frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 23 February 2023
DOI 10.3389/fevo.2023.1138297

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Phylogenetics, Phylogenomics, and Systematics, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 05 January 2023
ACCEPTED 08 February 2023
PUBLISHED 23 February 2023

CITATION
Ma Q, Li F, Zheng J, Liu C, Wang A, Yang Y and Gu Z (2023) Mitogenomic phylogeny of Cypraeidae (Gastropoda: Mesogastropoda). *Front. Ecol. Evol.* 11:1138297. doi: 10.3389/fevo.2023.1138297

Mitogenomic phylogeny of Cypraeidae (Gastropoda: Mesogastropoda)

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Cowries (Family Cypraeidae) are widely distributed in tropical and subtropical seas, with the highest diversity of cowries in the Indo-Pacific region. However, the classification of Cypraeidae, especially at the lower taxonomic levels, is still controversial. In the present study, we determined the complete mitochondrial genomes of 10 cowries. All the newly sequenced mtDNA encode 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) genes, two ribosomal RNA (rRNA) genes, and several non-coding regions. The reconstructed mitogenomic phylogeny of Cypraeidae recognized two monophyletic clades, with the first clade comprised of Erroneinae, Cypraeinae and Luriinae and the second clade formed by the single subfamily Erosarinae. The congeneric genetic distance values fall within 0.118–0.144, lower than those above genus level ranging from 0.163 to 0.271, consistent with the current division of genera within Cypraeidae. The divergence time estimated here indicated that the ancestor of Indo-Pacific cowries diversified during the Paleocene, and the closure of the Tethys Seaway might lead to the speciation events of several Indo-Pacific species. This study suggests that the complete mtDNA is a promising tool to improve the phylogenetic resolution of Cypraeidae, and mtDNA could also provide important information for future species delimitation especially within the cowries that possess different morphological phenotypes.

KEYWORDS

cowries, mitochondrial genome, phylogenetic analysis, genetic distance, divergence times

Introduction

Belonging to family Cypraeidae (Rafinesque, 1815), cowries are widely distributed in tropical and subtropical seas, although some species have been adapted to temperate water environment. The highest diversity of cowries was found in the Indo-Pacific region, especially along the boundary between East Indian and West Pacific Ocean (Paulay and Meyer, 2006; Passamonti, 2015). This region is also the richest species area of reef-building corals (Malay and Paulay, 2010), and considered as a center of maximum marine biodiversity (Hoeksema, 2007). Cowries are usually characteristic with a brilliant and shiny shell, since the retractable mantle that could cover the entire shell helps clean up the shell attachment. The presence of a beautiful shell also imparts some cowry species high collection values among shell markets.

Traditional taxonomy of Cypraeidae was mainly based on shell and anatomical characteristics (Schilder and Schilder, 1938; Kay, 1957; Schilder, 1966; Burgess, 1985). Although the division within Cypraeidae, especially at generic or subgeneric level, were controversial, most of the

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

Newly sequenced mt genomes			
Species	Length (bp)	Sampling time	Accession no.
Monetaria moneta	16,214	August, 2021	OP729418
Naria helvola	15,648	August, 2021	OP734446
Mauritia arabica	15,855	August, 2021	OP714184
Naria miliaris	16,123	October, 2021	OP747190
Naria erosa	16,020	November, 2021	OP738004
Purpuradusta gracilis	16,240	November, 2021	OP723877
Lyncina vitellus	16,269	November, 2021	OP714183
Erronea onyx	15,789	December, 2021	OP714185
Erronea caurica	15,857	December, 2021	OP714186
Monetaria caputserpentis	15,818	December, 2021	OP738519
Genbank mt genomes			
Species	Length (bp)	Accession no.	References
Monetaria annulus	16,087	LC469295	Fukumori et al. (2019)
Cypraea tigris	16,177	MK783263	Pu et al. (2019)
Bufonaria rana (Bursidae)	15,510	MT408027	Zhong et al. (2020)
Charonia lampas (Charoniidae)	15,405	MG181942	Choi and Hwang (2021)
Monoplex parthenopeus (Cymatiidae)	15,270	EU827200	Ashlin et al. (2020)

previously identified subfamilies and genera have also been recognized by molecular phylogenies (Meyer, 2003, 2004). The current classification of Cypraeidae is divided into nine subfamilies and 55 genera (MolluscaBase, 2022). Different from the stable taxonomies at higher levels, those at species level and below are quite subjective. The major reason was due to the absence of molecular data, which could help determine the validity of their taxonomic status. On the other hand, the increased species number of cowries has been triggered by economic factors in shell market, leading to unnecessary proliferation of taxonomic names (Passamonti, 2015).

The typical metazoan mitochondrial (mt) genome is a covalently circular molecule, encoding 37 genes including 13 protein-coding genes (PCGs), two ribosomal RNA (rRNA) genes and 22 transfer RNA (tRNA) genes (Boore, 1999), although some exceptions have been reported (Lavrov et al., 2013; Lavrov and Pett, 2016). Compared with single gene fragments, mitochondrial genome could provide considerable amount of variant information which has been used in species identification (Abalde et al., 2017a,b) and phylogenetic construction (Uribe and Zardoya, 2017; Uribe et al., 2019) within Mollusca. In the present study, the complete mtDNA of 10 cowries representing four subfamilies were sequenced and compared together with those of other cowries published before. The reconstructed phylogenetic relationships as well as the pairwise genetic distance values in the present study could provide important information for future species delimitation especially within the cowries that possess different morphological phenotypes.

Materials and methods

Samples and DNA extraction

All the specimens of cowries were collected in Sanya and Lingshui, Hainan Province, China (Table 1). Samples were then deposited in 95% ethanol at 4°C.

Genomic DNA was isolated from small pieces of foot tissue (less than 30 mg) using Tiangen Marine Animals DNA Kit (Tiangen Biotech, Beijing, China) following manufacturer's instructions.

PCR amplification, *de novo* sequencing, and mitogenome assembly

The complete mitochondrial genome was amplified by using universal primers in a total volume of 20 µl using 10 µl of 2 × Taq PCR Master Mix (with Taq DNA polymerase, dNTP mixture, $MgCl_2$, and PCR buffer), 0.5 µl of forward and reverse primers (10 µM), 3 µl of DNA and 6 µl of water. PCR conditions were set as follows: initial denaturation step was maintained at 94°C for 3 min, 40 denaturation cycles at 94°C for 30 s, annealing time at 46°C for 30 s, extension to 72°C for 1 min, and a final extension step at 72°C for 5 min. PCR products were sequenced at BGI (China).

Genomic DNA was sent to Novogene Company (Beijing, China) for library construction and high-throughput sequencing. A total of 10 libraries with insert sizes of approximately 300 bp were prepared and then sequenced as 150 bp paired-end runs on the Illumina NovaSeq 6000 platform. Finally, about 8 Gb of raw data were generated for each library. The clean reads were generated using Trimmomatic v.0.39 (Bolger et al., 2014), and imported into Geneious Prime 2021.0.1 (Kearse et al., 2012) for assembly following Irwin et al. (2021).

