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ORIGINAL ARTICLE

Phylogeny of Veneridae (Bivalvia) based on mitochondrial genomes

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Abstract
Veneridae is one of the most diverse families of bivalve molluscs. However, their phylogenetic relationships among subfamilies have been debated for years. To explore phylogenetic relationships of Veneridae, we sequenced 13 complete mitochondrial genome sequences from eight subfamilies and compared with available complete mitochondrial genome of other Veneridae taxa (18 previously reported sequences). Phylogenetic analyses using probabilistic methods recovered two highly supported clades. In addition, the protein-coding gene order revealed a highly conserved pattern among the same subclade lineages. According to our molecular analyses, Tapetinae should be recognized as a valid subfamily, but the genera formed para-polyphyletic clades. Chioninae was recovered not monophyletic that differs from a previously molecular phylogeny. Furthermore, the reconstructed chronogram calibrated with fossils recovered the Veneridae have originated during the early Permian (about 290 million years ago). Noticeably, programmed frameshift was found in the *nad4* gene of *Leukoma jedoensis*, *Anomalodiscus squamosus* and *Antigona lamellaris* and *cob* gene of *L. jedoensis*. This is the first time that the presence of the programmed frameshift has been found in the protein-coding genes of Heterodonta species. Our results improved the phylogenetic resolution within Veneridae, and a more taxonomic sampling analysis of the subfamily Chioninae is supposed to construct.

KEYWORDS
mitochondrial genomes, phylogeny, programmed frameshift, Veneridae

1 | INTRODUCTION

The Veneridae (Rafinesque, 1815), also known as venus clams, is one of the most diverse families of bivalve molluscs with more than 800 extant species (Kappner & Bieler, 2006). This family consists of 14 subfamilies (Habe, 1977; Keen, 1969) which are distributed across tropical, subtropical, temperate and polar marine ecosystems (Harte, 1998). Some members of Veneridae occupy diverse habitats including shallow sublittoral reefs, sandy bays and coarse substrates of the continental shelves, and a smaller number of species were restricted to deeper waters (Harte, 1998; Kappner & Bieler, 2006; Kondo, 1998). Studies on Veneridae have focused on diverse aspects of their biology, including fisheries (Baeta et al., 2018), aquaculture (Covernton et al., 2019; Medhioub et al., 2017), disease (Rahmani et al., 2019; Yang et al., 2017) and perhaps most prominently genetics and evolutionary biology (Kappner & Bieler, 2006; Ghiselli et al., 2012; Salvi & Mariottini, 2012; Chacón et al., 2020) due to its biological diversity and economical importance.

The current classification of Veneridae, which was largely established by Keen (1969), was divided into 12 subfamilies

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on the basis of systematically summarizing predecessors' work (Gray, 1847, 1853; Adams & Adams, 1858; Tryon, 1884; Fischer et al., 1887; Dall, 1902; Jukes-Browne, 1914; Marwick, 1927; Frizzell, 1936). Mostly following Keen's classification, Habe (1977) revised this family by dividing parts of Pitarinae into Lioconchinae and Callistinae. Different taxa in the family Veneridae were distinguished mainly based on the shell morphology (Glover & Taylor, 2010; Roopnarine & Vermeij, 2000), anatomical characteristics (Kappner & Bieler, 2006; Mikkelsen et al., 2006) and evidence of palaeontology (Case y, 1952; Gardner, 2005; Saul, 1993). Nevertheless, it is difficult to define taxa within Veneridae in some cases based on the morphological characters, which might be influenced by convergence evolution and phenotypic plasticity (Canapa et al., 1996, 2003). Therefore, the current classification system and phylogenetic relationship of Veneridae may conflict with the genetic interrelationships among the subfamily (Canapa et al., 1996; Chen et al., 2011; Harte, 1992; Keen, 1969), which has been supported by some molecular phylogenies (Canapa et al., 2003; Cheng et al., 2006; Taylor et al., 2007). Mitochondrial and nuclear fragment-based phylogenies, including the 16S rRNA (Canapa et al., 2003), the 28S rRNA and the COI (Chen et al., 2011; Kappner & Bieler, 2006), mitochondrial-nuclear combined data sets 16S + COI+28S + H3 (Mikkelsen et al., 2006) and 16S + COI+H3 (Chen et al., 2011; Kappner & Bieler, 2006), have implied that most subfamilies and many genera in Veneridae were non-monophyletic. A recent phylogenetic analysis based on the nuclear ITS2 rRNA primary sequence and secondary structure indicated Chioninae sistering to Venerinae is not monophyletic (Salvi & Mariottini, 2012). However, these results were poorly supported and often contradicted each other due to unbalanced taxon sampling.

The typical metazoan mitochondrial (mt) genome contains 37 genes: 13 protein-coding genes (PCGs), two ribosomal RNA (rRNA) and 22 transfer RNA (tRNA) genes (Boore, 1999). Due to their compact size and conserved features in their gene organization, rarity of recombination, maternal inheritance and higher mutation rate, mtDNA sequences are extensively used for comparative and evolutionary genomics and phylogenetic inference (Ballard & Whitlock, 2004; Gissi et al., 2008; Kurabayashi et al., 2008). Particularly, complete mtDNA has been proved that could be more informative at deep phylogenetic levels (Curole & Kocher, 1999; Kong et al., 2020; Li et al., 2015) and useful in recovering internal nodes with high statistical support compared with partial mt genes. Therefore, mtDNA has been widely used to reconstruct phylogenetic relationships in different bivalve groups, such as Heterodont (Ozawa et al., 2017), Pteriomorphia (Sun & Gao, 2017), Veneroida (Fernandez-Perez et al., 2017; Hwang et al., 2015) and Mytilidae (Lee et al., 2019).

