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Mitogenomic phylogeny of the Naticidae (Gastropoda: Littorinimorpha) reveals monophyly of the Polinicinae

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Abstract

The Naticidae is a species-rich family of predatory marine gastropods with substantial interspecific morphological diversity. The classification of the Naticidae has been traditionally based on morphology data, but the phylogenetic relationships within the family are debated due to conflicting molecular results, especially regarding the monophyly of subfamilies Polinicinae and Naticinae. To further resolve the phylogenetic controversies within the Naticidae, we undertake a phylogenetic approach using 14 newly sequenced complete or nearly complete (only lacking a control region) mitochondrial genomes. Both the maximum likelihood and Bayesian inference analyses supported monophyly of the Polinicinae, but paraphyly of the Naticinae due to the placement of the enigmatic genus *Notocochlis*. The ancestral character reconstruction suggests that the operculum, a character that currently defines the two subfamilies, evolved from an ancestor with a calcareous operculum in the evolutionary history of naticids. In addition, the chronogram estimates that naticids was originated in late Triassic (about 227 million years ago), consistent with previous hypotheses. Our study highlights the importance of using complete mitochondrial genomes while reconstructing phylogenetic relationships within the Naticidae. The evolution scenario of the naticid operculum contributes new insights into the classification of Naticidae.

KEYWORDS

mitochondrial genome, molecular phylogeny, Naticinae, operculum evolution, Polinicinae

1 | INTRODUCTION

With over 260 described species (Kabat, 1996), naticids (Family Naticidae, Guilding, 1834) are a group of predatory marine snails that are distributed worldwide. The species diversity of naticids is highest in tropical regions and is also plentiful in temperate, Arctic and Antarctic waters. They are found at a great variety of depths from deep water to the intertidal zone, associated with sandy substrates (Huelsken, Marek, Schreiber, Schmidt, & Hollmann, 2008). Naticids are best known for their drilling predation, preying on almost any mollusc including other naticid snails, *Conuber sordidum* was even shown to prey on the soldier crab *Mictyris longicarpus* (Cameron, 1966; Huelsken, 2011). Some species such as *Neverita didyma* are economically important shellfish along the coastal areas (Zhao, Kong, Yu, & Li, 2017).

The Naticidae belong to the superfamily Naticoidea (Caenogastropoda, Littorinimorpha) and are the only family in the Naticoidea (Bouchet et al., 2017). The isolated placement of the Naticidae was first recognized by Thiele (1929), based on cladistic analyses of conchological and anatomical data, and was later confirmed by Wenz (1941) who brought together a comprehensive taxonomy of naticids. Traditionally, the definition of naticid subfamilies

was based on shell characters and operculum material composition as originally described by Röding (1798) who placed naticids into three genera: *Sinum*, *Albula* and *Cochlis*. *Albula* corresponded to naticids with a corneous operculum and *Cochlis* corresponded to those with a calcareous operculum, which subsequently became the delimitation basis of the subfamilies Polinicinae and Naticinae, respectively. The subfamilial ranking of Naticidae was debated over the last century (Cossman, 1925; Marincovich, 1977; Marwick & Finlay, 1937; Thiele, 1929; Wenz, 1941). Disagreements were mostly based on different interpretations of morphological resemblance and anatomical characters. After reexamining the relevant type species and original descriptions, Kabat (1991) produced the first comprehensive monograph of the Naticidae classification and distinguished four subfamilies: Ampullospirinae, Naticinae, Polinicinae and Sininae. Some major changes of Naticidae classification were made by Bouchet et al. (2005) who removed the Ampullospirinae from the Naticidae and lumped the Naticinae with the Polinicinae into a single subfamily: Naticinae; three subfamilies were established: Globisininae, Naticinae and Sininae. Later, the taxonomy established by Torigoe and Inaba (2011) recognized Naticinae and Polinicinae as two distinct subfamilies and proposed a few rearrangements at the subgenus level.