Gene annotation and sequence analysis

The newly obtained mitochondrial genomes of cowries were annotated with Geneious Prime (Kearse et al., 2012). The 13 PCGs were defined by setting their similarity values to 75–80% as previously published mitochondrial genomes of cowries and modified manually. The tRNA secondary structures were determined by ARWEN (Laslett

TABLE 2 List of total size, AT content, AT skew and GC skew, for mitochondrial genomes of *Monetaria moneta* (*Cmm*), *Naria helvola* (*Cnh*), *Mauritia arabica* (*Cmar*), *Naria miliaris* (*Cnm*), *Naria erosa* (*Cne*), *Monetaria caputserpentis* (*Cmc*), *Purpuradusta gracilis* (*Cpg*), *Lyncina vitellus* (*Clv*), *Erronea onyx* (*Ceo*), *Erronea caurica* (*Cec*), *Cypraea tigris* (*Cct*), and *Monetaria annulus* (*Cma*).

	Cmm	*Cnh*	*Cmc*	*Cnm*	*Cne*	*Cmar*	*Cpg*	*Clv*	*Ceo*	*Cec*	*Cct*	*Cma*
Total size	16,214	15,648	15,818	16,123	16,020	15,855	16,240	16,269	15,789	15,857	16,177	16,087
%A + T	0.620	0.615	0.637	0.626	0.621	0.647	0.682	0.623	0.677	0.686	0.659	0.642
%A + T (tRNA)	0.649	0.647	0.656	0.650	0.659	0.651	0.660	0.652	0.667	0.668	0.657	0.658
%A + T (*rrnS*)	0.628	0.644	0.642	0.645	0.635	0.663	0.668	0.624	0.663	0.662	0.647	0.643
%A + T (*rrnL*)	0.682	0.696	0.699	0.688	0.678	0.706	0.724	0.678	0.726	0.735	0.711	0.699
rrnS	973	973	971	969	964	960	962	971	960	960	972	975
rrnL	1,393	1,400	1,400	1,396	1,393	1,398	1,406	1,400	1,398	1,406	1,388	1,407
AT skew mitogenome	−0.081	−0.083	−0.086	−0.064	−0.069	−0.125	−0.117	−0.136	−0.114	−0.120	−0.127	−0.069
AT skew all PCGs	−0.129	−0.136	−0.135	−0.116	−0.121	−0.181	−0.181	−0.208	−0.173	−0.174	−0.191	−0.121
AT skew rRNAs	0.073	0.077	0.068	0.076	0.077	0.035	0.034	0.061	0.061	0.058	0.041	0.069
GC skew mitogenome	−0.121	−0.112	−0.099	−0.128	−0.124	0.023	0.047	0.045	0.034	0.045	0.046	−0.117
GC skew all PCGs	−0.154	−0.146	−0.135	−0.162	−0.157	−0.006	0.025	0.018	0.006	0.013	0.026	−0.150
GC shew rRNAs	0.035	0.046	0.037	0.033	0.021	0.164	0.180	0.174	0.164	0.173	0.160	0.044

The last two mitogenomes are previously published.

and Canbäck, 2008). The boundaries of rRNA genes were identified by comparison with those of other cowries. Codon usage and pairwise genetic distances of 13 PCGs, and the nucleotide composition of the whole mitogenome, PCGS, tRNA and rRNA genes were calculated using MEGA X (Kumar et al., 2018). The base skew values were calculated as AT skew = (A − T)/(A + T) and GC skew = (G − C)/(G + C) (Perna and Kocher, 1995). The mitochondrial genome map was drawn by CGView (Grant and Stothard, 2008). The average pairwise ratio of nonsynonymous (Ka) to synonymous (Ks) between sequences for each gene was calculated using BUSTED analysis (Murrell et al., 2015) implemented on the Datamonkey server.[1]

Phylogenetic analysis

The phylogenetic analysis was conducted based on the concatenated nucleotide sequences of 13 PCGs and two rRNA genes. The PCGs were aligned with ClustalW implemented in MEGA X, while the rRNA alignment was conducted separately by MAFFT v7 (Katoh and Standley, 2013) with default parameters. Ambiguously aligned positions of rRNA alignments were removed using Gblocks v.0.91b (Castresana, 2000) with default parameters. Different gene alignments were concatenated together using Geneious Prime 2021.0.1. Sequences were converted into NEXUS and PHYLIP formats for further phylogenetic analyses using DAMBE5 (Xia, 2013).

Phylogenetic analyses were carried out using maximum likelihood (ML; Felsenstein, 1981) and Bayesian inference (BI; Huelsenbeck and Ronquist, 2001). ML analyses were carried out using IQtree 1.6.10 (Nguyen et al., 2015), allowing partitions to have different evolutionary rates (-spp option) and with 10,000 ultrafast bootstrap pseudoreplications (-bb option). BI was conducted using MrBayes v.3.1.2 (Ronquist and Huelsenbeck, 2003), running four Monte Carlo Markov chains (MCMC) simultaneously for 10,000,000 generations, sampling every 1,000 generations and discarding the first 25% generations as burn-in. Two independent runs were carried out to increase the chance of adequate mixing of the Markov chains and to increase the chance of detecting failure to converge, as determined using Tracer v1.6. The effective sample size (ESS) of all parameters was higher than 200, and the phylogenetic trees were visualized using FigTree v1.4.2.

The best partition schemes and best-fit substitution models were determined by PartitionFinder 2 (Lanfear et al., 2017) under the Bayesian Information Criterion (BIC; Schwarz, 1978). For the 13 PCGs, the partitions tested were all genes combined; all genes separated (except *atp6-atp8* and *nad4-nad4L*); and genes grouped by subunits (*atp*, *cob*, *cox*, and *nad*). Additionally, these three partition schemes were tested considering separately the three codon positions. The two rRNA genes were analysed with two different schemes (genes grouped or separated).

Divergence time estimation

Divergence times of Cypraeidae were estimated based on the same data set used for phylogenetic reconstruction. An uncorrelated relaxed molecular clock model was employed using BEAST v.1.10.4 (Drummond and Rambaut, 2007). For tree prior, the Yule Process was chosen. The Markov chains were run twice for 100 million generations, sampled every 10,000 generations, and the first 10% of the samples were discarded as burn-in. The effective sample size of all the parameters was higher than 200, and the convergence of the chains was checked based on Tracer v1.6. Finally, the tree was generated by TreeAnnotator and visualized using FigTree v1.4.2.

The posterior distribution of the estimated divergence times was obtained by specifying two calibration points from the fossil data as priors for the divergence times of the corresponding splits. The first calibration point was set for the origin of *Cypraea*. A lognormal distribution was applied, with a minimum of 28.4 Mya and a 95% upper limit of 33.9 Mya (offset, 28.4; mean, 1.5; SD, 1.5) based on the fossil record of *Cypraea sindiensis* (Iqbal, 1980). The second calibration

1 http://www.datamonkey.org/dataupload.php

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point was set at the divergence of *Monetaria* and *Naria*, with a minimum of 28.1 Mya and a 95% upper limit of 33.9 Mya (offset, 28.1; mean, 1.6; SD, 1.6) based on the fossil record of *Monetaria* found in Rupelian France (Cahuzac and Janssen, 2010).