In this study, we sequenced and assembled 13 mitochondrial genomes representing eight Veneridae subfamilies. Together with 18 publicly available ones, a total of 33 mitochondrial genomes (including 2 outgroup species) were used to reconstruct the phylogenetic relationships within Veneridae. Our aims were (a) to reconstruct a phylogeny of the Veneridae following assessment the monophyly of Chioninae and Venerinae; (b) to explore the genomic characteristics and evolutionary patterns of the taxa within Veneridae; and (c) to estimate the divergence time of major cladogenesis within Veneridae.

2 | MATERIALS AND METHODS

2.1 | DNA extraction, next-generation sequencing and sequence assembly

Specimens were mainly obtained from Hainan Province of China from April to June 2019 (Table 1). All tissues were preserved in ethanol and shell voucher are available from Ocean University of China in Qingdao, China. Genomic DNA from 13 Veneridae specimens was extracted from the adductor muscle using a modified phenol–chloroform procedure described by Li et al. (2002).

Genomic DNA was submitted to Novogene (Beijing, China) for library construction and high-throughput sequencing. Sequencing libraries with average insert sizes of approximately 300 bp were prepared and then sequenced as 150 bp paired-end runs on the Illumina HiSeq 4,000 platform. Finally, about 10 Gb of raw data were generated for each library. The clean data of mitochondrial genome sequences were assembled using Geneious Prime version 2020 0.3 (Hahn et al., 2013) with map to reference strategy based on the tutorial 'reconstructing mt genomes from mt barcode seeds'. The partial *cox1* sequence downloaded from NCBI was used for the barcode seed sequence. The following mapping parameters were used in Geneious: a minimum of 50 consecutive nucleotides (nt) perfectly matching the reference, a maximum 10% of single nt mismatch over the read length, a minimum of 98%nt similarity in overlap region and a maximum of 10% of gaps with a maximum gap size of 15 nt. Iterative mapping cycles were performed in order to elongate the sequence when the complete mitogenome was not recovered after the initial mapping round.

2.2 | Gene annotation and sequence analysis

All sequences for each of those mitochondrial genomes were submitted to the MITOS webserver (Bernt et al., 2013) for annotation, and the boundary of protein-coding genes (PCGs) was further determined using ORFfinder (https://www.ncbi.nlm.nih.gov/orffinder). Start and end codons of each gene were checked and edited manually. The tRNA genes were identified using ARWEN (Laslett & Canbäck, 2008), and the

TABLE 1 Complete mitochondrial genomes used for phylogenetic analysis in this study

Species	Subfamily	Location	Length (bp)	GenBank accession no.
*Gafrarium pectinatum**	Circinae	Sanya, China	21,132	MT737369
*Circe scripta**	Circinae	Sanya, China	20,182	MT737370
*Tapes belcheri**	Tapetinae	Sanya, China	18,393	MT737367
*Tapes dorsatus**	Tapetinae	Sanya, China	19,048	MT737378
*Katelysia hiantina**	Tapetinae	Sanya, China	20,924	MT737373
Paphia amabilis	Tapetinae		19,629	JF969276.1
Paphia euglypta	Tapetinae		18,643	GU269271.1
Paphia textile	Tapetinae		18,561	JF969277.1
Paphia undulata	Tapetinae		18,154	JF969278.1
Ruditapes decussatus	Tapetinae		18,995	KP089983.1
Ruditapes philippinarum	Tapetinae		22,089	KT001084.1
Macridiscus melanaegis	Tapetinae		20,738	MK394098.1
Macridiscus multifarius	Tapetinae		20,171	MK394099.1
*Callista erycina**	Calliistinae	Beihai, China	20,353	MT737374
Saxidomus purpuratus	Calliistinae		19,637	KP419933.1
*Placamen isabellina**	Chioninae	Qinzhou, China	18,602	MT737376
*Placamen foliaceum**	Chioninae	Beihai, China	17,789	MT737375
*Leukoma jedoensis**	Chioninae	Yantai, China	18,847	MT737372
*Anomalocardia producta**	Chioninae	Sanya, China	20,423	MT737371
*Anomalodiscus squamosus**	Chioninae	Sanya, China	17,699	MT737366
*Antigona lamellaris**	Venerinae	Beihai, China	18,209	MT737368
*Periglypta puerpera**	Venerinae	Beihai, China	16,855	MT737377
Dosinia altior	Dosininae		17,536	MG543473.1
Dosinia japonica	Dosininae		17,693	MF401432.1
Dosinia troscheli	Dosininae		17,229	MG543474.1
Cyclina sinensis	Cyclininae		21,799	KU097333.1
Meretrix lamarckii	Meretricinae		21,209	GU071281.1
Meretrix lusoria	Meretricinae		20,268	GQ903339.1
Meretrix lyrata	Meretricinae		21,625	NC_022924.1
Meretrix meretrix	Meretricinae		19,826	GQ463598.1
Meretrix petechialis	Meretricinae		19,567	EU145977.1

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

two rRNA genes were identified by sequence comparison with previously reported Veneridae rRNA genes. Alignment was performed with the Mauve alignment v.2.3.1 (Darling et al., 2004) in Geneious to find and visualize conserved sequence clusters of mtDNA among Veneridae species.

