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ORIGINAL ARTICLE

Mitogenomic phylogeny of Muricidae (Gastropoda: Neogastropoda)

Yi Yu[1] | **Lingfeng Kong**[1,2] | **Qi Li**[1,2]

[1]Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Qingdao, China

[2]Laboratory for Marine Fisheries Science and Food Production Processes, Qingdao National Laboratory for Marine Science and Technology, Qingdao, China

Correspondence
Qi Li, Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Yushan Rd. 5, Qingdao 266003, China.
Email: qili66@ouc.edu.cn

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Abstract

Muricidae is one of the most species-rich and morphologically diverse families in Gastropoda, with a worldwide distribution. The classification of Muricidae has traditionally been based on shell and radular characteristics; however, the phylogenetic relationships within the family are debated due to morphological convergence and plasticity. In this study, to explore the phylogenetic relationships of Muricidae, we sequenced 11 muricid mitochondrial (mt) genomes and compared them with 13 previously reported complete muricid mt genomes. All muricid mt genomes shared the same gene arrangement and exhibited conserved genome size and nucleotide composition. Three-nucleotide deletions in *atp8* and *nad4*, and three-nucleotide insertions in *nad2* were detected in Rapaninae. Both maximum likelihood and Bayesian inference analyses supported the monophyly of each subfamily studied (Ocenebrinae, Muricinae, Rapaninae and Ergalataxinae). Ergalataxinae was recovered as the sister taxon of Rapaninae, refuting the traditional morphology-based placement of Ergalataxinae within Rapaninae. In Rapaninae, *Indothais* was confirmed to be monophyletic and determined to be a valid genus. Similarly, *Drupina* was determined to be an independent genus rather than a subgenus of *Drupa*. *Purpura* was recovered as a paraphyletic group, with *Purpura panama* being sister to *Reishia* + *Rapana* + *Indothais* and clustering with *Purpura bufo*.

KEYWORDS

Gastropoda, mitochondrial genome, Muricidae, phylogeny

1 | INTRODUCTION

With approximately 1600 extant described species, Muricidae (Rafinesque, 1815) is one of the most speciose and morphologically diverse families of Gastropoda (Boss, 1971; Vermeij, 1996). Muricid species are distributed worldwide, and mainly in tropical waters (Taylor & Morris, 1988). Moreover, they have been found at different depths, from the intertidal zone to deep waters at depths of over 3000 m; however, most species inhabit shallow sea sand, rocks and coral reefs (Barco et al., 2010). Muricids are active predators, preying mainly on bivalves and barnacles (Taylor & Morris, 1988; Barco et al., 2010). Predation mainly involves drilling the shell of the prey animal via a combination of mechanical action of the radula and secretion of organic acids (Carriker, 1961). Because of their predatory behaviour, muricids are ecologically significant in marine benthic communities, and their complex predatory behaviours are reflected their adaptive radiation (Barco et al., 2010; Harding et al., 2007; Menge, 1974;

Morton, 1999, 2004; Peharda & Morton, 2005). Some muricids, such as *Rapana venosa* are an economically valuable food source in coastal regions (Leiva & Castilla, 2002).

The classification and phylogeny of Muricidae have long been controversial due to morphological convergence and plasticity within the group. The main controversies centred on the classification of subfamilies and the relationship between each subfamily in Muricidae. Tryon (1880) originally divided Muricidae into two subfamilies: Muricinae and Purpurinae. However, Cossmann (1903) recognized five subfamilies of Muricidae based on opercular characteristics: Muricinae, Ocenebrinae, Trophoninae, Typhinae and Rapaninae. He proposed Purpuridae to be a distinct family outside of Muricidae and proposed the subfamilies Rapaninae and Ocenebrinae for the first time. By comparing the shells of fossil and recent species, Keen and Mclean (1971) removed Rapaninae from Muricidae and formed a new family, Thaididae, comprising Rapaninae, Thaidinae and Drupinae. However, in the same year, Kuroda et al. (1971) reassigned some Thaididae species to the new subfamily Ergalataxinae in Muricidae. Additionally, based on shell, radula and egg capsule morphology, Radwin and D'Attilio (1971) synonymized Ergalataxinae with Muricinae in their subsequent monograph on muricids. Ponder and Warén (1988) divided Muricidae into three subfamilies (Muricinae, Thaidinae and Coralliophilinae) and moved all species in the other previously recognized subfamilies to the subfamily Muricinae. Based on gross anatomy, radular, opercular, protoconch morphology and shell ultrastructure, Ergalataxinae was synonymized with Rapaninae (Kool, 1993; Vermeij & Carlson, 2000). The current classification system of Muricidae is based on the study of Bouchet et al. (2005), in which Muricidae was considered a single family comprising 10 subfamilies (Muricinae, Muricopsinae Ocenebrinae, Trophoninae, Typhinae, Tripterotyphinae, Ergalataxinae, Rapaninae, Haustrinae and Coralliophilinae). Later, the genera *Pagodula*, *Xymenopsis*, *Xymene* and *Trophonella* in the Trophoninae were united in a new subfamily, Pagodulinae (Barco et al., 2012).

Some muricids exhibit ontogenetic changes in morphology (Fujioka, 1985; Herbert et al., 2007); for instance, shell and radular characters vary with age, season and sex (Tan, 1995; Tan & Sigurdsson, 1996), which can lead to an inaccurate understanding of muricid phylogeny when relying solely on morphological characteristics. Several attempts have been made to reconstruct the phylogeny of the Muricidae using molecular data. Marko and Vermeij (1999) reconstructed the phylogeny of Ocenebrinae in the eastern Pacific using the mitochondrial (mt) 12S rRNA and *cox1* genes, in which Ocenebrinae was proven to be monophyletic relative to Rapaninae as an outgroup. By analysing the mt 12S rRNA gene and nuclear ITS2, Oliverio et al. (2002) found that Rapaninae was the sister group to Coralliophilinae, while Muricinae was closely related to Muricopsinae but distantly related to Rapaninae, Coralliophilinae and Ocenebrinae. However, another study on muricid phylogeny using the 12S rRNA gene indicated that Rapaninae was not sister to Coralliophilinae and that the phylogenetic relationship between Muricinae and Rapaninae was relatively close, in contrast to the results of previous study (Oliverio & Modica, 2009). Analyses using the nuclear 28S rRNA and mt 16S rRNA genes demonstrated strong support for a sister relationship between Rapaninae + Ocenebrinae and Ergalataxinae (Claremont et al., 2008). In a study by Barco et al. (2010), Rapaninae and Ergalataxinae were recovered as sister groups, but the sister taxa relationship between Rapaninae and Ocenebrinae was not verified. To date, owing to the limited phylogenetic signal contained in short gene fragments, phylogenetic studies of Muricidae based on gene fragments have often produced contradictory results and are not always well-supported. Therefore, it is important to reconstruct a well-supported phylogenetic tree to solve the existing taxonomic problems of Muricidae.