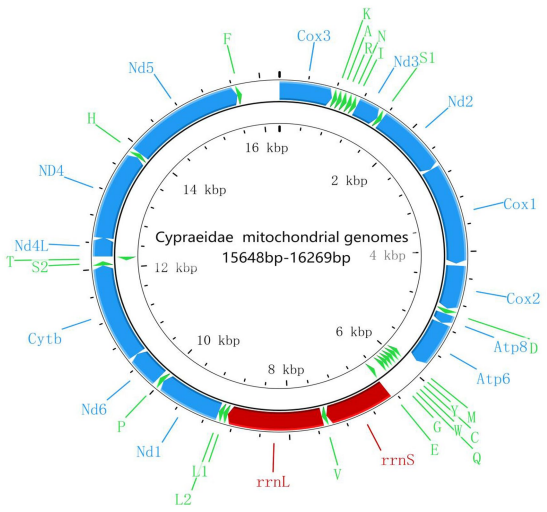

FIGURE 1
Gene map of the mt genomes of cowries.

Results and discussion

Genome structure, organization, and composition

Compared with other previously reported Cypraeidae mt genomes (Fukumori et al., 2019; Pu et al., 2019), all newly sequenced mt genomes in this study share very similar patterns in terms of genome size, nucleotide composition and AT content. The size of the 10 Cypraeidae mtDNA ranges from 15,648 (*N. helvola*) to 16,269 bp (*Lyncina vitellus*; Table 2). These Cypraeidae mt genomes are all composed of 13 PCGs, 22 tRNA genes and two rRNA genes, and the differences between these genomes are mainly in the non-coding regions. All the 13 PCGs, 14 tRNA genes (*trnD*, *trnV*, *trnL1*, *trnL2*, *trnP*, *trnS1*, *trnS2*, *trnH*, *trnF*, *trnK*, *trnA*, *trnR*, *trnN*, and *trnI*) and two rRNA genes (*rrnL* and *rrnS*) are encoded on the major strand, while the other eight tRNA genes are encoded on the minus strand (Figure 1).

The AT content, AT skew and GC skew of the 10 Cypraeidae mtDNA are shown in Table 2. The AT content of the 10 species ranges from 61.5 to 68.6%, similar to that reported for other molluscan taxa

TABLE 3 The length, start and stop codons for mitochondrial genes of *M. moneta* (*Cmm*), *N. helvola* (*Cnh*), *P. gracilis* (*Cpg*), *M. arabica* (*Cmar*), *N. miliaris* (*Cnm*), *L. vitellus* (*Clv*), *N. erosa* (*Cne*), *E. onyx* (*Ceo*), *E. caurica* (*Cec*), and *M. caputserpentis* (*Cmc*).

	Cmm	*Cpg*	*Cnh*	*Cmar*	*Cnm*	*Clv*	*Cne*	*Ceo*	*Cec*	*Cmc*
atp6	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAG)	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAA)	696 (ATG/TAA)
atp8	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAA)	159 (ATG/TAG)
cytb	1,152 (ATG/TAG)	1,146 (ATG/TAA)	1,152 (ATG/TAA)	1,140 (ATG/TAG)	1,152 (ATG/TAA)	1,140 (ATG/TAA)	1,152 (ATG/TAA)	1,140 (ATG/TAA)	1,140 (ATG/TAA)	1,152 (ATG/TAG)
cox1	1,536 (ATG/TAA)	1,539 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAA)	1,536 (ATG/TAG)	1,536 (ATG/TAA)
cox2	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)	687 (ATG/TAA)
cox3	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)	780 (ATG/TAA)
nad1	941 (ATG/TA)	942 (GTG/TAA)	957 (ATG/TAA)	942 (ATG/TAA)	957 (ATG/TAA)	942 (ATG/TAA)	941 (ATG/TA)	942 (ATG/TAA)	942 (ATG/TAG)	941 (ATG/TA)
nad2	1,062 (ATG/TAG)	1,062 (GTG/TAA)	1,062 (ATG/TAG)	1,062 (ATG/TAA)	1,062 (ATG/TAA)	1,062 (ATG/TAA)	1,062 (ATG/TAG)	1,062 (ATG/TAA)	1,062 (ATG/TAA)	1,062 (ATG/TAA)
nad3	354 (ATG/TAA)	354 (ATG/TAA)	354 (ATG/TAG)	354 (ATG/TAG)	354 (ATG/TAA)	354 (ATG/TAA)	354 (ATG/TAG)	354 (ATG/TAA)	354 (ATG/TAA)	354 (ATG/TAA)
nad4	1,371 (ATG/TAA)	1,371 (ATG/TAA)	1,371 (ATG/TAA)	1,356 (ATT/TAG)	1,356 (ATT/TAA)	1,371 (ATG/TAA)	1,371 (ATG/TAA)	1,371 (ATG/TAG)	1,371 (ATG/TAA)	1,359 (ATA/TAA)
nad4L	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)	297 (ATG/TAG)
nad5	1722 (ATG/TAG)	1722 (ATG/TAA)	1722 (ATG/TAG)	1722 (ATG/TAG)	1722 (ATG/TAG)	1722 (ATG/TAG)	1722 (ATG/TAG)	1722 (ATG/TAG)	1722 (ATG/TAA)	1722 (ATG/TAG)
nad6	504 (ATG/TAA)	504 (GTG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAA)	504 (ATG/TAG)

TABLE 4 Codon and relative synonymous codon usage (RSCU) of 13 PCGs in the mt genomes of *M. monetab* (*Cmm*), *N. helvola* (*Cnh*), *P. gracilis* (*Cpg*), *M. arabica* (*Cmar*), *N. miliaris* (*Cnm*), *L. vitellus* (*Clv*), *N. erosa* (*Cne*), *E. onyx* (*Ceo*), *E. caurica* (*Cec*), and *M. caputserpentis* (*Cmc*).