More recently, attempts have been made to reconstruct the phylogeny of Naticidae using molecular data. It is interesting to note that these reconstructed phylogenies were in stark contrast with the morphology-based taxonomy, as reflected by species of different subfamilies intermingling in several taxa, which seemed to suggest the currently recognized Naticinae and Polinicinae may not be monophyletic clades (Huelsken et al., 2008, 2012; Kang, Tan, & Liu., 2018). Huelsken et al. (2008) reconstructed the phylogenetic relationship of naticid species from Giglio Island using several molecular markers, including the nuclear 18S rRNA and Histone H3 (H3), mitochondrial (mt) 16S rRNA and cytochrome oxidase I (COI). The results showed *Euspira* as a sister to *Naticarius* + *Natica*, with this lineage grouped with *Tectonatica*, and *Neverita* was recovered as the sister group of the two clades. Monophyly of the Polinicinae and the Naticinae was therefore not supported. However, possibly due to unbalanced taxon sampling, this grouping was not recovered in a subsequent analysis (Huelsken et al., 2012) based on a concatenated data set (COI, 16S, 18S, 28S, H3), which demonstrated the close affinity of *Euspira* and *Polinices* + *Mammilla*, whereas *Neverita* were recovered as a sister to the lineage that includes *Sinum*, *Euspira*, *Polinices* and *Mammilla*. The work of Kang et al. (2018) based on COI and 16S yielded contradicting results in two trees, the relationships between *Euspira*, *Mammilla* and *Polinices* were equivocal, and provided no support for subfamily monophyly. These contradicting results obscured our understanding of potential monophyly of subfamilies as well as the phylogenetic relationships within the family. Thus, important aspects of Naticidae phylogeny still remain elusive and additional phylogenetic analyses are needed towards elucidating them.

A robust molecular phylogeny could aid greatly in the understanding of evolutionary relationships of major lineages and morphological character evolution, as in this case, resolving subfamily monophyly and the phylogenetic relationships within the Naticidae. Furthermore, it could potentially provide insights into the complexity of operculum evolution and diversification, which will greatly expand our understanding of this characteristic feature of naticids. Mt genomes have been extensively used in phylogenetic analyses due to their maternal inheritance, lack of recombination and a high rate of base substitution (Brown, George, & Wilson, 1979; Gissi, Iannelli, & Pesole, 2008; Krabayashi et al., 2008). Compared to gene fragments, mt genomes contain more information and have proven useful in recovering internal nodes with high statistical support, which have been widely used to reconstruct phylogenetic relationships in different gastropod groups, including the Neritimorpha (Uribe, Colgan, Castro, Kano, & Zardoya, 2016), Conidae (Uribe, Puillandre, & Zardoya, 2017), Caenogastropoda (Osca, Templado, & Zardoya, 2015) and Pulmonates (White et al., 2011). However, complete mitochondrial genome was publicly available for only two naticid species belonging to *Naticarius* (Osca et al., 2015) and *Glossaulax* (Li, Yang, Li, & Sun, 2018).

In this study, we newly sequenced 14 complete or nearly complete (without a control region, between *trnF* and *cox3*) Naticidae mt genomes, which represent nine main lineages of the Naticidae. Our aims were as follows: (a) to reconstruct a phylogeny of the Naticidae allowing assessment of the monophyly of the naticid subfamilies Naticinae and Polinicinae; (b) to gain insight into the complexity of operculum evolution of naticids; (c) to estimate the divergence time of major cladogenetic events within the Naticidae.

2 | MATERIALS AND METHODS

2.1 | Sample collection and DNA extraction

The specimens were collected personally during field surveys. We selected eight species of Polinicinae and six species of Naticinae (see Figures S1 and S2 for pictorial documentation). The collecting site of each specimen is listed in Table 1. After collection, specimens were immediately preserved in 95% ethanol. The total genomic DNA was isolated from 5 to 10 mg of foot tissue (one specimen per species was used for DNA extraction) followed by the cetyltrimethylammonium bromide extraction method