Researchers have found that genes at different loci may be subject to different selection pressures over the course of evolution. A single gene or fragment gene contains few information loci, which may not be representative of whole genome evolution when analysing phylogeny (Cunha et al., 2009; Uribe et al., 2016; Uribe, Williams et al., 2017). Therefore, phylogenetic studies based on fragment genes may lead to unreliable or erroneous results (Rokas et al., 2003; Zardoya & Meyer, 1996). The mt genome contains abundant sequence information and information on structural characteristics, which can provide a large number of genome-level features as signals for studying metazoan evolutionary relationships. Recently, mt genomes have been widely used in phylogenetic studies of gastropods, including Patellogastropoda (Xu et al., 2022), Lymnaeoidea (Young et al., 2021), Caenogastropoda (Uribe et al., 2018) and Conidae (Uribe, Puillandre & Zardoya, 2017). Although 13 complete muricid mt genomes are currently available in GenBank, a comprehensive phylogenetic analysis of Muricidae based on mt genomes has not been reported.

In the present study, we sequenced 11 complete mt genomes from Muricidae. Combined with the published mitogenome from GenBank, we reconstructed the phylogeny of Muricidae, including a total of 24 mt genomes, with the following aims: (a) to reconstruct the phylogeny of the Muricidae and resolve the phylogenetic position of controversial taxa; and (b) to explore mt genomic characteristics among different lineages.

2 | MATERIALS AND METHODS

2.1 | Sample collection, DNA extraction and sequencing

All specimens were collected in the field from the southern coastal areas of China (Table 1). The specimens were then fixed and preserved in 95% ethanol. We selected 11 muricid species belonging to eight genera for the following analyses. Total genomic DNA was extracted from 100 mg of foot tissue following a modified Cetyl Trimethyl Ammonium Bromide method (Winnepenninckx et al., 1993). DNA quality was assessed by agarose gel electrophoresis and DNA concentration was determined using NanoDrop 2000 (Thermo Scientific). Qualified samples were submitted to Novogene for library construction and high-throughput sequencing. Sequencing libraries were prepared with average insert sizes of approximately 300 bp and sequenced as 150 bp paired-end runs on an Illumina HiSeq X platform (Novogene). Finally, approximately 8 Gb of raw data were generated for each library.

2.2 | Genome assembly, gene annotation and sequence analysis

Raw reads were filtered using Trimomatics (Bolger et al., 2014). The resulting clean reads were assembled via de novo assembly in SPAdes (Bankevich et al., 2012) with *k*-mers of 21, 33, 55 and 77. To find the target mt genome, assembled results were searched against a nucleotide database constructed from the complete mt genome of *Rapana venosa* (KM213962) using BLASTN (http://www.ncbi.nlm.nih.gov/BLAST) with an *e*-value cut-off of 0.01. All newly sequenced mt genome sequences have been deposited in GenBank, with the accessions listed in Table 1.

TABLE 1 Mitochondrial (mt) genomes analysed in this study.

Species	Subfamily	Length (bp)	Location	GenBank acc. no.
Rapana venosa	Rapaninae	15,271	Qingdao, China	KM213962
*Indothais sacellum**	Rapaninae	15,237	Sanya, China	MW550293
Indothais lacera	Rapaninae	15,272	Beihai, China	MG099702
*Indothais javanica**	Rapaninae	15,219	Sanya, China	MW550295
Reishia clavigera	Rapaninae	15,285	Korea	DQ159954
Reishia luteostoma 1*	Rapaninae	15,262	Ningbo, China	MW550286
Reishia luteostoma 2	Rapaninae	15,301	Zhoushan, China	MG786490
*Purpura bufo**	Rapaninae	15,239	Sanya, China	MW550291
*Purpura panama**	Rapaninae	15,227	Sanya, China	MW550290
Menathais tuberosa	Rapaninae	15,294	Chuuk, Micronesia	KU747972
*Tylothais virgata**	Rapaninae	15,286	Sanya, China	MW550294
*Drupa morum**	Rapaninae	15,895	Sanya, China	MW550292
*Drupina grossularia**	Rapaninae	16,188	Sanya, China	MW550296
*Drupella margariticola**	Ergalataxinae	15,410	Danzhou, China	MW550287
*Tenguella granulata**	Ergalataxinae	15,387	Beihai, China	MW550288
*Tenguella musiva**	Ergalataxinae	15,218	Beihai, China	MW550289
Chicoreus torrefactus	Muricinae	15,359	Zhoushan, China	MG786489
Bolinus brandaris	Muricinae	15,380	Madrid, Spain	EU827194
Murex trapa	Muricinae	15,408	Beihai, China	MN462589
Boreotrophon candelabrum	Pagodulinae	15,265	Dalian, China	MK361104
Ceratostoma burnetti	Ocenebrinae	15,334	Dalian, China	MK411749
Ceratostoma rorifluum	Ocenebrinae	15,338	Dalian, China	MK411750
Ocinebrellus falcatus	Ocenebrinae	15,326	Dalian, China	MK348224
Ocinebrellus inornatus	Ocenebrinae	15,324	Dalian, China	MK395390

Note: The newly sequenced complete mt genomes are indicated with an asterisk (*).

The coding regions of 13 protein-coding genes (PCGs) were identified using ORF Finder (https://www.ncbi.nlm.nih.gov/orffinder) and MITOS web server (Bernt et al., 2013), using the invertebrate mt genetic code. Gene boundaries were examined and adjusted manually by comparison with the sequenced muricid mt genome. tRNA genes were identified using ARWEN (Laslett & Canbäck, 2008). The positions of the rRNA genes were determined using the MITOS web server. The inferred rRNA genes were identified by sequence comparison with previously reported muricid rRNA genes and were assumed to extend to the boundaries of adjacent genes (Boore et al., 2005).