M. moneta/Monetaria moneta					
Amino acid	Codon	Count (RSCU)	Amino acid	Codon	Count (RSCU)
Phe	UUU	184.0 (1.17)	**Ala**	GCU	76.0 (1.22)
	UUC	131.0 (0.83)		GCC	102.0 (1.63)
Leu	UUA	178.0 (1.81)		GCA	59.0 (0.94)
	UUG	39.0 (0.40)		GCG	13.0 (0.21)
	CUU	99.0 (1.01)	**Gly**	GGU	53.0 (0.86)
	CUC	96.0 (0.98)		GGC	48.0 (0.78)
	CUA	122.0 (1.24)		GGA	116.0 (1.88)
	CUG	56.0 (0.57)		GGG	30.0 (0.49)
Ile	AUU	200.0 (1.33)	**Arg**	CGU	10.0 (0.65)
	AUC	101.0 (0.67)		CGC	6.0 (0.39)
Met	AUA	125.0 (1.38)		CGA	38.0 (2.45)
	AUG	56.0 (0.62)		CGG	8.0 (0.52)
Val	GUU	76.0 (1.26)	**Tyr**	UAU	81.0 (1.12)
	GUC	46.0 (0.76)		UAC	64.0 (0.88)
	GUA	92.0 (1.53)	**His**	CAU	36.0 (0.89)
	GUG	27.0 (0.45)		CAC	45.0 (1.11)
Ser	UCU	65.0 (1.37)	**Gln**	CAA	55.0 (1.43)
	UCC	87.0 (1.83)		CAG	22.0 (0.57)
	UCA	75.0 (1.58)	**Asn**	AAU	58.0 (0.95)
	UCG	17.0 (0.36)		AAC	64.0 (1.05)
	AGU	25.0 (0.53)	**Lys**	AAA	75.0 (1.60)
	AGC	50.0 (1.05)		AAG	19.0 (0.40)
	AGA	44.0 (0.93)	**Asp**	GAU	41.0 (1.09)
	AGG	17.0 (0.36)		GAC	34.0 (0.91)
Pro	CCU	46.0 (1.23)	**Glu**	GAA	69.0 (1.53)
	CCC	37.0 (0.99)		GAG	21.0 (0.47)
	CCA	51.0 (1.36)	**Cys**	UGU	20.0 (1.03)
	CCG	16.0 (0.43)		UGC	19.0 (0.97)
Thr	ACU	61.0 (1.29)	**Trp**	UGA	87.0 (1.55)
	ACC	59.0 (1.25)		UGG	25.0 (0.45)
	ACA	53.0 (1.12)	*	UAA	8.0 (1.33)
	ACG	16.0 (0.34)		UAG	4.0 (0.67)

For other tables, see Supplementary Table S1.

(Grande et al., 2008; Xu et al., 2012). All mitochondrial genomes show an A bias toward T (AT skew from −0.136 to −0.064), which is also seen in Vetigastropoda (Williams et al., 2014) and Neritimorpha (Arquez et al., 2014). Among the 10 mitogenomes, those of *M. moneta*, *N. helvola*, *N. miliaris*, *N. erosa*, and *M. caputserpentis* show a bias from G to C (GC skew from −0.128 to −0.099), with the same composition as *M. annulus*. The other five, including those of *P. gracilis*, *M. arabica*, *L. vitellus*, *E. onyx*, and *E. caurica* all show a bias from C to G (GC skew from 0.023 to 0.047) and similar to that of *C. tigris*. Both positive and negative GC skews have been reported within Metazoa (Saccone et al., 1999).

Protein-coding genes, transfer RNA, and ribosomal RNA genes

For the PCGs, 10 mitogenomes show negative AT skew, while GC skew was both positive and negative. All PCGs of the 10 newly sequenced Cypraeidae mt genomes started with the typical codons ATG and ATA except for the *nad1*,*nad2*, and *nad6* genes of *P. gracilis*, and *nad4* genes of *M. arabica* and *N. miliaris*, which used the alternative start codons GTG and ATT, respectively (Table 3). The latter alternative start codons ATT and GTG have also been reported in other gastropods (White et al., 2011; Osca et al., 2015; Uribe et al., 2016).

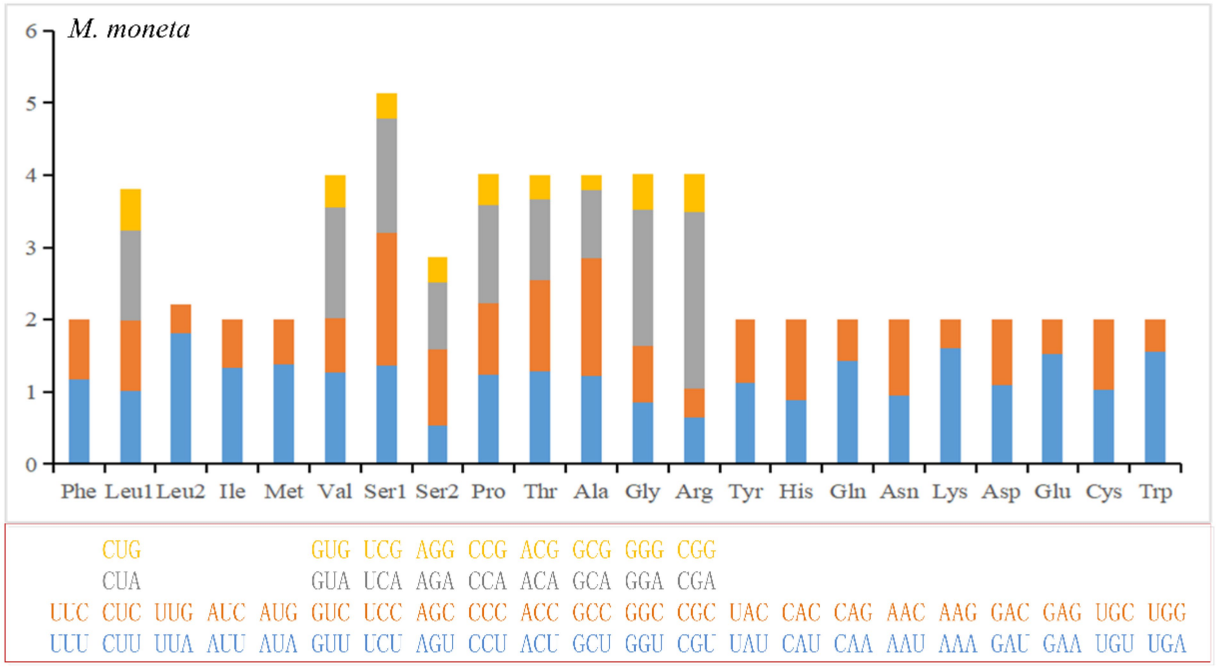

FIGURE 2
Relative Synonymoud Codon Usage (RSCU) of mitochondrial genomes for *E. moneta*. For other species, see Supplementary Figure S1.

All PCGs of the sequenced mitochondrial genomes terminate with complete stop codons TAA and TAG, except for the nad1 genes of *M. moneta*, *N. erosa*, and *M. caputserpentis*, which terminate with an incomplete stop codon TA. Incomplete stop codons may be modified to the TAA codon by polyadenylation of the transcribed messenger RNA (Ojala et al., 1981). The use of incomplete TA has also been reported in other gastropod species, such as *Pyramidella dolabrata* and *Siphonaria pectinata* (Grande et al., 2008).