TABLE 1 Mitochondrial (mt) genomes analysed in this study

New mt genomes Species	Family	Subfamily	Locality	GenBank Acc. No.
Neverita sp.	Naticidae	Polinicinae	Dongying, Shandong Province	MK500870
Neverita didyma[*] (Röding, 1798)	Naticidae	Polinicinae	Dalian, Liaoning Province	MK478017
Glossaulax reiniana[*] (Dunker, 1877)	Naticidae	Polinicinae	Lianyungang, Jiangsu Province	MK478019
Euspira gilva[*] (Philippi, 1851)	Naticidae	Polinicinae	Haitouzhen, Jiangsu Province	MK478016
Euspira pila (Pilsbry, 1911)	Naticidae	Polinicinae	Ganyu, Jiangsu Province	MK500869
Mammilla mammata[*] (Röding, 1798)	Naticidae	Polinicinae	Beihai, Guangxi Province	MK433194
Mammilla kurodai[*] (Taki, 1944)	Naticidae	Polinicinae	Sanniang Bay, Guangxi Province	MK433193
Polinices sagamiensis[*] (Pilsbry, 1904)	Naticidae	Polinicinae	Fangcheng Bay, Guangxi Province	MK478018
Cryptonatica janthostoma (Deshayes, 1839)	Naticidae	Naticinae	Ganyu, Jiangsu Province	MK500871
Cryptonatica andoi [*](Nomura, 1935)	Naticidae	Naticinae	Qingdao, Shandong Province	MK433195
Notocochlis gualtieriana (Récluz, 1844)	Naticidae	Naticinae	Luhuitou, Hainan Province	MK500872
Notocochlis sp.	Naticidae	Naticinae	Fangcheng Bay, Guangxi Province	MK507895
Tanea lineata (Röding, 1798)	Naticidae	Naticinae	Zhanjiang, Guangdong Province	MK507894
Paratectonatica tigrine (Röding, 1798)	Naticidae	Naticinae	Beihai, Guangxi Province	MK507893
GenBank mt genomes Species	Family	Subfamily	GeneBank Acc. No.	Reference
Naticarius hebraeus (Martyn, 1786)	Naticidae	Naticinae	KP716634	Osca et al., (2015)
Conomurex luhuanus (Linnaeus, 1758)	Strombidae	—	KY853669	Zhao, Tu, Bai, and Cui, (2017).
Strombus gigas (Linnaeus, 1758)	Strombidae	—	KM245630	Marquez et al., (2016)

Note: Complete mt genomes are indicated with an asterisk (*).

(Winnepenninckx, Backeljau, & Dewachter, 1993). RNA was removed using RNase during the extraction. One specimen per species were used for DNA extraction. Finally, the quality of the DNA was visualized on 1.0% agarose gels.

2.2 | Mitochondrial genome assemblies and annotation

The total genomic DNA was sequenced on an Illumina HiSeq X sequencer using a PE150 protocol. The raw reads were filtered using Trimomatics (Bolger, Lohse, & Usadel, 2014). Short-read DNA sequences were assembled using de novo assembly in CLC Genomics Workbench 11 (CLC Bio) and Ray (Boisvert, Laviolette, & Corbeil, 2010) with a k-mer of 31. In order to find the target mt genome, assembly results were searched against a nucleotide database constructed from the complete mitochondrial genome of *Naticarius hebraeus* (KP716634) using BLASTN (http://www.ncbi.nlm.nih.gov/BLAST) with an *e*-value cut-off of 0.01. All the newly sequenced mitochondrial genome sequences have already been deposited in GenBank, and the accession numbers are listed in Table 1.

Locations of the protein-coding genes (PCGs) were determined using the MITOS web server (Bernt et al., 2013) and Open Reading Frame Finder (https://www.ncbi.nlm.nih.gov/orffinder/). Gene boundaries were examined and subsequently adjusted manually by comparison with the sequenced naticid mt genome. The positions of tRNA genes were determined by ARWEN (Laslett & Canbäck, 2008) and DOGMA (Wyman, Jansen, & Boore, 2004) using the invertebrate mitochondrial genetic code and the default search mode. The rRNA genes were identified by their similarity of inferred sequences to the mt genome of *Na. hebraeus* (Osca et al., 2015) by BLAST search and assumed to extend to the boundaries of adjacent genes (Boore, Macey, & Medina, 2005).

2.3 | Sequence alignment and analysis

The newly sequenced complete or nearly complete mt genomes (only lacking a control region) were aligned with the available naticid mt genome in NCBI (Table 1). A total of 17 taxa were used for the phylogenetic analysis, with *Conomurex luhuanus* (KY853669) and *Strombus gigas* (KM245630) from the family Strombidae (Caenogastropoda, Stromboidea) selected as outgroups. Two data sets were constructed and analysed: one with 13 PCGs at the amino acid level, hereafter referred to as the AA data set; one with 13 PCGs at the nucleotide level, hereafter refer to as the NT data set. The nucleotide sequences and deduced amino acid sequences of 13 PCGs were aligned

separately with Clustal W (Thompson, Higgins, & Gibson, 1994) in MEGA 7 (Kumar, Stecher, & Tamura, 2016) and further verified manually. The ambiguously aligned positions were removed using Gblocks v.0.91b (Castresana, 2000) with less stringent settings. Finally, the different single alignments were concatenated using Sequence Matrix 1.7.8 (Vaidya, Lohman, & Meier, 2011). Sequences where format-converted for further analyses and saturation position exclusion using DAMBE (Xia & Xie, 2001). Pairwise genetic distances for 13 PCGs were calculated using the NT data set in MEGA 7 (Kumar et al., 2016) under the maximum composite likelihood model.

