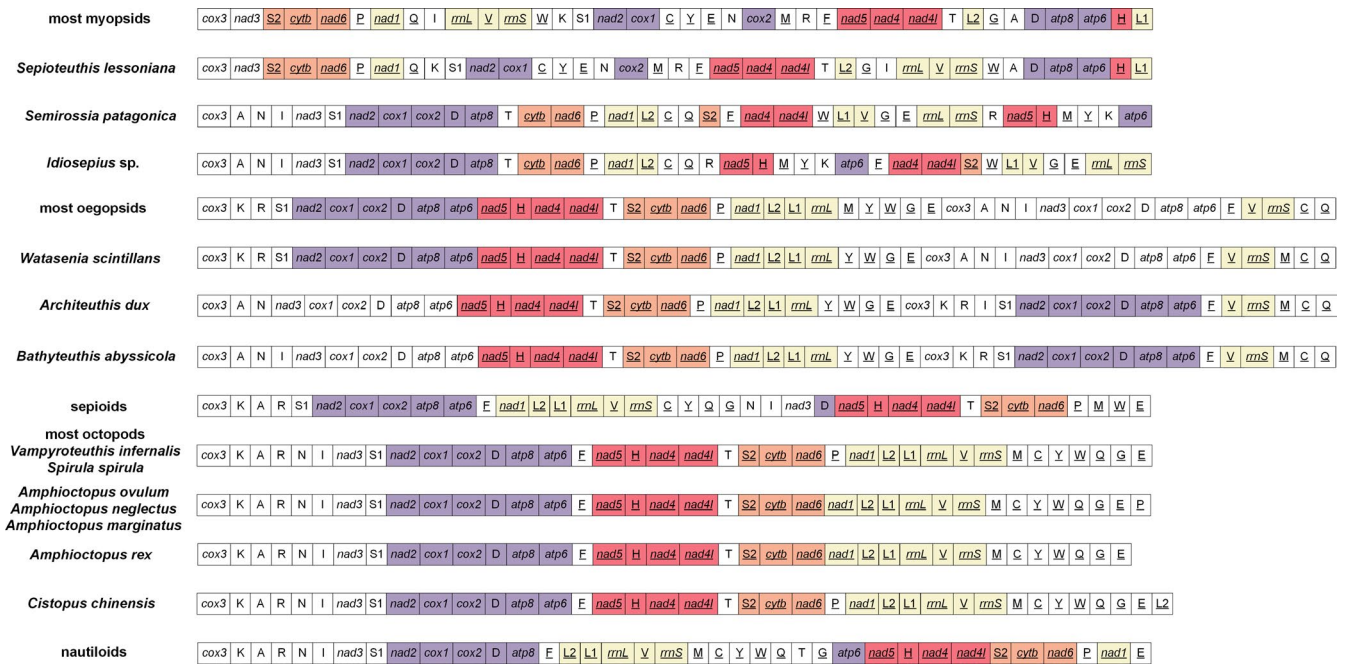

FIGURE 2 Gene arrangement of Cephalopoda. The four colored squares represented four conserved blocks found in previous studies (Bernt, Bleidorn, et al., 2013; Guerra et al., 2018). Lines under gene names indicate the gene coded on the minus strand

or U most frequently, which is common in metazoans (Jennings & Halanych, 2005; Palomares-Rius et al., 2017; Sun et al., 2016; Yang et al., 2020). A possible explanation for this might be mutational bias alone or both mutation bias and natural selection (Wei et al., 2014; Yang et al., 2020).

3.2 | Gene arrangement patterns

According to previous studies (Bernt, Bleidorn, et al., 2013; Guerra et al., 2018), four gene blocks were found in Bilateria and defined as conserved blocks. In this study, four conserved blocks were found intact in some cephalopods, differing only in the identity of the tRNA gene between *cox2* and *atp8*, which in cephalopods is *trnD* rather than *trnK*. The four conserved blocks were (a) *nad2-cox1-cox2-trnD-atp8-atp6*; (b) *nad4l-nad4-trnH-nad5*; (c) *rrnS-trnV-rrnL-trnL1-trnL2-nad1*; and (d) *nad6-cytb-trnS2*, which are highlighted with four different colors in the gene arrangements in Figure 2.