The newly determined complete mt genomes were aligned with all orthologous muricid mt genomes available in GenBank (Table 1). The substitution saturation of PCGs and rRNA genes was tested in DAMBE (Xia, 2018). All codons of *atp8* gene and the 3rd codons of other PCGs were discarded due to high saturation (Tables S1 and S2). The saturation of rRNA genes and conservation of tRNA genes were determined to be inappropriate for muricid phylogenetic analyses (Chris et al., 1994; Yang, 1998). Therefore, three datasets were constructed and analysed. The first (hereafter referred to as the MA dataset) was aimed at testing the internal phylogenetic relationships of Muricidae, including the amino acid sequences of 13 PCGs. The second dataset (MD) was the nucleotide sequences of the first two codons of 12 PCGs, except *atp8* gene. The third (MN) dataset was used to calculate pairwise genetic distances with the nucleotide sequences of the 13 PCGs and two rRNA genes. The amino acid and nucleotide sequences of the 13 PCGs were aligned separately using Clustal W (Thompson et al., 1994) in MEGA 7 (Kumar et al., 2016). The nucleotide sequences of the two rRNA genes were aligned separately with MAFFT 7 (Katoh et al., 2013) and further verified manually. The ambiguously aligned positions were removed using Gblocks v.0.91b (Castresana, 2000) with the following settings: -*t*=*d*, −b1=50%+1, −b2=b1, −b3=8, −b4=2, −b5=*a*. Finally, the different single alignments were concatenated using Sequence Matrix 1.7.8 (Vaidya et al., 2011). The AT content values and nucleotide frequencies were computed using the EditSeq program from DNASTAR (Burland, 2000). The GC and AT skew were calculated according to the following formulae: AT skew=(A−T)/(A+T); GC skew=(G−C)/(G+C).

2.3 | Phylogenetic analysis

Pairwise genetic distances were estimated based on the MN dataset in MEGA 7 (Kumar et al., 2016) under the maximum composite likelihood model. Phylogenetic

TABLE 2 List of total size, AT content, AT skew and GC skew, for mitochondrial genomes of *Indothais sacellum* (*Isa*), *Indothais javanica* (*Ija*), *Reishia luteostoma* (*Rlu*), *Purpura bufo* (*Pbu*), *Purpura panama* (*Ppa*), *Tylothais virgata* (*Tvi*), *Drupa morum* (*Dmo*), *Drupina grossularia* (*Dgr*), *Drupella margariticola* (*Dma*), *Tenguella granulata* (*Tgr*) and *Tenguella musiva* (*Tmu*).

	Isa	*Ija*	*Rlu*	*Pbu*	*Ppa*	*Tvi*	*Dmo*	*Dgr*	*Dma*	*Tgr*	*Tmu*
Total size	15,237	15,219	15,262	15,239	15,227	15,286	15,895	16,187	15,411	15,387	15,218
%A+T	69.51	66.95	66.29	66.67	68.78	64.89	60.42	61.83	69.09	66.99	68.64
rrnS	955	962	963	958	962	963	963	966	942	946	944
rrnL	1358	1360	1356	1356	1353	1347	1341	1348	1359	1359	1363
AT skew mitogenome	−0.133	−0.140	−0.144	−0.134	−0.135	−0.141	−0.146	−0.121	−0.130	−0.125	−0.128
GC skew mitogenome	0.056	0.052	0.050	0.036	0.072	0.018	0.021	0.003	0.049	0.040	0.048

analyses were conducted using the maximum likelihood (ML; Felsenstein, 1981) and Bayesian inference (BI; Huelsenbeck & Ronquist, 2001) approaches using the MA and MD datasets. ML analyses were performed using IQtree v. 1.6.8 (Nguyen et al., 2015) with 10,000 bootstrap replicates and the ultrafast bootstrap feature. BI analyses were conducted using MrBayes v.3.2 (Ronquist et al., 2012) running four simultaneous Monte Carlo Markov chains for 10,000,000 generations sampling every 1000 generations. The first 25% of the generations were discarded as burn-in. Subsequently, two independent Bayesian inference runs were performed. Parameter convergence was achieved within 10,000,000 generations with a standard deviation of split frequencies of less than 0.01. The effective sample size (ESS) values for all sampled parameters were checked with Tracer 1.7 (Rambaut et al., 2018) to ensure convergence was reached (ESS > 200). Node support was assessed based on Bayesian posterior probabilities (PP), and a PP higher than 0.95 was considered as high statistical support. The phylogenetic trees and node labels were visualized in FigTree v1.4.2 (Rambaut, 2014). The best partition schemes and best-fit models of substitution for the datasets were identified using Partition Finder Protein 2 and Partition Finder 2 (Lanfear et al., 2016) with the Bayesian Information Criterion (Schwarz, 1978). The partitions tested were as follows: all genes grouped, all genes separated, and genes grouped by enzymatic complexes (*nad*, *cox*, *atp* and *cytb*). The selected best-fit partitions and models are listed in Tables S3 and S4.

3 | RESULTS AND DISCUSSION

3.1 | Mitochondrial genome organization and structural features

The newly sequenced mt genomes in the present study showed similar patterns of genome size, AT contents and AT skews. The size of the 11 mitogenomes ranged from 15,218 bp (*Tenguella musiva*) to 16,187 bp (*Drupina grossularia*) (Table 2). All mitogenomes were AT-rich (>60%), with *Indothais sacellum* having the highest (69.51%) and *Drupa morum* having the lowest (60.42%) AT content (Table 2). The nucleotide compositions were strongly skewed away from C in favour of G (the GC skews ranged from 0.003 to 0.072) and from A in favour of T (the AT skews ranged from −0.146 to −0.121) (Table 2). The positive GC skews and negative AT skews were consistent with those of other neogastropod species reported in previous study (Cunha et al., 2009) and were caused by the asymmetric replication and transcription of mt genomes (Clayton, 1982; Reyes et al., 1998; Tanaka & Ozawa, 1994).