The numbers of PCG codons for the 10 Cypraeidae mt genomes are from 3,745 (*M. arabica*) to 3,759 (*N. helvola*; including termination codons). The most encoded amino acid is leucine and the least encoded is cysteine (Table 4 and Supplementary Table S1, Figure 2 and Supplementary Figure S1). The most frequently used codon for *E. onyx* and *P. gracilis* is UUA (Leu). UUU (Phe) is the most frequently used codon for *L. vitellus*, *M. caputserpentis*, *E. caurica*, and *M. arabica*. While the most frequently used codon in *E. erosa*, *M. moneta*, *N. helvola,* and *N. miliaris* is AUU (Ile). The least frequently used codon in most mitogenomes is CGC (Arg), which is also reported in other invertebrates (Palomares-Rius et al., 2017). The least frequently used codons UCG(Ser), ACG(Thr), CGU(Arg), and GCG (Ala) are found in that of *E. caurica*, *E. erosa*, *N. helvola*, and *N. miliaris*, respectively. These frequently used codons, such as UUA (Leu), AUU (Ile), and UUU (Phe), all end in A or U and thus have a strong A + T bias at the third codon position, which results in an increased A + T content in the mitochondrial genome. These commonly used codons have also been observed in other invertebrates, such as Maldanidae and Siboglinidae in Annelida (Jennings and Halanych, 2005), and Longidoridae in Nematoda (Palomares-Rius et al., 2017).

The Ka/Ks ratios for each gene were all under 1.0, indicating the evidence of purifying selection (Figure 3). The highest average pairwise Ka/Ks ratio was found in *atp8* gene with Ka/Ks = 0.054,

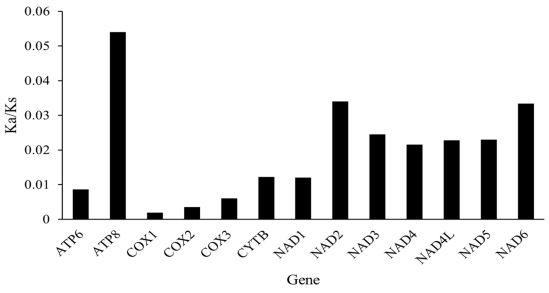

FIGURE 3
The Ka/Ks ratios of the 13 different mitochondrial genes in Cypraeidae species.

followed by *nad2*, *nad6* and *nad3* genes with values ranging from 0.034 to 0.025. Whereas the lowest Ka/Ks ratio was found in *cox1* with Ka/Ks = 0.002, followed by *cox2*, *cox3*, and *atp6* genes (with values between 0.004 and 0.009; Figure 3). This result reveals that the NADH complex genes of cowries are suffering a more relaxed purifying selection compared with the COX genes which appear more conservative. Similar trends have also been detected in other gastropod taxa (Yang et al., 2018).

Most metazoan mitochondrial genomes contain 22 tRNAs, including two serines and two leucines (Podsiadlowski et al., 2008). The 10 Cypraeidae mt genomes also contain 22 tRNAs. The average AT content of tRNAs ranges from 64.7% (*N. helvola*) to 66.8% (*E. caurica*; Table 2). The tRNAs of these 10 Cypraeidae mt genomes are essentially the same length, ranging from 62 bp to 75 bp (Table 5 and Supplementary Table S2). And most of them can form a clover-like secondary structure, but the DHU arms of *trnS*-AGN are missing

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TABLE 5 Gene annotation of the complete mt genome of *M. moneta*.

Gene	Strand	Location	Size(bp)	Start codon	Stop codon	Intergenic nucleotides
cox3	H	1–780	780	ATG	TAA	15
tRNA-*Lys*	H	796–864	69			1
tRNA-*Ala*	H	866–937	72			1
tRNA-*Arg*	H	939–1,009	71			9
tRNA-*Asn*	H	1,019–1,089	71			3
tRNA-*Ile*	H	1,093–1,162	70			4
nad3	H	1,167–1,520	354	ATG	TAA	0
tRNA-*Ser*	H	1,521–1,588	68			0
nda2	H	1,589–2,650	1,062	ATG	TAA	10
cox1	H	2,661–4,196	1,536	ATG	TAG	29
cox2	H	4,226–4,912	687	ATG	TAA	8
tRNA-*Asp*	H	4,921–4,990	70			0
atp8	H	4,991–5,149	159	ATG	TAA	3
atp6	H	5,153–5,848	696	ATG	TAA	36
tRNA-*Met*	L	5,885–5,952	68			1
tRNA-*Tyr*	L	5,954–6,022	69			6
tRNA-*Cys*	L	6,029–6,098	70			−2
tRNA-*Trp*	L	6,097–6,166	70			1
tRNA-*Gln*	L	6,168–6,230	63			4
tRNA-*Gly*	L	6,235–6,301	67			1
tRNA-*Glu*	L	6,303–6,373	71			0
12 s	H	6,374–7,346	973			0
tRNA-*Val*	H	7,347–7,416	70			0
16 s	H	7,417–8,809	1,393			0
tRNA-*Leu*	H	8,810–8,880	71			10
tRNA-*Leu*	H	8,891–8,960	70			1
nad1	H	8,962–9,902	941	ATG	TA	0
tRNA-*Pro*	H	9,903–9,969	67			1
nad6	H	9,971–10,474	504	ATG	TAA	3
cytb	H	10,478–11,629	1,152	ATG	TAG	−2
tRNA-*Ser*	H	11,628–11,693	67			7
tRNA-*Thr*	L	11,701–11,767	67			5
nad4L	H	11,773–12,069	297	ATG	TAG	−7
nad4	H	12,063–13,433	1,371	ATG	TAA	4
tRNA-*His*	H	13,438–13,505	68			1
nad5	H	13,507–15,228	1722	ATG	TAG	−1
tRNA-*Phe*	H	15,228–15,298	71			—

The annotation tables for the other nine are shown in Supplementary Table S2.

(Figure 4). The absence of the DHU arms of *trnS*-AGN are also common in metazoan mitogenomes (Garey and Wolstenholme, 1989), such as in those of *Mytilus edulis* (Hoffmann et al., 1992), *Acanthocardia tuberculata* and *Hiatella arctica* (Dreyer and Steiner, 2006).

The *rrnL* genes of these 10 Cypraeidae mt genomes are from 1,393 bp (*M. moneta* and *N. erosa*) to 1,406 bp (*P. gracilis*) in length, with AT content ranging from 67.8 to 73.5%. The length of *rrnS* genes are from 960 bp (*M. arabica*, *E. onyx*, and *E. caurica*) to 973 bp (*M. moneta* and *N. helvola*), with AT content from 62.4 to 66.8%. The *rrnL* gene is surrounded by *trnL* and *trnV*, and the *rrnS* gene is located between *trnV* and *trnE*. The AT skew of rRNAs for the 10 species is from 0.034 to 0.077, all showing an A skew towards T. And the GC skew of rRNAs ranges from 0.021 to 0.180, all showing a C skew toward G (Table 2).