In this study, we compared all the gene arrangements among the Cephalopoda sequenced so far. In octopods, all reported mitogenomes contained the four conserved blocks mentioned above. The gene arrangements in this taxon were nearly identical except for the transpositions and loss of a few tRNA genes. In oegopsids, six duplicated genes (*cox3*, *cox1-cox2-trnD-atp8-atp6*) were detected, which is a common feature in oegopsid mitogenomes. The mitogenome of *T. rhombus* shared consistent gene arrangement with those of the following Ommastrephidae species: *O. bartramii*, *Dosidicus gigas* (d'Orbigny, 1835), *Sthenoteuthis oualaniensis* (Lesson, 1830), *Todarodes pacificus* (Steenstrup, 1880), and *Illex argentinus* (Castellanos, 1960) (Figure 2). Three conserved blocks were detected in the mitogenomes, and only one part of the gene block (i.e., *trnV-rrnS*) was transferred downstream. In our study, all oegopsids can be roughly divided into two groups based on the positions of the conserved gene blocks in their mitogenomes (Figure 2). One group included Enoploteuthidae, Ommastrephidae, and Thysanoteuthidae; the other group was formed by Architeuthidae. The mitogenomes of myopsids formed two arrangement patterns, with *Sepioteuthis lessoniana* d'Orbigny, 1826 having a different pattern compared with those of the other species. The species in this taxon reported to date were highly rearranged in mitochondrial genes compared with ancestral arrangements, especially in conserved gene blocks with barely shared patterns of arrangement among them. The mitogenomes within the sepioids showed congruent arrangement patterns, which retained three of the four conserved gene blocks. Only one mitogenome has been reported for each of the Sepiolida Keferstein, 1866 (=Sepiolina), Idiosepiidae Appellöf, 1898 and Spirulida Haeckel, 1896 taxa (only one species, *Spirula spirula* (Linnaeus, 1758), exists within Spirulida). Comparing gene arrangements of Octopodiformes, both the tRNA and PCGs of Sepiolida and Idiosepiidae were highly rearranged, whereas the gene arrangement of Spirulida was identical to the ancestral state of the most recent common ancestor of coleoid cephalopods (Figure 2), suggesting that other mitogenome arrangements within Decapodiformes are derived states (Strugnell et al., 2017).

3.3 | Rearrangement features

Of the nine taxa, Myopsida Naef, 1916, Sepiolida and Idiosepiidae had high RS values, indicating that they had relatively frequent

mitochondrial gene rearrangements. Compared to the ancestral pattern, Sepioidea Naef, 1916, had the least obvious differences in gene arrangement within Decapodiformes, without considering Spirulida (Figure S2A). To further understand the rearrangement features within the four taxa (i.e., Octopoda Leach, 1818, Sepioidea, Oegopsida, and Myopsida) containing more than eight species, we summarized the proportion of different mitogenome rearrangement patterns in these taxa (Figure 3). For the RS of mitogenomes, Oegopsida and Octopoda are the most complex in terms of their rearrangement patterns compositions. In contrast, only one pattern was found in Sepioidea. Within Myopsida, although only two rearrangement patterns were detected, the mitogenome of Myopsida was highly rearranged among the four taxa (Figure 3). Almost all the genes were not rearranged in Octopodiformes, except for a few genes with low-frequency rearrangements (Figure S2A).

Among the 37 genes of mitogenomes in Coleoidea, the genes with high-frequency rearrangements were mainly concentrated in several tRNA genes, especially in the "*trnM*, *trnW*, *trnQ*, *trnR*" (Figure S2B). In addition, the RS of *rrnS* was higher than that of *rrnL* (Figure S2B). The rearranged genes in 13 PCGs were mainly *cox3*, *nad3*, and *nad5*, and *nad2* was highly conserved with no rearrangement. Previous studies reported that *cox3*, *nad3*, and *nad5* are genes with high nucleotide diversity (Cheng et al., 2013; Tang et al., 2020), which accorded with our observations on rearranged genes and indicated that genomic rearrangements and sequence evolution are correlated, even if it is still unclear how (Xu et al., 2006).