2.4 | Phylogenetic analysis

The phylogenetic analyses of the AA data set and the NT data set (without the 3rd codon of all PCGs since a high saturation were detected on this position) were conducted with maximum likelihood (ML, Felsenstein, 1981) and Bayesian inference (BI, Huelsenbeck & Ronquist, 2001). ML analyses were carried out using RAxML v. 8.2.1 (Stamatakis, 2006) with the rapid hill-climbing algorithm and 10,000 bootstraps (BP). BP values <50, between 50 and 70, and >70 were considered to indicate non-significant, moderate and high statistical support, respectively. BI analyses were performed with MrBayes v.3.1.2 (Ronquist et al., 2012), running four simultaneous Monte Carlo Markov chains for 10 million generations (sampling every 1,000 generations). The first 25% generations were discarded as burn-in to prevent sampling before reaching stationarity. Two independent BI runs were performed. Parameter convergence was achieved within 10 million generations, and the standard deviation of split frequencies was <0.01. All parameters were checked with Tracer v. 1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018). Node support was assessed based on Bayesian posterior probabilities (BPP). We consider BPP values higher than 0.95 as high statistical support. The resulting phylogenetic trees were visualized in Fig Tree v1.4.2 (Rambaut, 2014).

The best partition schemes and best-fit models of substitution for the data sets were identified using Partition Finder 2 and Partition Finder Protein 2 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) with the Bayesian Information Criterion (Schwarz, 1978). The partitions tested were as follows: all genes grouped; all genes separated (except *nad4*/*4L* and *atp6*/*8*); and genes grouped by enzymatic complexes (*nad*, *cox*, *atp*, *cob*). The selected best-fit partitions and models are provided in Tables S1 and S2.

2.5 | Divergence time estimation

Divergence times of major clades were estimated based on the AA data set in BEAST 1.7 (Drummond, Suchard, Xie, & Rambaut, 2012) using the relaxed uncorrelated lognormal clocks. For the tree prior, we used random starting trees and the Yule speciation model. The final Markov chain was run twice for 100 million generations, sampling every 10,000 generations. The first 25% of samples were discarded as burn-in, according to the convergence of chains checked with Tracer v. 1.7 (Rambaut et al., 2018), and the ESS value of all the parameters was above 200.

The posterior distribution of the estimated divergence times was obtained by setting three calibration points as priors for divergence times of the corresponding splits. All the calibration points were based on fossil records. We chose the earliest known representative for a particular clade and then calculated the mean age for the fossil. All fossil ages were set as the lower limit (minimum age) at their respective nodes to estimate the divergence time of the most recent common ancestry of their respective lineages. The first calibration point was set at the split between *Polinices* and *Mammilla*. The most ancient fossil is *Polinices concinnus* (Hall & Meek, 1856) recovered from the Cretaceous of the United States (Bergquist, 1944). The presence of this fossil suggests the ancestor diverged prior to this period. The 95% lower and upper limits were set to 99.7 and 94.3 million years ago (MYA) to represent the most recent common ancestor of this clade (normal distribution, mean: 97; *SD*: 1.3). The second calibration point was set between *Tanea* and *Naticarius*. Fossils of *Tanea lineata* (Röding, 1798) became recognized in the Paleocene of the United States (Dickerson, 1914). The 95% upper and lower limits were set to 55.8 and 66.0 MYA (normal distribution, mean: 60.9; *SD*: 3.1). For the third calibration point, the earliest fossil of *Neverita*, *Neverita potomacensis* (Govoni, 1983), was reported from the Paleocene, United States. We set the 95% lower limit to 61.7 MYA (normal distribution, mean: 63.8; *SD*: 1.1). The maximum clade credibility tree was determined and annotated in TreeAnnotator v. 2.4.1 (part of the Beast package) after removal of 10% of the trees as burn-in.