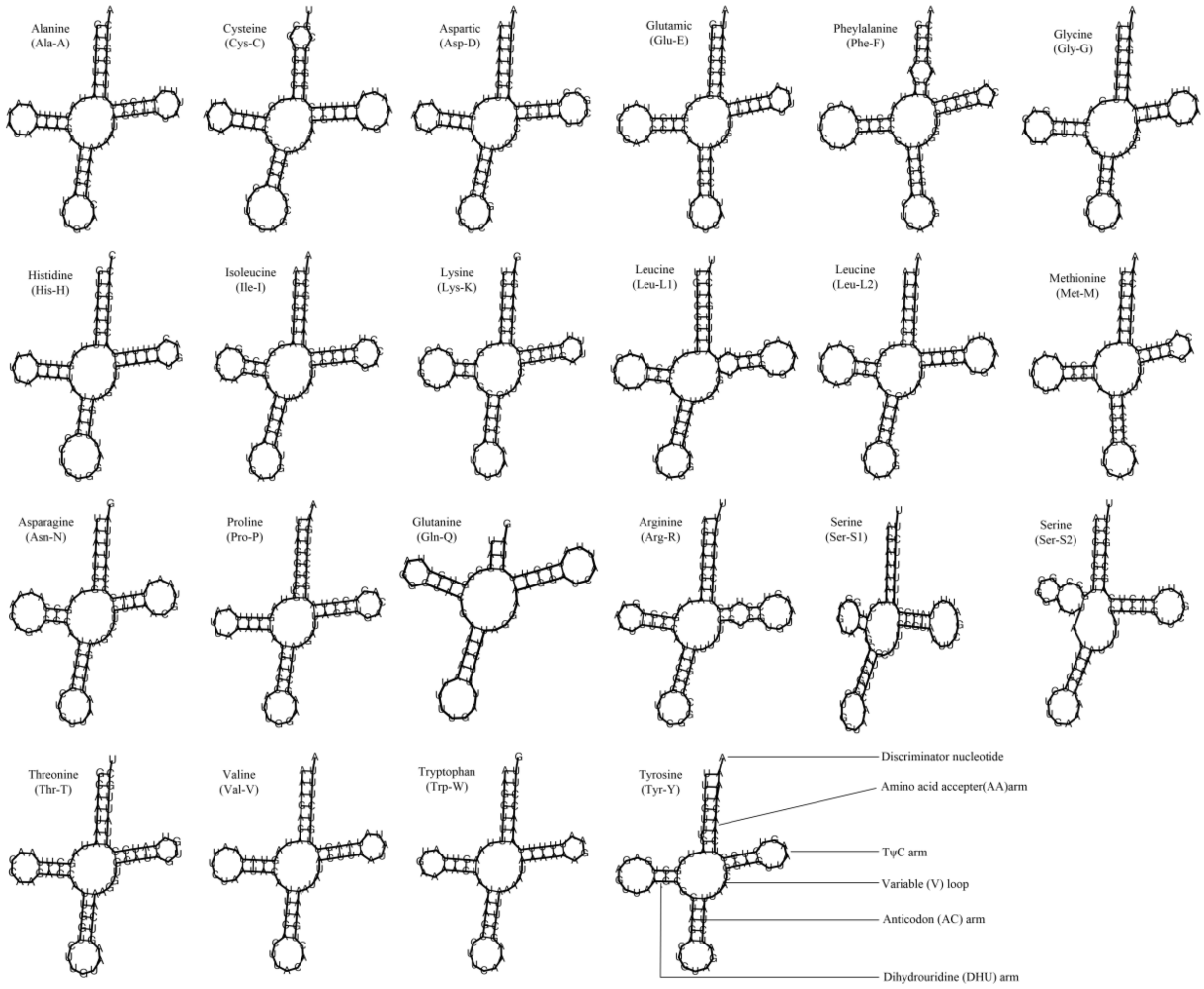

FIGURE 4
Inferred secondary structures of 22 tRNAs from *Lyncina vitellus*.

Phylogenetic relationship

Phylogenetic relationships of Cypraeidae were reconstructed based on the nucleotide sequences of the concatenated 13 PCGs and two rRNA genes using probabilistic methods. The final matrix was 13,323 bp in length. According to the BIC, the best partition scheme for the PCGs was the one combining genes by subunits but analysing each codon position separately (Supplementary Table S3). For the rRNA genes, the best partition scheme was the one combining together *rrnL* and *rrnS* genes. Both ML (−lnL = 133,593.77) and BI (−lnL = 133,905.39 for run 1; −lnL = 133,908.66 for run 2) analyses arrived at identical topologies (Figure 5).

According to the reconstructed phylogeny, a total of two clades are recognized and fully supported. The first clade (Clade I) is comprised of three monophyletic subfamilies including Erroneinae, Cypraeinae and Luriinae. The second clade (Clade II) is formed by the single subfamily Erosarinae. Within Clade I, Luriinae represented by the single species *L. vitellus*, is sister to Erroneinae + Cypraeinae. The radular morphology of a reduced shaft on all teeth is typical of the Luriinae. A previous study supported three lineages within *Lyncina*, with *L. vitellus* as sister to another Indo-West Pacific species *L. lynx* (Meyer, 2003). However, it also indicated that the internal phylogenetic relationships within Luriinae (especially between some genera, e.g., *Chelycypraea*, *Austrocypraea*, *Miolyncina*, *Arestoides*, *Callistocypraea*, and *Lyncina*) remained uncertain. Future mitogenomic phylogenies with a higher coverage of Luriinae are necessary to resolve the phylogenetic swarm. A second lineage of Clade I formed by *Cypraea tigris* and *Mauritia arabica* comprise Cypraeinae. Both two species are widely distributed in the Indo-West Pacific and contain several endemic subspecies (Meyer, 2003; Meyer and Tweedt, 2017; Cossignani and Allary, 2022), whose taxonomic ranges still need to be checked molecularly. In addition to *Cypraea* and *Mauritia*, Cypraeinae also includes another Indo-Pacific group *Leporicypraea* as well as the east Pacific clade including *Muracypraea* and *Macrocypraea* (MolluscaBase, 2022). And their phylogenetic relationships have been better resolved (Meyer, 2003). The last lineage of Clade I formed by *Erronea* and *Purpuradusta* correspond to Erroneinae. Both *E. caurica* and *E. onyx* include geographical subspecies that are not included in the present study.

Clade II is grouped by *Monetaria* and *Naria*, which all belong to subfamily Erosarinae. Within the former genus that is usually