3.4 | Phylogenetic analyses

The phylogenetic analyses were conducted using two datasets from 48 taxa (Figure 4, Figures S3 and S4). Both the ML and BI analyses based on the nucleotide sequences retrieved consistent topologies with high bootstrap support values (BS) and posterior probabilities (PP; Figure 4). The phylogenetic trees constructed using amino acids showed minor differences (Figures S3 and S4). The Coleoidea was divided into two major clades containing Octopodiformes and Decapodiformes (Figure 4, Figures S3 and S4). Sepioidea formed a monophyletic group and had a sister relationship with the remaining Decapodiformes with strong nodal support (Figure 4, Figures S3 and S4; BS = 100%, PP = 100%). It should be noted that a clade containing Oegopsida, Bathyteuthoidea Vecchione, Young, & Sweeney, 2004, Spirulida and Myopsida clustered together with Sepiolida and Idiosepiidae in BI and ML analyses constructed using nucleotides (Figure 4). A similar topology was seen in the BI tree based on amino acid dataset, mainly differing with regards to a polytomy with three other lineages (Oegopsida, Bathyteuthoidea, and Spirulida + Myopsida + Sepiolida; Figure S3). Meanwhile, the conflicts in the ML analysis based on amino acids detected that a clade containing Sepiolida, Idiosepiidae, and Myopsida had a sister group relationship with the clade containing Oegopsida and Bathyteuthoidea, clustered together with Spirulida (Figure S4). Previous studies (Strugnell et al., 2017; Tang et al., 2019) favored the first topology, and the relationship of Idiosepiidae + (Sepiolida + (Myopsida + (Oegopsida + (Spirulida + Bathyteuthoidea)))) was also supported by morphological characteristics; the cornea and circularis muscle in the suckers were absent in Oegopsida, Spirulida, and Bathyteuthoidea (Vecchione et al., 2000; Young et al., 1998) but present in Sepioidea, Idiosepiidae, Sepiolida, and Myopsida, reflecting the transition from a neritic or benthic lifestyle to a pelagic lifestyle (Strugnell et al., 2017). Within Myopsida, *Sepioteuthis lessoniana* was found to be sister to the remaining myopsid squids analyzed (Figure 4, Figures S3 and S4). Within Oegopsida, *I. argentinus* and *T. pacificus* clustered together and were revealed as the sister group of (*D. gigas* + *S. oualaniensis*) + *O. bartramii*. All our findings supported that Thysanoteuthidae showed a closer relationship with Ommastrephidae than with Enoploteuthidae and Architeuthidae, which was supported by recent observations (Sanchez et al., 2016). Further accumulation of mitogenomic data from various species will be necessary to confirm the phylogenetic relationships within Cephalopoda, especially in relation to Decapodiformes.

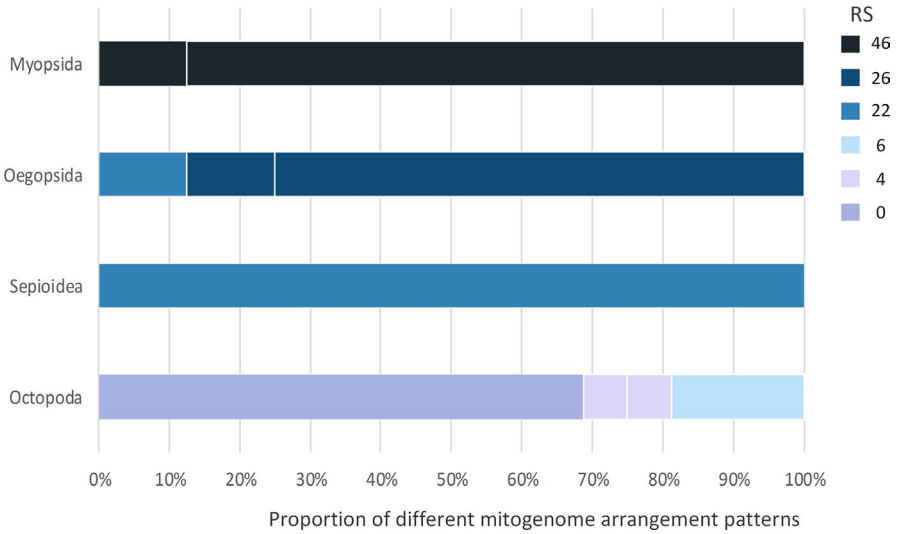

FIGURE 3 Proportion of different mitogenome rearrangement patterns in Myopsida, Oegopsida, Sepioidea and Octopoda