2.3 | PCR amplification

The *nad4* genes of *Leukoma jedoensis*, *Anomalodiscus squamosus* and *Antigona lamellaris* and *cob* gene of *L. jedoensis* were amplified using the specific primer sets (Table S1), respectively, to test whether frameshift site is a sequencing artefact. PCRs were carried out in 25 µl total volume reactions containing 12.5 µl 2 × *Taq* Plus Master Mix II (Dys plus), 1 µl of each primer (10 µM), 15 µl double distilled water and 0.5 µl of template DNA (approximately 100 ng). The thermal cycling profile was as follows: denaturation step start at 95°C for 3 min followed by 35 cycles of denaturation at 95°C for 15 s, annealing at 60°C for 20 s and elongation at 72°C for 60 s per kb, and a final extension at 72°C for 5 min. PCR products were confirmed on a 1% agarose gel

electrophoresis followed by stained with ethidium bromide to evaluate the quality of amplification products. PCR products were sent to Sangon Biotech for Sanger sequencing using an ABI 3,730 XL analyzer (Applied Biosystems) by primer walking.

2.4 | Phylogenetic analyses

We used 33 mitochondrial genome sequences (including the 13 newly sequenced species) representing eight subfamilies for phylogenetic analyses (Table 1), with *Arctica islandica* (Arcticidae) and *Calyptogena magnifica* (Vesicomyidae) as the outgroups.

Preliminary analyses using DAMBE (Xia, 2018) showed that use of DNA sequences in phylogenetic analyses was judged inappropriate given likely saturation. Since five species (*Paphia euglypta*, *Ruditapes philippinarum*, *Macridiscus melanaegis*, M*acridiscus multifarious* and *Saxidomus purpuratus*) download from GenBank had no *atp8* gene annotated, amino acid sequences for 12 protein-coding genes were concatenated, excluding *atp8*. The amino acid sequences for the 12 protein-coding genes excluding the *atp8* were aligned using MAFFT (http://mafft.cbrc.jp/alignment/server/) with default parameters, respectively. Using Gblocks v.0.91b (Cruickshank, 2000) with default settings to obtain conserved regions of the aligned amino acid sequences for each of the 12 PCGs. Each of the amino acid sequence of 12PCGs was treated as a separate partition. The best partition schemes and best-fit substitution model for the data set were identified using PartitionFinder 2.1.1 (Lanfear et al., 2017) with the Bayesian information criterion (BIC). The partitions tested were as follows: all genes grouped; all genes separated; and genes grouped by enzymatic complexes (*atp*, *cox*, *cob*, *nad*). The selected best-fit partitions and models are provided in Table S2. Phylogenetic relationships were inferred using maximum likelihood (ML) with IQ-TREE v.1.6.8 (Nguyen et al., 2015) and Bayesian inference (BI) with MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001). The ML tree was performed with 10,000 bootstrap replicates and automatic algorithm. The BI analysis was performed using four 4 parallel Markov chain Monte Carlo (MCMC) chains for 10,000,000 generations, sampling every 1,000 generations and discarding the first 2,500,000 generations as burn-in. All parameters were confirmed with Tracer v. 1.7 (Rambaut et al., 2018).

2.5 | Divergence time estimation

Divergence times among subfamilies were estimated using the amino acid sequences of 12 PCGs with a relaxed clock lognormal model in BEAST v.1.7 (Drummond et al., 2012). The model of Yule process was selected for the tree prior. For estimating divergence time calibration, two calibration points were used as priors for divergence times of the corresponding splits. Fossil ages were incorporated based on available data in the Paleobiology Database (https://paleobiodb.org/). Priors for fossil ages were drawn from uniform distributions, and the root *Dosinia* was constrained between 99.7 and 94.3 million year ago (MYA) (Perrilliat et al., 2006). And the 106.2 Ma point calibration was set as the root rate of *Paphia* based on the fossil of *Paphia peruana* (112.6–99.7 MYA) (Kummel, 1948). The final Markov chain was run twice for 100 million generations, sampling every 10,000 generations. The first 10% generations were discarded as burn-in, according to the convergence of chains checked with Tracer v. 1.7 and the ESS value of all the parameters were above 200. Maximum clade credibility tree was generated in TreeAnnotator v. 2.4.1 (part of the Beast package) and was visualized in FigTree v.1.4.3 (Rambaut, 2014).

3 | RESULTS

3.1 | General features and gene arrangements of the mitochondrial genome

The complete mitochondrial genomes of the 13 newly determined Veneridae species are all circular molecules ranging from 16,856 bp (*Periglypta puerpera*) to 21,134 bp (*Gafrarium pectinatum*) in size, which is similar to previously reported bivalve species (Table 1). The size of the control regions is highly variable, as well documented from many other metazoan taxa, contributing to the overall genome size variation (Tables S3-S15). All tRNAs could be folded into cloverleaf secondary structures.

All of the sampled genomes encode all protein-coding, rRNA and tRNA genes on the forward strand in the same orientation and are A/T rich, with a similar AT content from 65% to 72%. The nucleotide compositions were all strongly skewed away from C in favour of G (the GC-skews are from 0.304 to 0.516) and from A in favour of T (the AT skews are from −0.289 to −0.097).