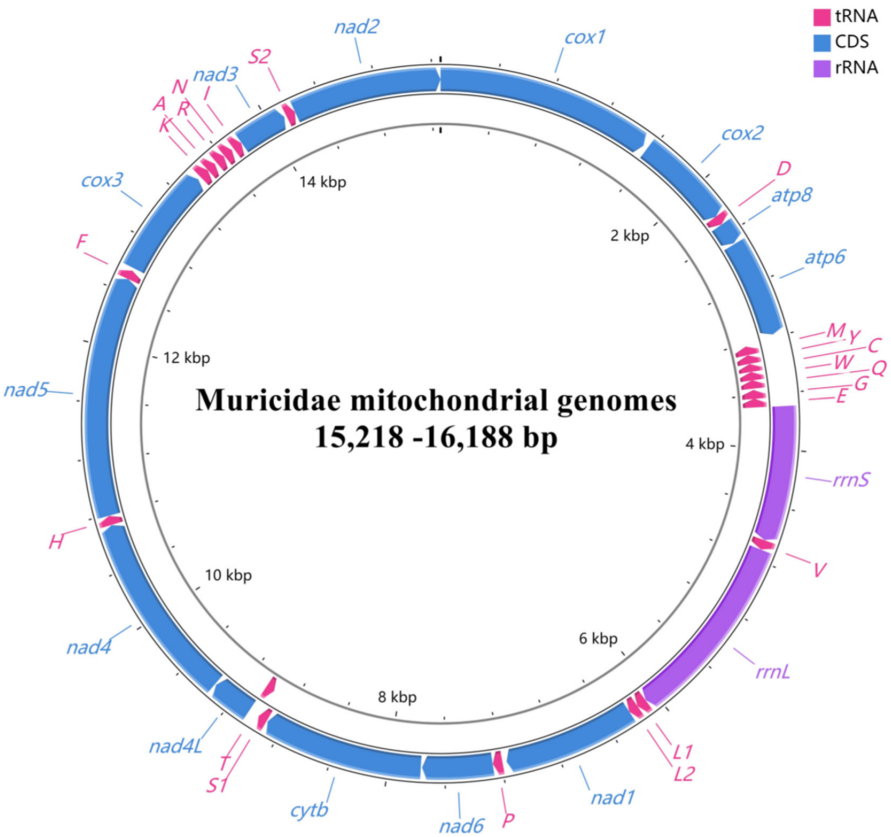

FIGURE 1 Gene map of the mt genomes of 11 Muricidae species.

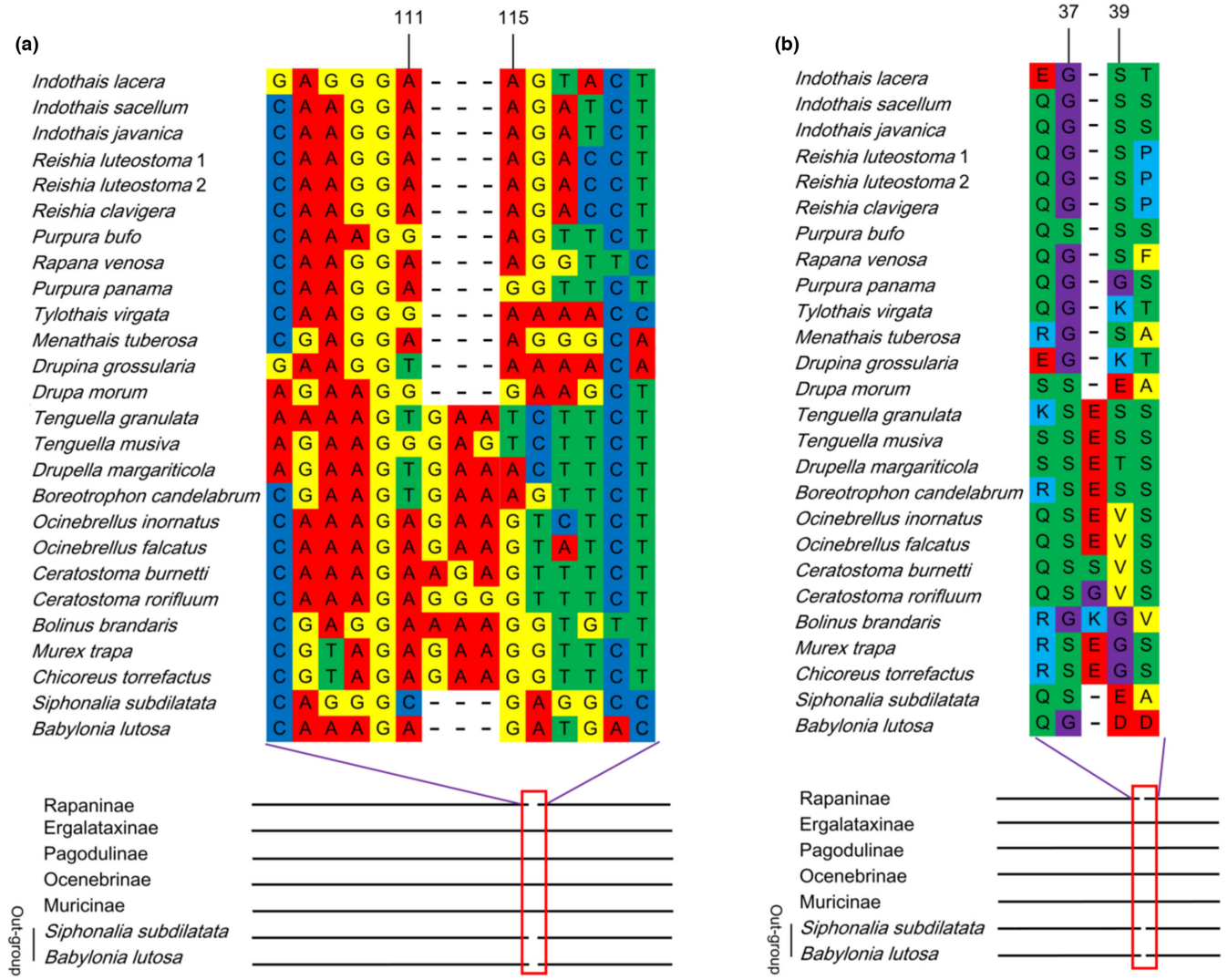

FIGURE 2 *Atp8* sequence differences in 24 muricids and two outgroup species. Nucleotide (a) and amino acid (b) alignments of a portion of *atp8* gene indicate that Rapaninae lack three continuous nucleotides present in other muricids.

Similar to those of most metazoans (Boore, 1999), muricid mt genomes contained 13 PCGs, 22 tRNAs and 2 rRNAs. Among these genes, 13 PCGs, 14 tRNAs (*trnD*, *trnV*, *trnL1*, *trnL2*, *trnP*, *trnS1*, *trnH*, *trnF*, *trnK*, *trnA*, *trnR*, *trnN*, *trnI* and *trnS2*), and 2 rRNAs (*rrnS* and *rrnL*) were encoded on the major strand, whereas the other eight tRNAs (*trnM*, *trnY*, *trnC*, *trnW*, *trnQ*, *trnG*, *trnE* and *trnT*) were encoded on the minor strand. The gene order of the 11 muricid mt genomes (Figure 1) was identical to that of other reported neogastropod mt genomes (Brauer et al., 2012; Cunha et al., 2009; Yang et al., 2020; Zhong et al., 2019).