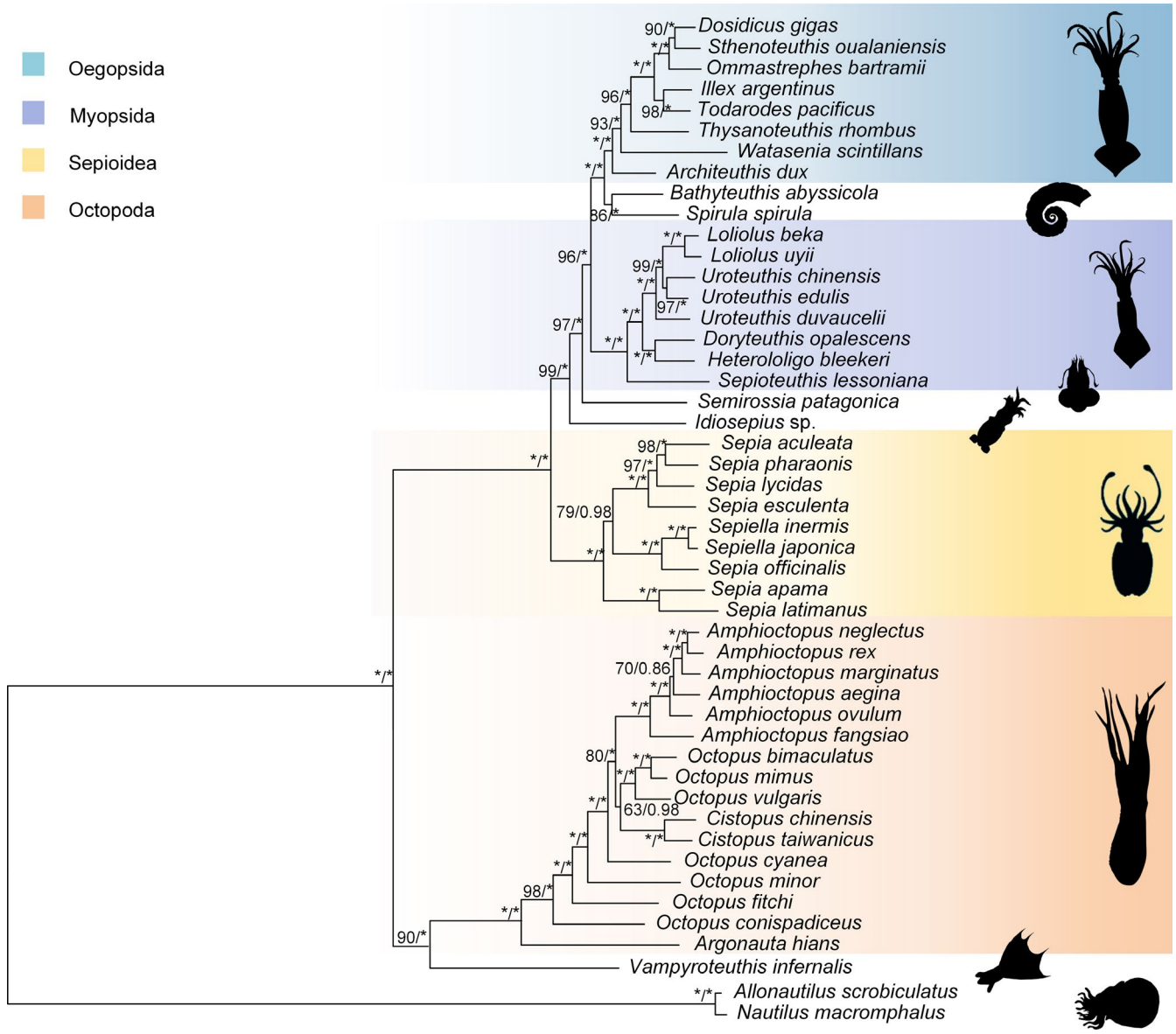

FIGURE 4 Phylogenetic trees of Cephalopoda constructed using nucleotides of 13 protein-coding genes (PCGs) and two ribosomal RNAs (rRNAs). The numbers separated by "/" near the nodes represent bootstraps of maximum likelihood (ML) and posterior probabilities of Bayesian inference (BI) analyses, respectively. Each value of 100% or 1.0 is indicated by an asterisk