Gene order of all genes and the number of tRNA genes are significantly different among Veneridae as is common in other bivalves (Lee et al., 2019; Williams et al., 2017). Gene order among the species, particularly among different subfamilies, is as variable as indicated by mtDNA alignments produced by Mauve v. 2.3.1 (Darling et al., 2004) in Geneious (Figure S1). The syntenic blocks of same subfamily species were much more similar to each other than to members among different subfamilies (Figure 1). However, protein-coding gene order was identical for species belonging to different subfamilies: Callistinae, Dosininae, Meretricinae and two species of Chioninae (*Placamen foliaceum, Placamen*

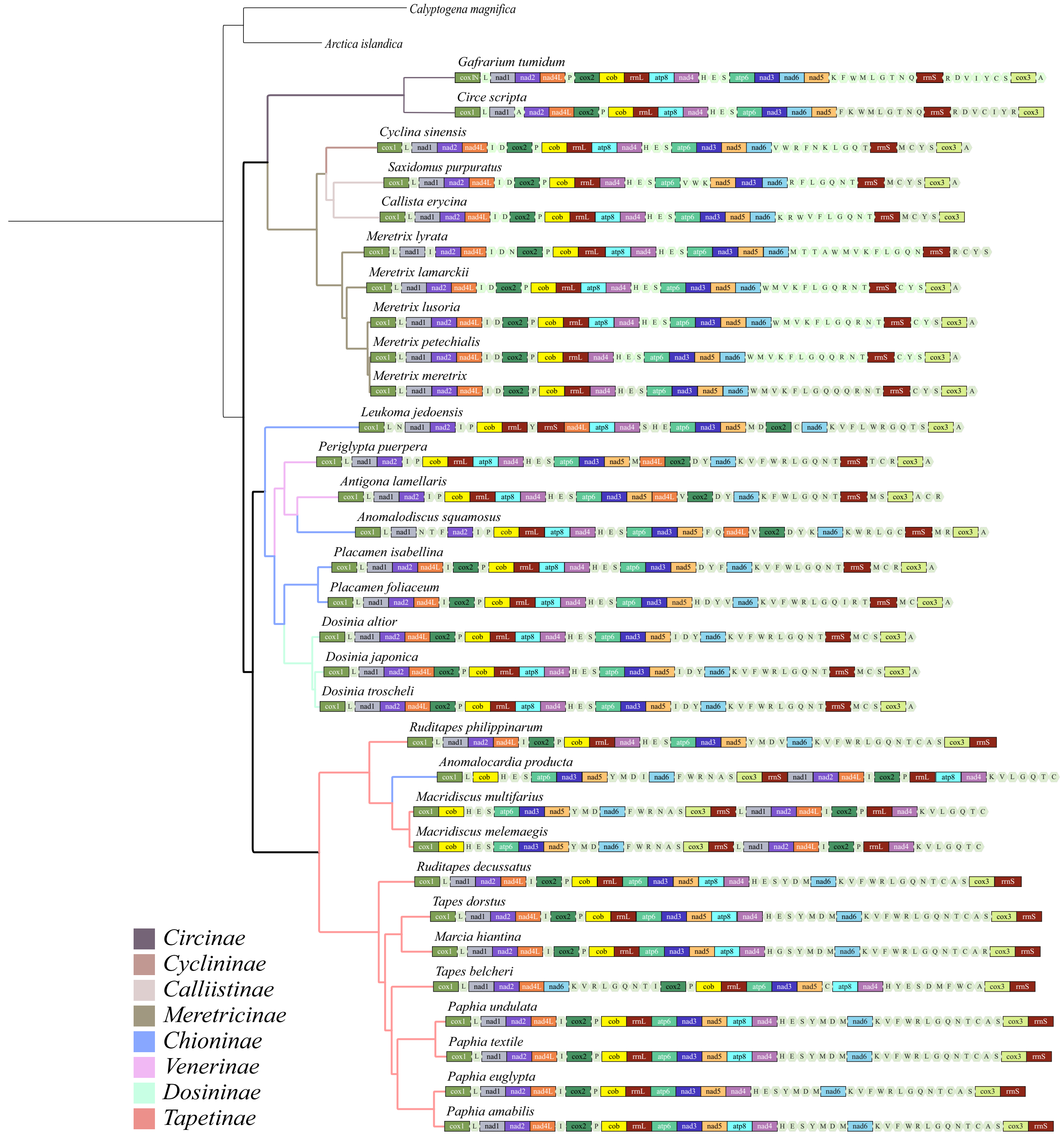

FIGURE 1 Linearized mitochondrial gene order of Veneridae species superimposed on the phylogenetic tree (see Figure 2 for detailed relationships among Veneridae species). Gene and genome size are not scaled according to length. PCGs are denoted by standard abbreviations, and tRNA genes are labelled using the single-letter codes of the encoded amino acids [Colour figure can be viewed at wileyonlinelibrary.com]

isabellina) share the same gene order for protein-coding gene. In addition to the lack of ATP8, the other protein-coding gene in *S. purpuratus* has the same order as other species in Callistinae. Although *M. melanaegis* and *M. multifarius* belong to Tapetinae, their gene order differs from *Ruditapes decussatus* which belongs to Tapetinae too. On the contrary, their gene order is the same as *Anomalocardia producta* of Chioninae. The mitochondrial genomes of *A. lamellaris, Callista erycina*, *Circe scripta*, *G. pectinatum*, *L. jedoensis*, *P. isabelline*, *Tapes belcheri* and *Tapes dorsatus* contain 13 PCGs, 2 rRNA and 22 tRNA genes. *A. producta*, *Marcia hiantina* and *P. puerpera* contain 13 PCGs, 2 rRNA and 23