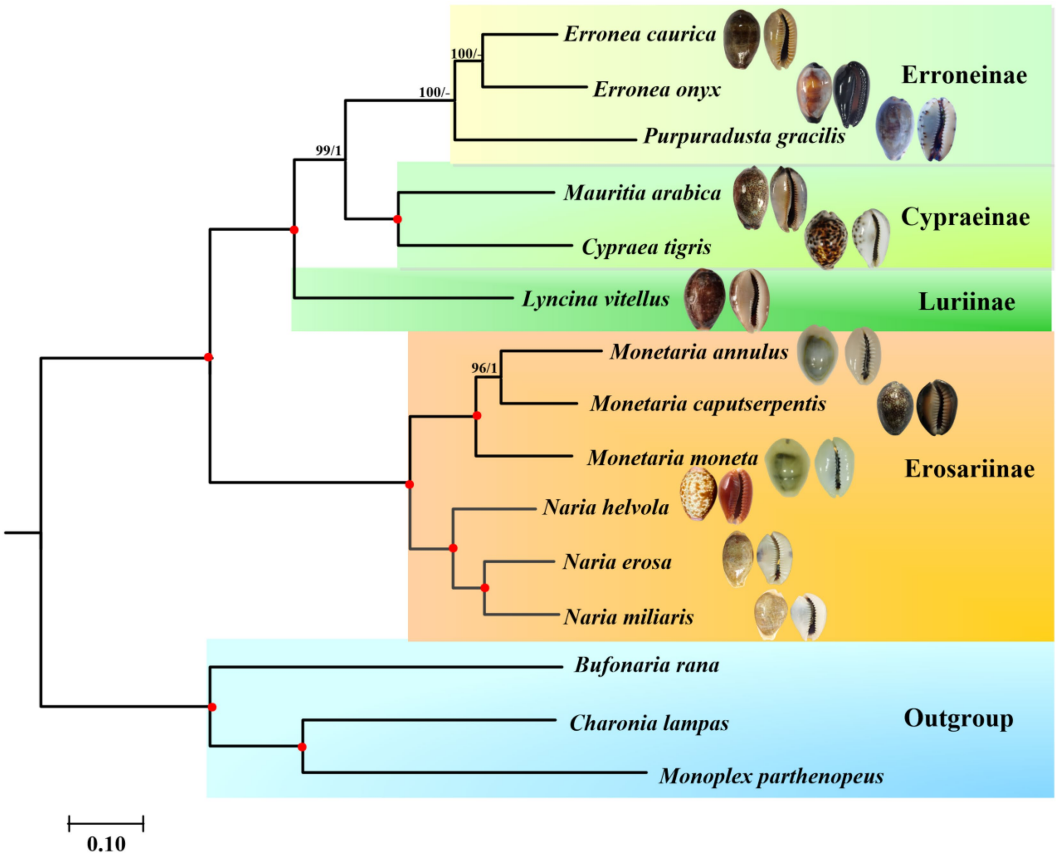

FIGURE 5
Phylogenetic relationships of Cypraeidae based on the nucleotide sequences of 13 mitochondrial protein-coding genes (PCGs) and 2 ribosomal RNA (rRNA) genes, with *Bufonaria rana*, *Charonia lampas*, and *Monoplex parthenopeus* as outgroups. The first number on each node is the bootstrap proportion (BP) of the maximum likelihood (ML) analysis. The second number is the Bayesian posterior probability (PP). Nodes with maximum statistical support (BP=100; PP=1) are marked with red solid circles.

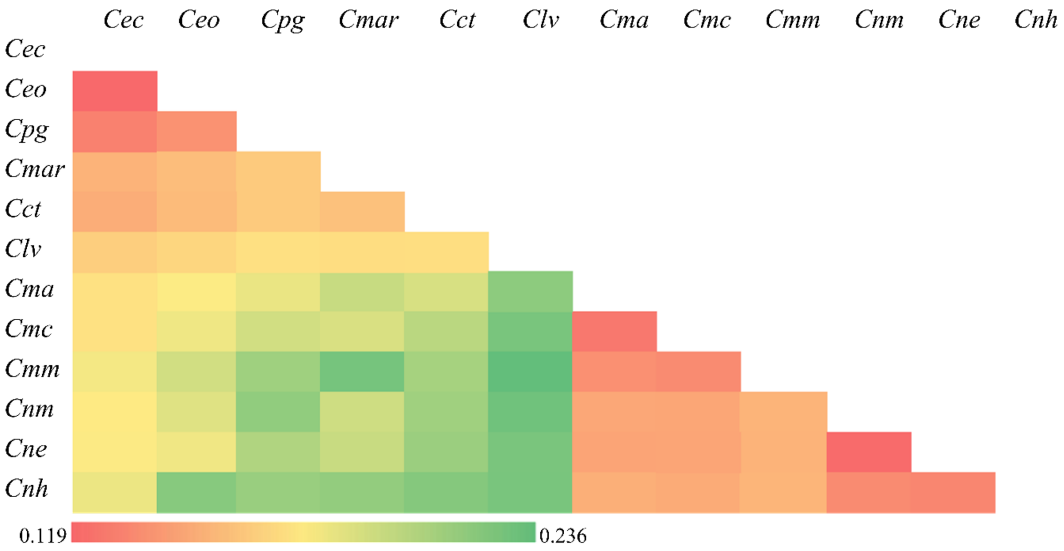

FIGURE 6
Heatmap of pairwise genetic distance of 13 PCGs of *Monetaria moneta* (*Cmm*), *Naria helvola* (*Cnh*), *Mauritia arabica* (*Cmar*), *Naria miliaris* (*Cnm*), *Naria erosa* (*Cne*), *Monetaria caputserpentis* (*Cmc*), *Purpuradusta gracilis* (*Cpg*), *Lyncina vitellus* (*Clv*), *Erronea onyx* (*Ceo*), *Erronea caurica* (*Cec*), *Cypraea tigris* (*Cct*), and *Monetaria annulus* (*Cma*).