3.5 | Estimation of the history of rearrangements

According to congruent phylogenies based on nucleotides, we inferred the gene rearrangement history using TreeREx with its default options (Bernt et al., 2008). As shown in Figure 5, six transpositions (T) and 18 tandem duplication-random loss events (TDRL) occurred, forming the current gene arrangement patterns of the Cephalopoda. Except for the nodes of several Decapodiformes, most nodes exhibited highly consistent levels, especially in Octopoda and Sepioidea, indicating consistency in exploring the phylogenetic relationships of these taxa based on gene sequences versus those based on gene arrangements. Only two transposition events of *trnP* were detected (Figures 2 and 5) in Octopoda, implicating the evolutionary conservation of gene arrangements in this taxon. The gene arrangement of *Vampyroteuthis* Chun, 1903 and most octopods are identical and are similar to the polyplachophoran *Katharina tunicata* and the gastropod *Lophiotoma cerithiformis* rather than to the cephalopod *N. macromphalus*, reflecting that more ancestral structures have been maintained in octopus-like mitogenomes than those in nautiloid mitogenomes (Guerra et al., 2018; Kawashima et al., 2013; Strugnell et al., 2017). Four TDRLs and one transposition event occurred to form the current gene arrangements of Sepioidea observed from those of Octopoda. Myopsida and the clade containing Oegopsida, Bathyteuthoidea, and Spirulida were separated by three TDRL events (node A16 in Figure 5). The TDRL+T and the transposition of *trnM* supported the split of *Architeuthis dux* and