Within muricids, most PCGs use conventional start codons (ATG and ATA). Deviations were observed in *nad4* (*T. musiva* and *T. granulata*), which started with GTG. Most PCGs were terminated with the complete termination codons TAA and TAG, but *nad2* of Ergalataxinae and *nad6* of *D. morum* ended with an incomplete stop codon (T). During transcription, the incomplete stop codon performs termination functions in the form of mRNA polyadenylation to modify the TAA termini (Maria et al., 2011; Ojala et al., 1981). When the PCGs of 24 muricids were aligned, the mt sequences of Rapaninae species were found to contain a deletion of three continuous nucleotides in *atp8* (Figure 2) and *nad4* (Figure 3), leading to the deletion of one amino acid, which reflected unusual constraints on proteins in these taxa. Continuous nucleotide deletions in gastropod have been reported in previous studies, which occurred in *nad2* and *nad6* (Sevigny et al., 2015; Yang et al., 2018). Additionally, a continuous six-nucleotide insertion was found in *nad2* of Rapaninae (Figure 4), which led to two amino acid insertions. Nucleotide insertions and deletions (indels) are among the main sources of evolutionary changes at the molecular level (Tao et al., 2008). Similar indels have not been found in the subfamily Ergalataxinae. The characteristics of deletions and insertions within *nad2* and *nad4*

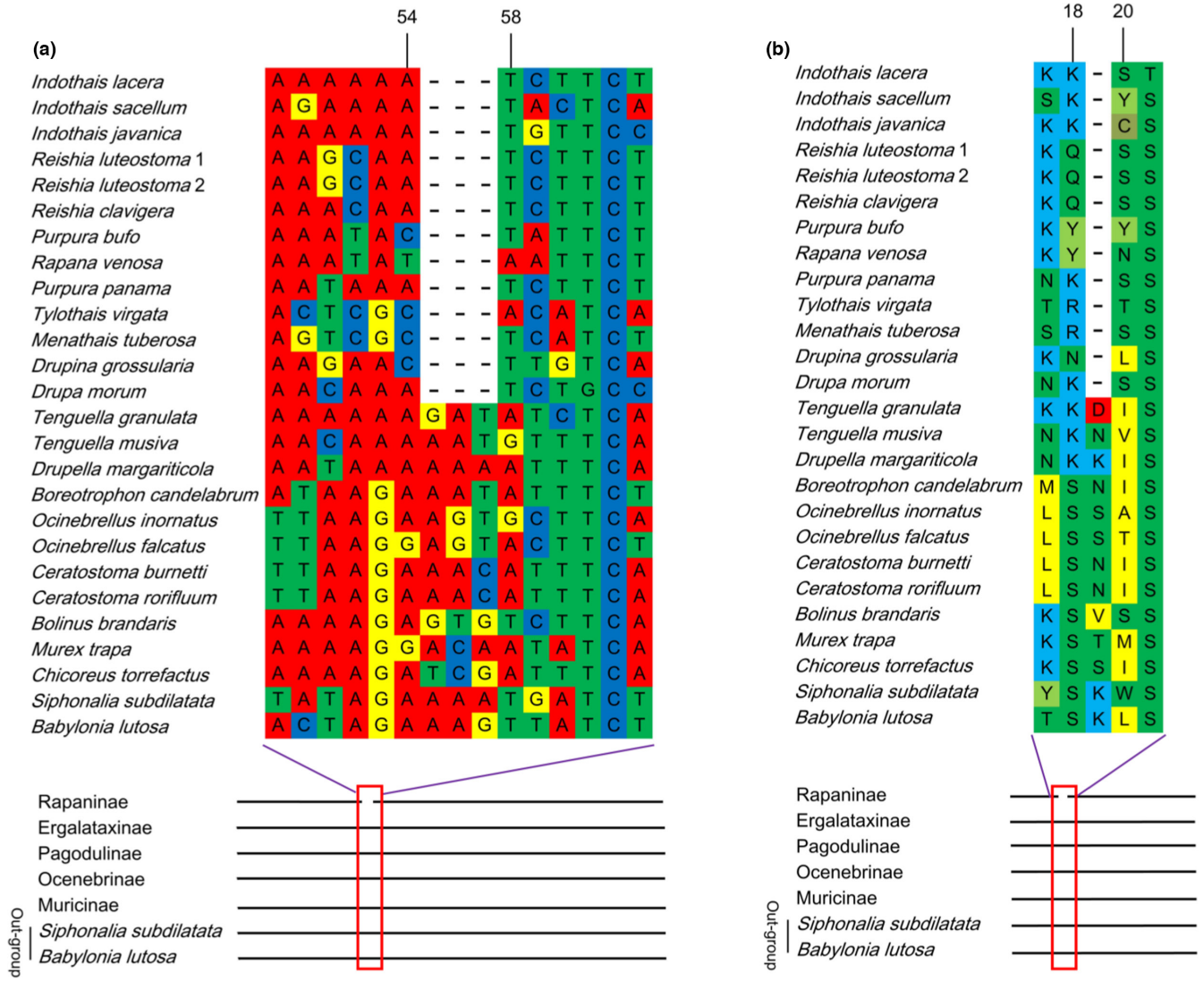

FIGURE 3 *Nad4* sequence differences in 24 muricids and two outgroup species. Nucleotide (a) and amino acid (b) alignments of a portion of *nad4* gene indicate that Rapaninae lack three continuous nucleotides present in other muricids.

support the hypothesis that Ergalataxinae is not nested within Rapaninae, which refutes previous studies based on morphology (Vermeij & Carlson, 2000). Interestingly, the indels in atp8 (Figure 2) provide support for a monophyletic clade comprising Ergalataxinae, Muricinae, Pagodulinae and Ocenebrinae as sister to Rapaninae. In the newly sequenced mt genomes, the 12 PCGs (except *nad4* gene) showed almost the same length in different species, whereas the length of *nad4* genes varied among subfamilies. The length of *nad4* genes in Ocenebrinae, Ergalataxinae and Pagodulinae was up to 1374 bp, while that in Rapaninae and Muricinae was only 1353 and 1356 bp, respectively. When the *nad4* genes were aligned, only rapanine species were found to contain a deletion of three continuous nucleotides, which demonstrated that the variation in *nad4* gene length was caused by the different positions of the start codon.

3.2 | Phylogenetic analyses

A total of 26 taxa were selected for phylogenetic analyses, including 23 muricid species belonging to 16 genera and five subfamilies (Rapaninae, Ergalataxinae, Muricinae, Ocenebrinae and Pagodulinae; Table 1). *Siphonalia subdilatata* (MG827217) from Buccinidae and *Babylonia lutosa* (Q424447) from Babyloniidae were used as outgroups. The phylogenetic trees constructed here covered the most comprehensive muricid mt genomes. However, most species included in this analysis were from the Indo-Pacific Ocean, and several valid subfamilies of Muricidae in World Register of Marine Species were still not represented in our dataset.