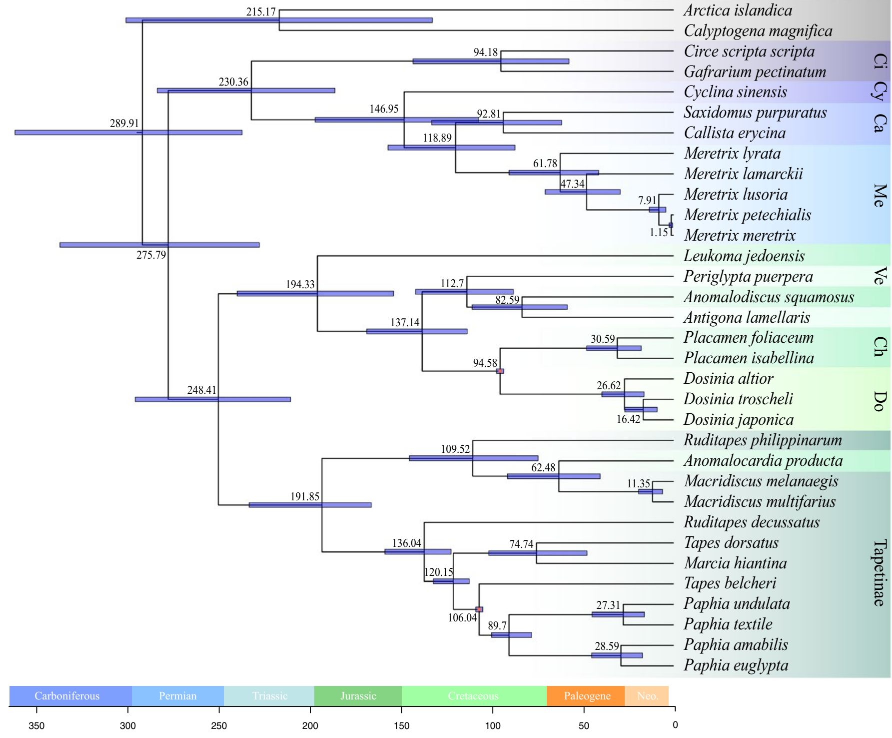

FIGURE 2 Phylogenetic trees of Veneridae derived from maximum likelihood and Bayesian inference analyses based on amid animo sequences of 12 mitochondrial protein-coding genes. Maximum likelihood bootstrap/Bayesian posterior probability are shown in the branches [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Gene of programmed frameshift in this study

	Nucleotides	Acids	Seven nucleotide sequence	Region
Leukoma jedoensis (cob)	1,198	398	TAC TAA T	463 ~ 469
Leukoma jedoensis (nad4)	1,354	450	TGG TAG T	502 ~ 508
Antigona lamellaris (nad4)	1,366	453	GAT TAG G	484 ~ 490
Anomalodiscus squamosus (nad4)	1,354	450	TGG TAG A	502 ~ 508

tRNA genes. *A. squamosus* and *P. foliaceum* contain 13 PCGs, 2 rRNA and 24 tRNA genes.

3.2 | Programmed translational frameshifting

The protein products of the *nad4* gene of *L. jedoensis*, *A. squamosus* and *A. lamellaris* and cob gene of *L. jedoensis* (Table 2) are not directly encoded in the DNA as a single ORF, but in two overlapping reading frames. That phenomenon suggests gene mentioned above contain stop codons that would result in a truncated protein if normally translated. If a + 1 frameshift occurs at the particular site, then the resulting amino acid sequence surrounding the site would show similarities to the other taxa of Veneridae and produce a functional polypeptide. In order to verify that the premature stop codons really exist in the sequence, we have sequenced additional 3 individuals of the three species respectively for the region in question. We found no deviation from the original sequence, which indicates premature termination codons in the protein-coding sequences are not sequencing artefacts.

3.3 | Phylogenetic relationships

Phylogenetic trees based on the concatenated data set of amino acid (containing 3,501 sites) inferred from 12 PCGs among Veneridae subfamilies were reconstructed using ML and BI methods. The ML phylogram and the BI consensus tree had identical topologies revealing the family Veneridae is subdivided into two clades and the overall relationships among their subfamilies.

Clade 1 (BS: 100%, PP: 1.00): Clade 1 contained four subfamilies Callistinae, Circinae, Cyclininae (represented by one taxon, *C. sinensis*) and Meretricinae. Only one subfamily (Circinae) is included within Clade 1a with a strong branch support value (100% BS, 1.00 PP). The single representative

of Cyclininae was recovered as sister to Callistinae represented by *C. erycina* and *S. purpuratus* (56% BS, 0.75 PP) and they were placed sister to Meretricinae within Clade 1b (100% BS, 1.00 PP).

Clade 2 (BS: 100%, PP: 1.00): The Chioninae taxon *L. jedoensis* occupied the basal position (BS: 99%, PP: 1.00) and a Chioninae lineage of two species was sister to *Dosinia* within Clade 1a (100% BS, 1.00 PP). *Anomalodiscus squamosus* was grouped with a Venerinae branch of *A. lamellaris* and *P. puerpera* both with high branch support values. Two subclades were in this clade having high supporting values (100% BS, 1.00 PP). The members of *Tapetine* taxa (*Macridiscus*) with one Chioninae species (*A. producta*) formed in one group (Clade 1b), with significant support (100% BS, 1.00 PP). Within Clade 1b, the taxonomic relationship of Tapetine is also very confusing: *T. belcheri* (*Tapes*) was more closely related to *Paphia* than *T. doratus*. Moreover, *T. doratus* was the sister group to the *Marcia* and *Ruditapes* with high support (100% BS, 1.00 PP). Two species of *Ruditapes*, *R. decussatus* (100% BS, 1.00 PP) and *R. philippinarum* (100% BS, 1.00 PP) were nested within different subclade.