2.6 | Ancestral character state reconstruction

Ancestral character state reconstruction of the evolution of the operculum was performed using the ML approach with Mesquite v3.02 (Madison & Madison, 2015). Two character states of the operculum (corneous and calcareous) were mapped onto the completely resolved BI tree; that is, the one recovered with BI analysis based on 13 PCGs analysed on the amino acid level. We employed the Markov k-state one-parameter model (Mk1) for character evolution.

3 | RESULTS

3.1 | Mitochondrial genomes features

Within Naticidae, the mt genomes that were determined complete are indicated with an asterisk in Table 1, the nearly complete mt genomes only lacked the control region (between *trnF* and *cox3*). The newly sequenced complete or nearly complete mt genomes possessed the typical 13 PCGs, 22 tRNAs and 2 rRNAs. All of the analysed Naticidae mt genomes share the same gene arrangement (see Figure S3). The 13 PCGs, 14 tRNAs (*trnD*, *trnV*, *trnL1*, *trnL2*, *trnP*, *trnS1*, *trnS2*, *trnH*, *trnF*, *trnK*, *trnA*, *trnR*, *trnN* and *trnI*) and 2 rRNAs (*rrnL* and *rrnS*) are encoded on the major strand, while the other eight tRNAs are encoded on the minor strand. Within fifteen Naticidae mt genomes, the size of *rrnS*, flanked by genes *trnE* and *trnV*, ranges from 946 bp (*N. didyma*) to 967 bp (*Polinices sagamiensis*). The length of the *rrnL* gene, located between *trnV* and *trnL1*, varies from 1,342 (*N. didyma*) to 1,384 bp (*Mammilla mammata*).

All the PCGs of analysed mt genomes share an identical initiation codon (ATG) except *nad4* in *Notocochlis* sp. and *Na. hebraeus*, which employ the alternative initiation codon GTG; most of the genes are terminated with the full termination codons TAA and TAG, except for *nad6* in *Notocochlis* that ends with an incomplete stop codon (T). When the *nad2* genes of fifteen naticids were aligned, a deletion of three continuous nucleotides was discovered in all the sequences except for *Notocochlis*, which only led to the deletion of one amino acid and did not cause other changes in the deduced amino acid sequences.

The heatmap of pairwise genetic distances of analysed species based on 13 PCGs is provided in Figure 1. The intraspecific pairwise genetic distance of *Glossaulax reiniana* is 0.003. The close affinities of *Neverita* to *Glossaulax* and *Mammilla* to *Polinices* are indicated with genetic distances of 0.105–106 and 0.131–0.142, respectively. The distances between *Euspira gilva* and *E. pila* is 0.153, larger than the distance between the congeneric species *Notocochlis gualtieriana* and *Notocochlis* sp. (0.130). Distinct divergence between members of the Polinicinae and the Naticinae was not observed in this study. For example, the genetic distance between *N. didyma* and *Cryptonatica andoi* is 0.208, while the distance between *N. didyma* and *M. mammata* is 0.220. It is important to note that the highest genetic distance values are detected between *Notocochlis* and other analysed Naticidae genera (0.244–0.268).

3.2 | Phylogenetic relationship

The ML and BI analyses using the AA data set (containing 3,737 sites) provided identical topologies. All nodes in the BI tree were strongly supported, but some nodes in the ML tree received moderate or low statistical support (Figure 2). In terms of higher-level relationships, the monophyly of the Naticidae received maximal support. *Notocochlis* was

	Nes	*Glr*	*Ned*	*Eug*	*Eup*	*Mam*	*Mak*	*Pos*	*Cra*	*Crj*	*Nah*	*Tal*	*Pat*	*Nog*	*Nos*	*Col*	*Stg*
Nes																	
Glr	0.106																
Ned	0.047	0.105															
Eug	0.199	0.198	0.199														
Eup	0.200	0.197	0.202	0.153													
Mam	0.226	0.228	0.220	0.213	0.223												
Mak	0.218	0.218	0.214	0.203	0.214	0.103											
Pos	0.212	0.212	0.213	0.204	0.214	0.142	0.131										
Cra	0.209	0.207	0.208	0.201	0.200	0.211	0.205	0.202									
Crj	0.211	0.210	0.210	0.202	0.202	0.213	0.207	0.204	0.040								
Nah	0.204	0.206	0.200	0.195	0.204	0.203	0.194	0.197	0.172	0.175							
Tal	0.231	0.229	0.227	0.223	0.227	0.220	0.213	0.218	0.201	0.204	0.193						
Pat	0.223	0.224	0.222	0.215	0.224	0.211	0.213	0.210	0.201	0.204	0.179	0.208					
Nog	0.260	0.256	0.258	0.247	0.258	0.257	0.249	0.247	0.249	0.252	0.244	0.254	0.257				
Nos	0.268	0.263	0.264	0.250	0.265	0.263	0.254	0.254	0.253	0.254	0.253	0.260	0.256	0.130			
Col	0.346	0.339	0.347	0.341	0.348	0.348	0.340	0.335	0.339	0.339	0.333	0.338	0.339	0.358	0.356		
Stg	0.338	0.336	0.336	0.334	0.342	0.340	0.338	0.336	0.336	0.338	0.325	0.343	0.337	0.361	0.364	0.229	