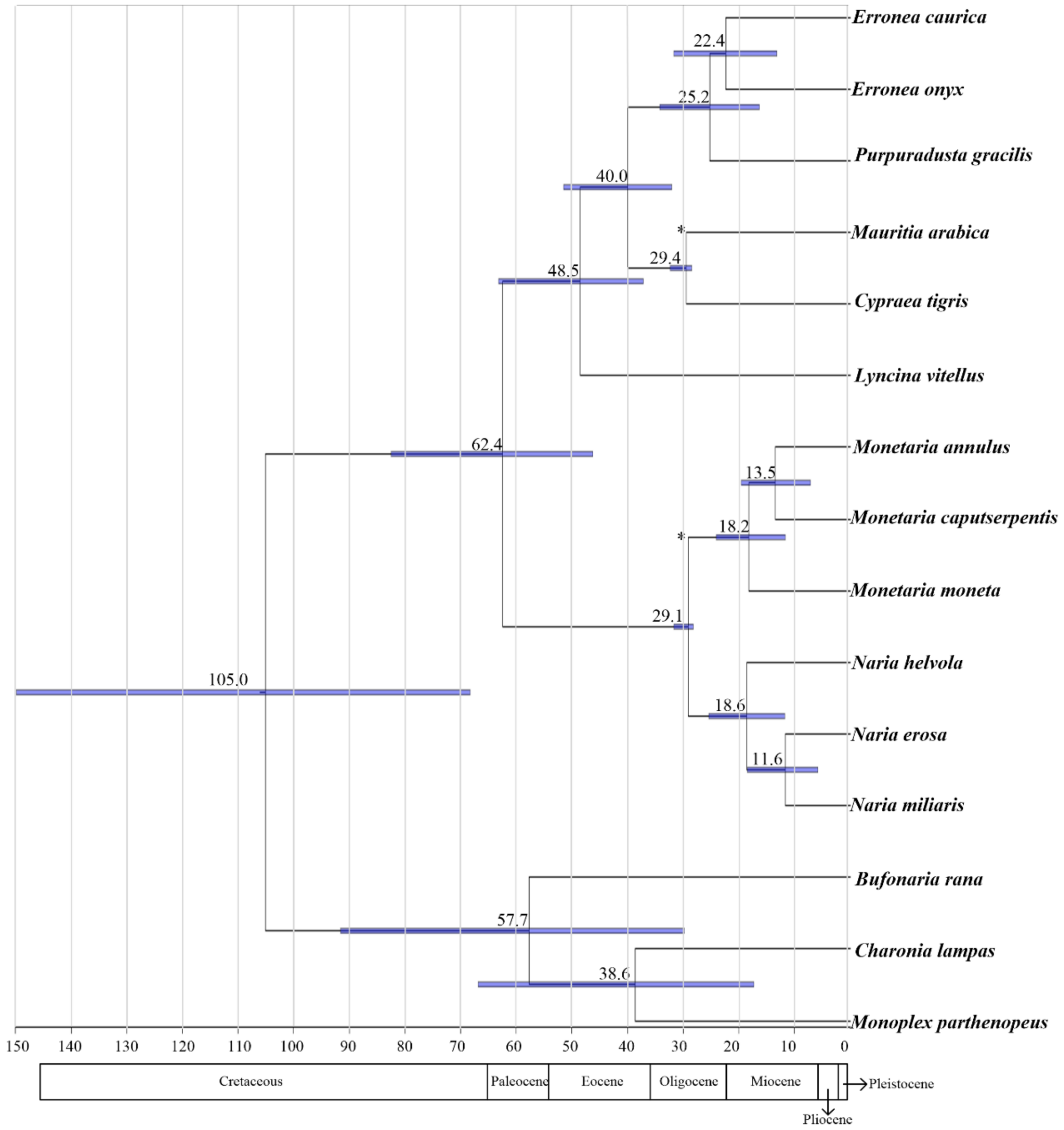

FIGURE 7
Divergences time estimations for the Cypraeidae using Bayesian relaxed dating methods (BEAST). Dates (and credibility intervals) are in millions of years, and horizontal bars represent 95% credibility intervals of relevant nodes.

mentioned as money cowries, the Indo-West Pacific distributed *M. annulus* was divided into five geographical subspecies based on the morphological characteristics (Schilder and Schilder, 1938; Iredale, 1939). It has been revealed that the geographical variation of shell morphology (especially the callus thickness) was significantly related to seawater temperature instead of genetic differentiation (Irie, 2006). Although similar trends have also been detected in *M. caputserpentis* (Irie, 1997; Irie and Iwasa, 2003), this species contained two evolutionarily significant units (ESUs) that corresponded to Hawaii and the remaining Indo-Pacific region, respectively. On the contrary, no ESUs were discovered within the widely distributed *M. moneta* (Meyer, 2003). The latter genus *Naria* is comprised of *N. helvola* + (*N. miliaris* + *N. erosa*). This topology is consistent with that of Meyer (2003), in which *N. miliaris* was relatively more related to *N. erosa*. Furthermore, in another COI-based phylogenetic analysis *N. helvola* was recovered as sister to *N. erosa* (Hao, 2007), contradicting either Meyer (2003) or the present study. It has been indicated that different datasets or methods might result in different topologies (Irwin et al., 2021). Compared with previous single gene-based phylogenies, the phylogenetic relationship within *Naria* derived from complete mitochondrial genomes here is fully supported and considered better resolved. Among the three members of *Naria*, only *N. erosa* and *N. helvola* possessed ESUs (Meyer, 2003).

The pairwise genetic distance values within Cypraeidae are shown in Figure 6. The genetic distance is 0.119–0.236. The congeneric genetic distance values fall within0.119–0.149, lower than those above genus level which are mostly higher than 0.150 (Supplementary Table S4). This result is consistent with the current division of genera within Cypraeidae. At species level, the pairwise genetic distance analysis has been proved to be useful in species identification, especially among the cases of phenotypic convergence or phenotypic plasticity (Abalde et al., 2017a,b; Yang

et al., 2018). It is necessary to include those previously identified species which were triggered by economic factors and determine their validity since many species were named subjectively.

Divergence times

The speciation events within Cypraeidae were dated from about 62.4–11.6 Mya (Figure 7), with most diversifications falling after 30 Mya. In the present study, the primitive divergence of Cypraeidae was dated to 62.4 Mya, consistent with the fossil record of earlist Indo-Pacific coweries that was dated to the Paleocene (Kay, 1990). The ancestors of Indo-Pacific cowries diversified in the ancient Tethys which connected the Mediterranean Sea and Indo-Pacific. Most speciation events derived in this study happened during this epoch. The continental drift happened about 19 Mya led to the collision of Laurasia and Gondwana and the final closure of the Eastern Tethys Seaway around 14 Mya (Okay et al., 2010). After that the faunas of the Mediterranean and the Indo-Pacific evolved separately. The major diversifications within *Naria* and *Monetaria* estimated here (18.6–11.6 Mya, Figure 7) were likely correlated with this paleogeological change, and fossil records suggested the diversifications of these species were restricted to the Indo-Pacific (Kay, 1990).

Conclusion

In this study, we present the comparative mitogenomic analysis of family Cypraeidae. All the newly sequenced mtDNA together with those published before show similar patterns in terms of genome size, nucleotide composition and gene order. The pairwise genetic distance and phylogenetic analyses indicate the validity of current classification. The present study also calls for the inclusion of complete mtDNA of cowries with morphological phenotypes, whose taxonomic status are not determined. The divergence time estimated here suggest the ancestor of Indo-Pacific cowries diversified during the Paleocene, and the closure of the Tethys Seaway might lead to the speciation events of several Indo-Pacific species.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://www.ncbi.nlm.nih.gov/genbank/, OP729418; https://www.ncbi.nlm.nih.gov/genbank/, OP734446; https://www.ncbi.nlm.nih.gov/genbank/, OP714184; https://www.ncbi.nlm.nih.gov/genbank/, OP747190; https://www.ncbi.nlm.nih.gov/genbank/, OP738004; https://www.ncbi.nlm.nih.gov/genbank/, OP723877; https://www.ncbi.nlm.nih.gov/genbank/, OP714183; https://www.ncbi.nlm.nih.gov/genbank/, OP714185; https://www.ncbi.nlm.nih.gov/genbank/, OP714186; https://www.ncbi.nlm.nih.gov/genbank/, OP738519.

Author contributions

QM: data curation, formal analysis, investigation, and writing—original draft preparation. FL: data curation, investigation, and writing—review and editing. JZ: data curation and investigation. CL: software and supervision. AW: supervision and funding acquisition. YY: data curation, formal analysis, methodology, funding acquisition, supervision, and writing—review and editing. ZG: supervision and funding acquisition. All authors contributed to the article and approved the submitted version.

Funding

This research was funded by the National Key Research and Development Program of China (2019YFD0901301), the Hainan Provincial Natural Science Foundation of China (322QN260), and Key Research and Development Project of Hainan Province (ZDYF2021SHFZ269).

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1138297/full#supplementary-material

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