3.4 | Divergence times

The divergence dates within Veneridae were estimated using two fossil calibration points with horizontal bars representing the 95% highest posterior density (HPD) intervals for each node (Figure 3). The resulting topology recovered the familiar relationships to topologies derived from the IQ-TREE (Figure 1) and MrBayes analyses (Figure 2) with an exception. The Cyclininae was the sister lineage to (Callistinae + Meretricinae) in the time-calibrated phylogeny with an inferred divergence time of approximately 146.95 MYA. According to the chronogram, the divergence time of the Veneridae was estimated to be approximately 289.91 MYA (Permian). The two major Veneridae clades (Clade 1 and Clade 2) were estimated to have split around 275.79 MYA (95% HPD interval 334.91–226.02 MYA) in the early Permian period. The radiation of the analysed subfamily species is estimated to have occurred from the mid-Triassic to the mid-Cretaceous (230–96 MYA).

4 | DISCUSSION

4.1 | Frameshift site and mechanism

Frameshifting exists widely in animal and viruses that occur in the course of the translation and transcription. In viruses and bacteria, frameshifting is used to expand the information content of their genomes (Brakier-Gingras et al., 2012; Chandler & Fayet, 1993). Recent results have implicated the roles of −1 programmed frameshifting in quality control of mRNA and DNA stability in eukaryotes (Belew et al., 2014). Frameshifting in *Euplotes* was expected to be harmful to high expressed genes and the phenotypic difference between gene variants with and without frameshift sites is unlikely to be high (Lobanov et al., 2017).

In this study, if translation of the sequence terminated prematurely, then sequence downstream of the termination codon would be freed from the pressure of purifying selection, and should therefore exhibit a higher frequency of non-synonymous polymorphisms and indels (Beckenbach

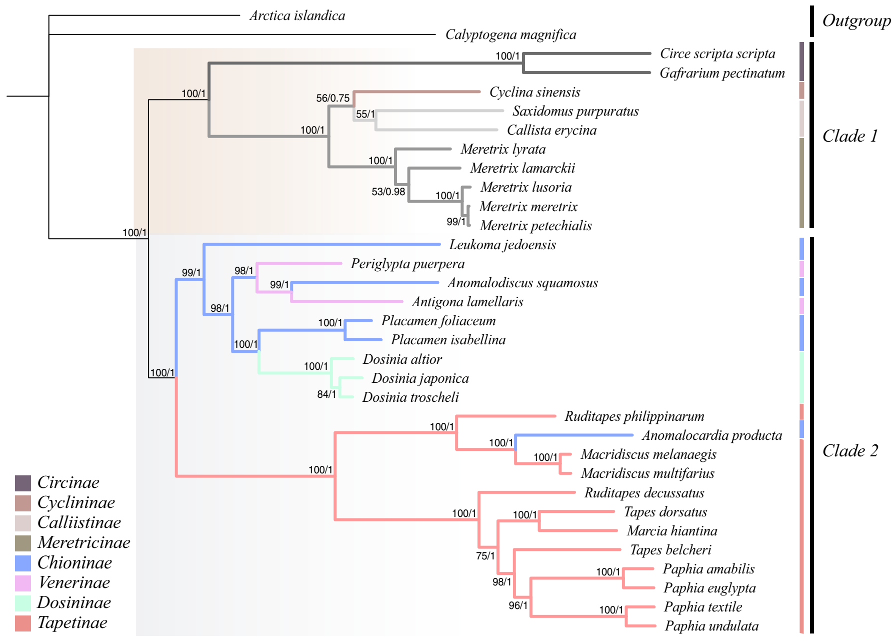

FIGURE 3 Divergence time estimation analysis of Veneridae inferred via Bayesian inference under the uncorrelated relaxed lognormal clock model. Fossil samples used to calibrate internal nodes are represented by red circle. 95% HPD is reported as blue bars, and Bayesian posterior probabilities are reported for each node [Colour figure can be viewed at wileyonlinelibrary.com]

Nad4

Species	Sequence	
Leukoma jedoensis	L F S T F N W V V I S M V S F G S D N M L L A K M S G	27
Anomalodiscus squamosus	F C P C F G N T I M Y L K G F G S D S M L L M K M V S	27
AntigonaSchumacher	F F S S V I S L L V F W G E V G T D N M L L V K M S S	27
Placamen foliaceum	S L P L L V G F L V F W S L V G S D N M L L S K M V S	27
Placamen isabellina	S L P L L V G F L V F W S L V G S D N M L L S K M V S	27
Dosinia altior	S L P L L V G M L V M S W K V G S D N M L L T K M N G	27
Dosinia japonica	S L P L L V G M L V M S W K M G S D N M L L T K M N S	27
Dosinia troscheli	S L P L L V G M L I M S W K M G S D N M L L A K M N S	27
Periglypta puerpera	S L P L L I S L L A F W W E L G S D N M L L I K M V G	27