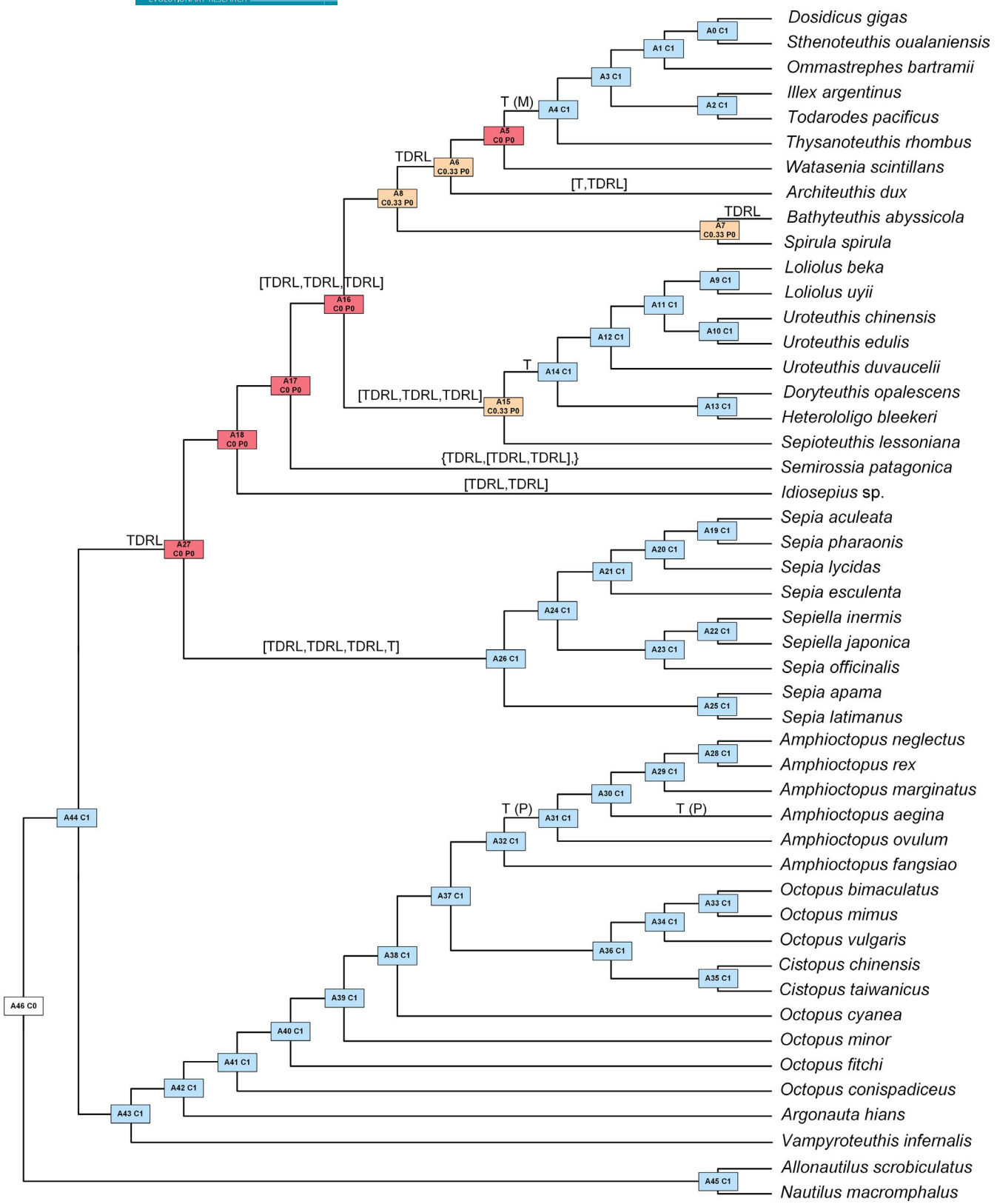

FIGURE 5 Evolutionary history of gene rearrangements in Cephalopoda inferred using TreeREx based on data matrix 3. Each node is marked with a different color (i.e., blue: consistent reconstructed node; orange: 1-consistent reconstructed; red: fallback). The rearrangement scenarios are represented using abbreviations

Watasenia scintillans from Oegopsida, successively. The evolutionary pathways of rearrangements based on the three matrices generated similar results (Figure 5, Figures S5 and S6). Several Decapodiformes were poorly supported, which might be related to the limited sampling and lineage-specific rearrangements of their mitogenomes (Zheng et al., 2018). The high consistency of node A4 reconfirmed

the phylogenetic position of *T. rhombus* + (((*D. gigas* + *S. oualaniensis*) + *O. bartramii*) + (*I. argentines* + *T. pacificus*)), supporting the reliability of the inferred topology of phylogenetic analyses. All mitogenome structures of the studied oegopsids shared the same wide-range duplication, and retained their common and specific patterns in *Architeuthis dux*, *Watasenia scintillans*, and other oegopsids, which may explain the phylogenetic relationship above.

ACKNOWLEDGEMENTS

We would like to thank Editage (www.editage.cn) for English language editing. This study was supported by research grants from National Natural Science Foundation of China (31672257) and Fundamental Research Funds for the Central Universities (201822022).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Figure S1. Predicted motif sequence alignments of long non-coding regions.

Figure S2. Rearrangement score (RS) for each species and rearrangement frequency (RF) for each gene among Coleoidea.

Figure S3. Bayesian Inference phylogenetic tree of Cephalopoda constructed using amino acids of 13 protein-coding genes (PCGs).

Figure S4. Maximum Likelihood phylogenetic tree of Cephalopoda constructed using amino acids of 13 protein-coding genes (PCGs).

Figure S5. Evolutionary history of gene rearrangements in Cephalopoda inferred using TreeREx based on data matrix 1.

Figure S6. Evolutionary history of gene rearrangements in Oegopsida and *Bathyteuthis abyssicola* inferred using TreeREx based on data matrix 2.

Table S1. Primers information used for amplification of mitogenome of *Thysanoteuthis rhombus*.

Table S2. The list of gene names and abbreviations used in our study.

Table S3. The information of cephalopods mitogenome used in constructing phylogenetic tree.

Table S4. Best partition scheme and substitution models for the Maximum Likelihood in IQ-TREE and Bayesian Inference in MrBayes.

Table S5. Organization of the mitochondrial genome of *Thysanoteuthis rhombus*.

Table S6. The nucleotide composition and skew analysis of *Thysanoteuthis rhombus*.

Table S7. Codon and relative synonymous codon usage (RSCU) of 13 protein-coding genes (PCGs) in the mitogenome of *Thysanoteuthis rhombus*.

Alignment S1. Nucleotide sequence alignment of 13 PCGs and 2 rRNA genes used in this study.

Alignment S2. Amino acid sequence alignment of 13 PCGs used in this study.

How to cite this article: Tang Y, Zhang X, Ma Y, Zheng X. Descriptive study of the mitogenome of the diamondback squid (*Thysanoteuthis rhombus* Troschel, 1857) and the evolution of mitogenome arrangement in oceanic squids. *J Zool Syst Evol Res*. 2021;00:1–11. https://doi.org/10.1111/jzs.12478