In the present study, almost all nodes in the BI tree were strongly supported, while some nodes in the ML tree received moderate statistical support (Figure 5). The

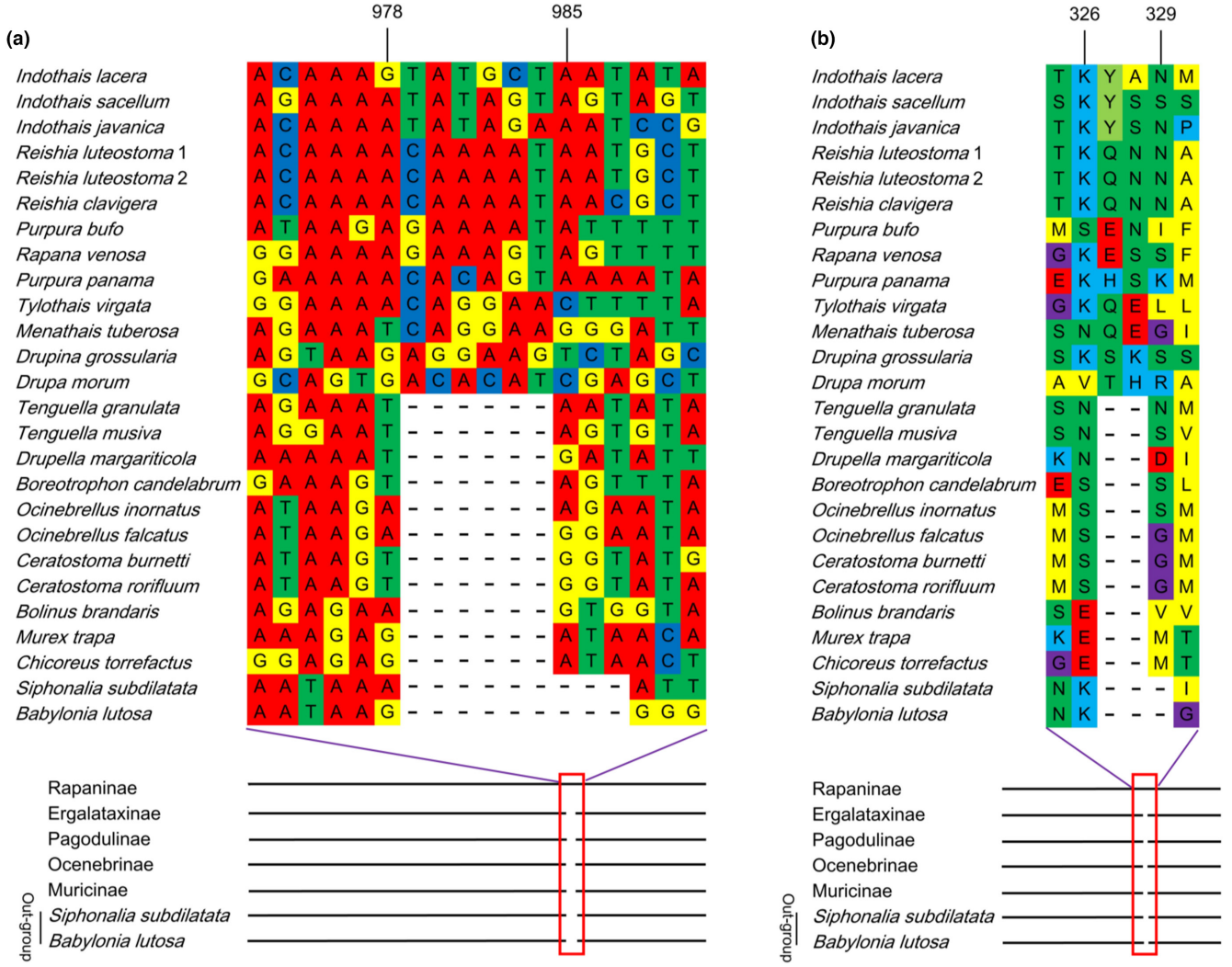

FIGURE 4 *Nad2* sequence differences in 24 muricids and two outgroup species. Nucleotide (a) and amino acid (b) alignments of a portion of *nad2* gene indicate that the six-nucleotide insertion present in Rapaninae.

monophyly of each subfamily (Rapaninae, Ergalataxinae, Ocenebrinae and Muricinae) was strongly supported, consistent with previous studies using partial sequences of mt and nuclear genes (Barco, 2015; Barco et al., 2010, 2016; Claremont et al., 2013). Ergalataxinae was recovered as the sister taxon of Rapaninae (BS: 100%, PP: 1.00), which refuted the results of morphological classification where Ergalataxinae was placed within Rapaninae (Kool, 1993; Vermeij & Carlson, 2000). The clade of Muricinae + Pagodulinae was sister to the clade of Ergalataxinae + Rapaninae (PP: 0.78) in the BI analysis, but recovered as a sister taxon to Ocenebrinae in the ML analysis (BS: 50%). A previous study using the 12S rRNA gene demonstrated that Muricinae was sister to Rapaninae + Ergalataxinae (Oliverio et al., 2009), which was consistent with our BI analysis, while the molecular phylogeny of Barco et al. (2010) showed the same results as our ML analysis. According to Claremont et al. (2008), Ergalataxinae was sister to Ocenebrinae + Rapaninae and then clustered with Muricinae. Our BI and ML analyses both refute that Ocenebrinae is a sister group of Rapaninae (Claremont et al., 2008). Therefore, to analyse the phylogeny of Muricinae (and Pagodulinae), further research with larger datasets is needed owing to the low node support values (0.78 PP and 50% BS, respectively).