Cob

Species	Sequence	
Leukoma jedoensis	N I I L S R N R N T N L F S A I P Y V G T T L V E W L	27
Anomalodiscus squamosus	M S F W G A T V I T N L F S A I P Y V G S D L V L W I	27
AntigonaSchumacher	M S F W G A T V I S N L F S A I P Y I G P D F V T W L	27
Placamen foliaceum	M S F W G A T V I T N L A S A I P Y V G T N L V E W L	27
Placamen isabellina	M S F W G A T V I T N L A S A I P Y V G T S L V E W L	27
Dosinia altior	M S F W G A T V I T N L F S A I P Y I G P S L V E W M	27
Dosinia japonica	M S F W G A T V I T N L F S A I P Y I G P N L V E W M	27
Dosinia troscheli	M S F W G A T V I T N L F S A I P Y I G P S L V E W M	27
Periglypta puerpera	M S F W G A T V I T N L F S A I P Y I G P D L V K W I	27

FIGURE 4 Partial nad4/cob amino acid sequences of 9 Veneridae taxa aligned to demonstrate conservation upstream and downstream of the premature termination codon (location indicated by triangle). Inferred amino sequence for gene with + 1 frameshifting is presented

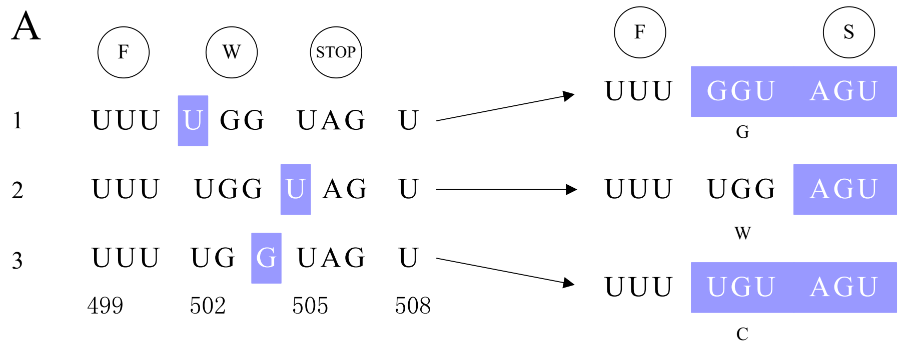

FIGURE 5 Alternative interpretations of the same frameshift event in nad4 gene of *Leukoma jedoensis*. The methods were reported by Vimaladithan and Farabaugh (1994), Russell and Beckenbach (2008), and Mindell et al. (1998) [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2005; Milbury & Gaffney, 2005; (Mindell, Sorenson, & Dimcheff, 1998). The downstream sequence in fact shows as much amino acid sequence similarity to other taxa of Venetidae as the upstream region (Figure 4). This observation suggests that the full-length protein is functional and therefore transcribed correctly despite the premature stop codon (Milbury & Gaffney, 2005). RNA editing as a possible cause could produce a full-length PCG sequence. However, Milbury and Gaffney (2005); Russell and Beckenbach (2008) have proved the mitochondrial transcripts of corresponding region all contain the extra frameshift-causing nucleotide in *Gallus gallus* and *Crassostrea virginica*, respectively. There was no evidence in the sequence traces of sequence lacking the frameshift mutation. If a + 1 frameshift occurred during translation at the site, a full-length amino acid sequence and functional polypeptide would produce, with significant homology to the sequence of other Veneridae taxa (Figure 4).

Different frameshift sites and mechanisms described in previous research (Farabaugh, 1996; Farabaugh et al., 1993; Matsufuji et al., 1995; Mindell et al., 1998; Russell & Beckenbach, 2008) have two such elements in common. The first element is a stalling in translation at the shift site, caused by the slow decoding of codon in the next 0-frame position and possibly aided by the presence of mRNA secondary structure. The second is a peptidyl-site codon that has poor wobble-position pairing with the corresponding tRNA and often good pairing with the same tRNA if shifted + 1 (Russell & Beckenbach, 2008). The frameshift sites observed in this study were suggest that occurs by occlusion of the nucleotide within seven nucleotide sequence, instead by slippage of the peptidyl-tRNA. Three possible frameshift sites could produce full-enough amino acid sequence. Taking the *nad4* gene of *L. jedoensis* as an example, the frameshift is caused by either a translational pause at a codon UUU (frame shift at position 502) or slow decoding of the TAG termination codon, allowing the + 1 frameshift to AGT (frame shift at position 505) as described by Vimaladithan and Farabaugh (1994), Russell and Beckenbach (2008). The alternative explanation of Mindell

et al. (1998) is that position 504 is ignored due to a + 1 slippage. The three possibilities affect only two codons (Figure 5).

In order to find out which of the three cases is more likely a multiple sequence alignment of the taxa within Clade1a has been created with ClustalX (Larkin et al., 2007) in MEGA7. The conservation pattern strongly favours the frameshift position at 502. The amino acid sequence around the frameshift position is nearly perfectly conserved (consensus without position 502 is FGSD) (Figure 4). The frameshift positions occur at the other species in this study also favours the same option as *L. jedoensis*. Therefore, *A. lamellaris* (nad4) occurs frameshift at position 465, *A. squamosus* (*nad4*) occurs frameshift at position 502, and *L. jedoensis* (cob) occurs frameshift at position 486 (Figure S2). The shift occurs with peptidyl-tRNA abound in the ribosomal P site during a translational pause, which may be facilitated by (a) the low availability of the cognate tRNA for the A site codon (Vimaladithan & Farabaugh, 1994), (b) the starving of cells for appropriate amino acids (Weiss et al., 1988) and (c) downstream mRNA secondary structure that impedes translation. In addition, a potential stem-loop structure at the frameshift site may promote a translational pause, allowing frameshifting (Mindell et al., 1998).