Claremont et al. (2013) first proposed *Indothais* by using four genes (28S rRNA, 16S rRNA, 12S rRNA and *cox1*), which mainly consists of species formerly belonging to *Reishia* in the Indo-West Pacific. In this study, *Indothais* was confirmed to be monophyletic (BS: 100%, PP: 1.00). *R. venosa* was sister to *Indothais* (BS: 87%, PP: 1.00) and clustered with *Reishia* (BS: 85%, PP: 1.00). The genetic distances between *Indothais* and *Reishia* were 0.186–0.211 (Figure 6), higher than the maximum distances between the congeneric species (*Reishia*, 0.078; *Tenguella*, 0.141; *Ceratostoma*, 0.062; *Ocinebrellus*, 0.077; *Indothais*, 0.180). This further shows that *Indothais* was a valid genus. *Drupina* was recovered at the base of

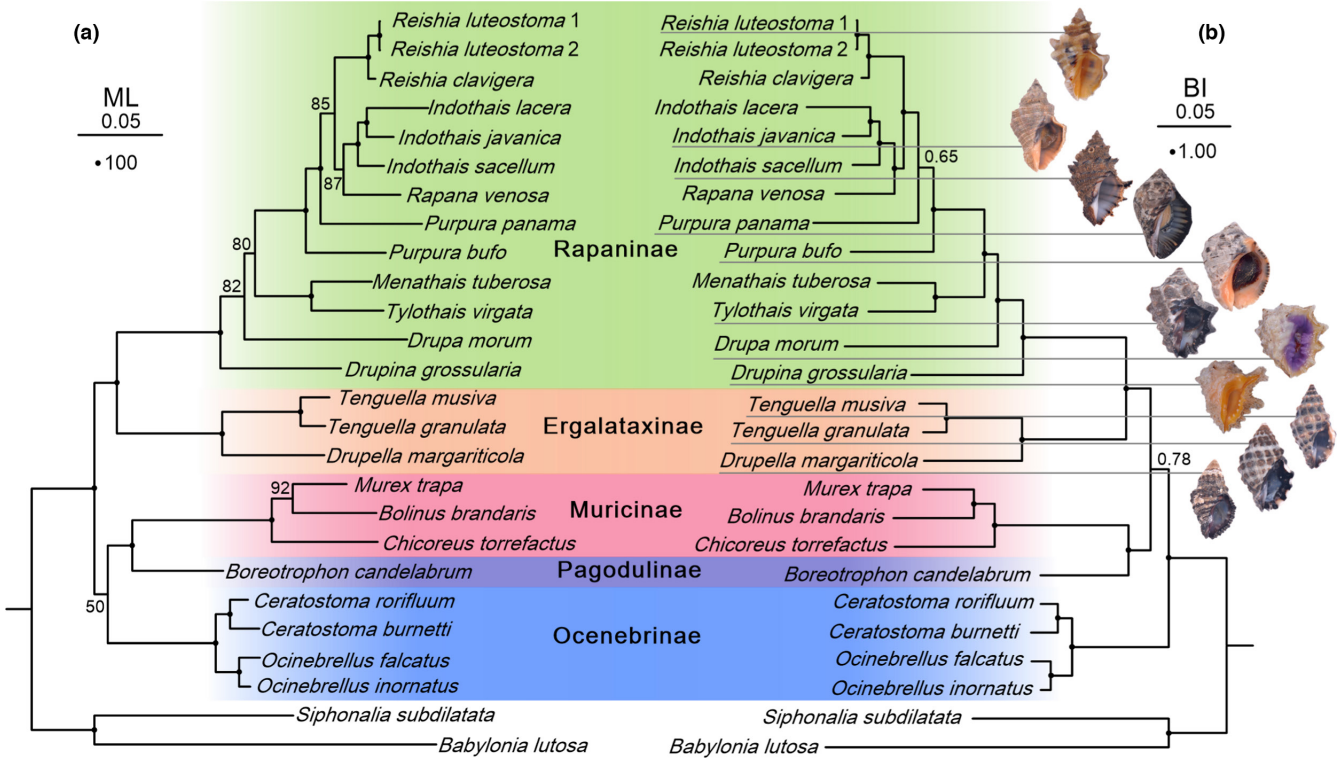

FIGURE 5 Phylogenetic relationships of Muricidae based on the MA dataset. The ML phylograms are shown in the (a). The BI phylograms are shown in the (b). Numbers at nodes are statistical support values for ML (bootstrap proportions in percentage)/BI (posterior probabilities). Solid black circles represent nodes with posterior probabilities ≥0.95 and bootstrap proportions ≥90. Shells of all the specimens sequenced in this study are illustrated.

	Rve	*Isa*	*Ila*	*Ija*	*Rcl*	*Rlu* 1	*Rlu* 2	*Pbu*	*Ppa*	*Mtu*	*Tvi*	*Dmo*	*Dgr*	*Dma*	*Tgr*	*Tmu*	*Cto*	*Bbr*	*Mtr*	*Bca*	*Cbu*	*Cro*	*Ofa*	*Oin*	*Blu*	*Ssu*
Rve																										
Isa	0.175																									
Ila	0.194	0.172																								
Ija	0.194	0.162	0.180																							
Rcl	0.194	0.192	0.211	0.200																						
Rlu 1	0.191	0.186	0.209	0.203	0.078																					
Rlu 2	0.191	0.186	0.209	0.203	0.078	0.004																				
Pbu	0.212	0.215	0.227	0.228	0.216	0.216	0.217																			
Ppa	0.207	0.201	0.221	0.218	0.210	0.210	0.209	0.228																		
Mtu	0.244	0.247	0.260	0.257	0.254	0.254	0.256	0.262	0.255																	
Tvi	0.254	0.255	0.257	0.264	0.257	0.257	0.258	0.271	0.264	0.215																
Dmo	0.293	0.298	0.303	0.299	0.295	0.295	0.293	0.306	0.305	0.302	0.299															
Dgr	0.286	0.285	0.294	0.288	0.284	0.284	0.283	0.296	0.290	0.287	0.285	0.304														
Dma	0.272	0.274	0.288	0.283	0.292	0.292	0.290	0.289	0.274	0.288	0.297	0.338	0.311													
Tgr	0.283	0.283	0.291	0.292	0.297	0.297	0.297	0.295	0.287	0.305	0.307	0.337	0.322	0.228												
Tmu	0.270	0.271	0.287	0.282	0.290	0.290	0.287	0.287	0.278	0.300	0.302	0.340	0.320	0.216	0.141											
Cto	0.301	0.296	0.305	0.309	0.312	0.312	0.311	0.308	0.305	0.311	0.318	0.350	0.327	0.296	0.316	0.302										
Bbr	0.291	0.291	0.297	0.304	0.307	0.307	0.304	0.306	0.295	0.312	0.316	0.345	0.334	0.294	0.296	0.288	0.222									
Mtr	0.297	0.299	0.300	0.305	0.301	0.301	0.304	0.302	0.294	0.313	0.314	0.347	0.327	0.293	0.302	0.292	0.223	0.197								
Bca	0.256	0.257	0.270	0.263	0.273	0.273	0.272	0.276	0.266	0.282	0.292	0.323	0.311	0.253	0.267	0.256	0.270	0.259	0.258							
Cbu	0.265	0.253	0.272	0.276	0.276	0.276	0.279	0.280	0.269	0.289	0.301	0.333	0.316	0.267	0.289	0.272	0.281	0.274	0.277	0.233						
Cro	0.267	0.253	0.274	0.274	0.276	0.276	0.276	0.284	0.268	0.288	0.297	0.330	0.312	0.268	0.287	0.274	0.279	0.273	0.277	0.235	0.062					
Ofa	0.272	0.260	0.276	0.275	0.280	0.280	0.279	0.288	0.278	0.292	0.300	0.319	0.321	0.275	0.287	0.281	0.287	0.282	0.285	0.233	0.148	0.148				
Oin	0.271	0.257	0.274	0.277	0.276	0.276	0.277	0.285	0.277	0.295	0.295	0.319	0.315	0.276	0.287	0.280	0.284	0.282	0.286	0.234	0.145	0.142	0.077			
Blu	0.311	0.310	0.324	0.318	0.322	0.322	0.322	0.321	0.317	0.331	0.326	0.358	0.352	0.310	0.319	0.308	0.326	0.328	0.317	0.295	0.298	0.300	0.303	0.303		
Ssu	0.296	0.288	0.299	0.306	0.312	0.312	0.308	0.316	0.308	0.315	0.316	0.359	0.338	0.295	0.307	0.299	0.318	0.304	0.308	0.273	0.274	0.275	0.284	0.279	0.297	

FIGURE 6 Pairwise genetic distances based on MN dataset of *Rapana venosa* (*Rve*), *Indothais sacellum* (*Isa*), *Indothais lacera* (*Ila*), *Indothais javanica* (*Ija*), *Reishia clavigera* (*Rcl*), *Reishia luteostoma*1 (*Rlu1*), *Reishia luteostoma2* (*Rlu2*), *Purpura bufo* (*Pbu*), *Purpura panama* (*Ppa*), *Menathais tuberosa* (*Mtu*), *Tylothais virgata* (*Tvi*), *Drupa morum* (*Dmo*), *Drupina grossularia* (*Dgr*), *Drupella margariticola* (*Dma*), *Tenguella granulata* (*Tgr*), *Tenguella musiva* (*Tmu*), *Chicoreus torrefactus* (*Cto*), *Bolinus brandaris* (*Bbr*), *Murex trapa* (*Mtr*), *Boreotrophon candelabrum* (*Bca*), *Ceratostoma burnetti* (*Cbu*), *Ceratostoma rorifluum* (*Cro*), *Ocinebrellus falcatus* (*Ofa*), *Ocinebrellus inornatus* (*Oin*), *Babylonia lutosa* (*Blu*), *Siphonalia subdilatata* (*Ssu*).

Rapaninae (BS: 100%, PP: 1.00), and *Drupa* was sister to the remaining species in Rapaninae (BS: 82%, PP: 1.00). *Drupina* had generally been considered a subgenus of *Drupa* (Emerson & Cernohorsky, 1973; Monsecour & Wuyts, 2007), but a previous study based on 12S rRNA, *cox1*, and nuclear 28S genes recognized *Drupina* as a valid genus (Claremont et al., 2012). The clustering relationship between *Drupina* and *Drupa* in our phylogenetic analysis was consistent with a study based on fragment genes, which demonstrated that *Drupina* was an independent genus rather than a subgenus of *Drupa*. Additionally, the genetic distances reflected the same result, with 0.304 (Figure 6) between *Drupina* and *Drupa* being larger than the genetic distances within the same genus (*Reishia*, 0.078; *Tenguella*, 0.141; *Ceratostoma*, 0.062; *Ocinebrellus*, 0.077; *Indothais*, 0.180). *Purpura* was not recovered as a monophyletic group in our analyses. In the MA dataset analysis, *Purpura panama* was recovered as sister to the clade *Reishia* + *Rapana* + *Indothais* (BS: 100%, PP: 0.65) and then clustered with *Purpura bufo* (BS: 100%, PP: 1.00). However, in the MD dataset analysis, *P. bufo* was sister to *Reishia* (BS: 100%, PP: 0.65). *P. panama* was recovered as a sister to the clade (*Reishia* + *P. bufo*) + (*Rapana* + *Indothais*) (BS: 100%, PP: 1.00; Figure S2). The evolutionary status of *P. bufo* is unclear. In previous morphological studies, *P. bufo* was classified as *Thais* (*Reishia*) and *Mancinella* (Cernohorsky, 1972; Kilburn & Rippey, 1982). Molecular analysis performed by Claremont et al. (2013) recovered *P. bufo* at the base of the clade comprising *Purpura*, *Reishia* and *Indothais*; however, none of these branches were particularly well-supported. The genetic distances between *P. bufo* and *Reishia* were 0.216–0.217, higher than the maximum distance within *Reishia* (0.078), which supported that *P. bufo* should be considered as a distinct clade instead of clustering with *Reishia*. However, the genetic distance between *P. bufo* and *P. panama* (0.228) was higher than the maximum distance among the congeneric species (*Reishia*, 0.078; *Tenguella*, 0.141; *Ceratostoma*, 0.062; *Ocinebrellus*, 0.077; *Indothais*, 0.180). The type species of *Purpura* (*P. persica*) resembles *P. panama* in terms of shell morphology. Therefore, the generic status of '*Purpura*' *bufo* in the current taxonomy is dubious and should be reconsidered in future studies.

4 | CONCLUSIONS

The mt genomes of 11 muricid species were conserved in genome size, nucleotide content and gene order. However, compared to other subfamilies, rapanine species have nucleotide indels in some PCGs of their mt genomes, which provides important phylogenetic signals. The reconstructed mitogenomic tree strongly supports the monophyly of each subfamily in Muricidae. This strongly supported a sister taxon relationship between Ergalataxinae and Rapaninae, supporting the taxonomic validity status of Ergalataxinae. However, the phylogeny of Muricinae needs to be further confirmed with nuclear data and larger sampling. Within Rapaninae, *Indothais* was determined to be a valid genus comprising species that formerly belonged to *Reishia*. The phylogenetic relationship between *Drupina* and *Drupa* indicated that *Drupina* was a full genus rather than a subgenus of *Drupa*. *Purpura* was not recovered as a monophyletic group, which necessitates revision of the classification of *P. bufo* by increasing the number of samples and datasets.

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ORCID

Yi Yu https://orcid.org/0000-0001-5570-2681
Lingfeng Kong https://orcid.org/0000-0001-5263-1697
Qi Li https://orcid.org/0000-0002-3937-9324

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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