4.2 | Origin of the frameshift site

Russell and Beckenbach (2008) had highlighted that translational frameshift has been either (a) originated as a single event at common ancestor; or (b) the frameshift mutation appeared independently. Three species with frameshift site nested within the clade 2a with high support, respectively, lends credence to the possibility that the frameshift site first occurred in a common ancestor of these species and has been retained since that time. Programmed frameshifts in two genes in budding yeasts, ABP140 and EST3, where the mutations appear to trace back ~150 myr, are evidence for ancient origin (Farabaugh et al., 2006). Expanding the taxon sampling to include more data from Venerinae as well as Chioninae will further elucidate the derivation of programmed frameshift in Veneridae.

4.3 | Phylogenetic analysis

Maximum Likelihood and BI analyses of the amino acid sequence data set reconstructed the same eight lineages of Veneridae taxa and produced similar topologies (Figure 1 for ML phylogram; Figure 2 for BI) which supported by the molecular analyses of Canapa et al. (2003), Mikkelsen et al. (2006), and Chen et al. (2011), Lv et al. (2018). Mt genomes of Venetidae analysed in the present study (Figure 1) are relatively conserved in terms of gene arrangements when compared to other molluscous groups (e.g. Bivalvia; Lee et al., 2019; Gastropoda; Yang et al., 2019; and Caudofoveata; Mikkelsen et al., 2018), and this similarity in mitochondrial genome structure is additional evidence of phylogenetic relationship (Figure S1). According to present molecular analyses, Circinae, Dosiniinae, Meretricinae and Tapetinae should be recognized as valid subfamilies. However, the traditional arrangements of some taxa needed revision. Dosiniinae was sister to Chioninae within Clade 2a, which contradicts a proposed molecular phylogeny using combined data set of mitochondrial and nuclear gene sequences where Dosiniinae was placed sister to Venerinae (Chen et al., 2011). The Chioninae is not monophyletic, with the majority of the species did not cluster with the same clade, which differs from a previous morphological study that argued Chioninae was monophyletic with all taxa in the Chioninae clade showing the characteristic of fused siphons and absence of an anterior lateral tooth (Kappner & Bieler, 2006). In addition, the gene order of *A. squamosus* is substantially different from *Placamen* (Chioninae) taxa, but both mitochondrial gene order comparison and the Mauve alignment analysis showed the highest similarity between it and the two Venerinae species. Therefore, the synonymization of the two subfamilies Venerinae and Chioninae is rejected by the present molecular analyses (Coan & Scott, 1997; Coan et al., 2000). Tapetinae should be recognized as a valid subfamily owing to the well-supported monophyly of Clade 2b, but taxonomic revision should be further considered combining morphological and molecular analyses with increased taxon sampling. The same PCGs order is conserved between *A. producta* and *Macridiscus* supporting topology of phylogenetic tree. The Cyclininae linage was represented by *C. sinensis* nested within the Calliistinae both recovered in the trees and indicated by PCGs order which agrees with a recent study (Lv et al., 2018). However, we are not able to test whether Cyclininae is polyphyletic, since only one Cyclininae representative is included in this analysis. Therefore, a taxonomic revision of the Cyclininae will be necessary. Moreover, molecular phylogenetics have largely supported the relationship showing in the present study with Veneridae forming two clades suggests the characteristics used as synapomorphies for the family should be re-examined (Smedley et al., 2019).

4.4 | Divergence time estimation

Our time-calibrated phylogeny based on a relaxed molecular clock model indicated the Veneridae originated 290 MYA ago (95% highest posterior density interval [HPD] =359.45–235.49 MYA), in agreement with a previous molecular study suggested that Veneridae appeared in the Carboniferous period (around 345 MYA) (Plazzi & Passamonti, 2010). However, the result provided by our analysis is different from the origin of the Veneridae estimated in a previous analyses. Case y (1952) indicated Veneridae first appeared in the Late Jurassic period (with Eocallista as the ancestral group) based on the fossil records. This probably resulted from the confusion in

fossil record which were identified by various taxonomic approaches and influenced by different experiences and expertise (Sepkoski, 1998). Veneridae fossil record requires a complete revision based on the insight derived of our findings, especially their ascriptions to the different subfamilies.

The Veneridae have split in two major clades (Clade 1 and Clade 2) in the early Permian period with 95% highest posterior density (HPD) in present study supports a previous analysis based on the morphology of shell, which suggested Veneridae was at least diphyletic (Gardner, 2005). The high subfamily and genera diversity of Veneridae built up from the middle Jurassic period and the expansions occurred in the Cretaceous periods which is a component of the well-known Mesozoic Marine Revolution (MMR; Thayer, 1979). Few published phylogenies have estimated the divergence times of the Veneridae, and those that do have been inferred from palaeontological data of the small subset of Veneridae taxa (e.g. Alvarez, 2019; Roopnarine, 1997). In contrast, our estimation of divergence times for the Veneridae is based on a larger taxonomic sampling including eight of the twelve families. We were able to independently estimate age of the family through this sampling strategy. Phylogenetically analyses including more fossil taxa will be critical for interpreting patterns of diversification and extinction for the group.

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SUPPORTING INFORMATION

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

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