FIGURE 1 Heatmap of pairwise genetic distances of 13 PCGs of *Neverita* sp.(*Nes*), *Euspira gilva* (*Eug*), *Glossaulax reiniana* (*Glr*), *Mammilla mammata* (*Mam*), *Mammilla kurodai* (*Mak*), *Neverita didyma* (*Ned*), *Cryptonatica andoi* (*Cra*), *Polinices sagamiensis* (*Pos*), *Notocochlis gualtieriana* (*Nog*), *Cryptonatica janthostoma* (*Crj*), *Euspira pila* (*Eup*), *Notocochlis* sp. (*Nos*), *Tanea lineata* (*Tal*), *Paratectonatica tigrina* (*Pat*), *Conomurex luhuanus* (*Col*), *Strombus gigas* (*Stg*), *Naticarius hebraeus* (*Nah*) [Colour figure can be viewed at wileyonlinelibrary.com]

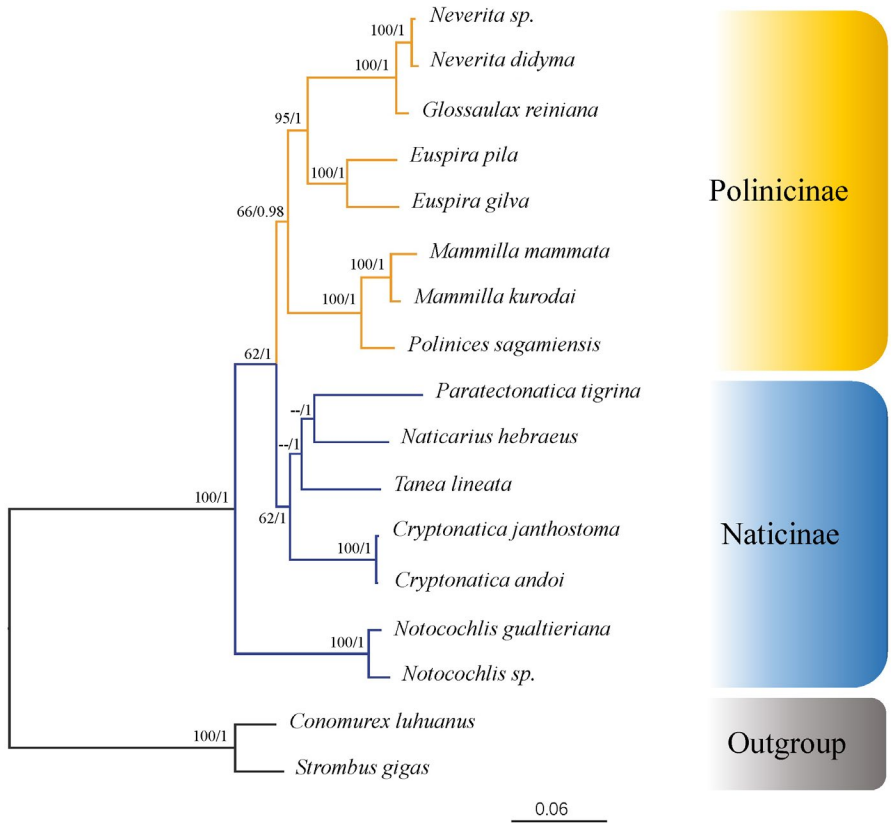


FIGURE 2 Phylogenetic relationships of Naticidae based on the AA data set. The ML phylograms are shown. The subfamily Naticinae is indicated in blue and the Polinicinae in yellow, the grey colour in the tree applies to outgroup taxa. Numbers at nodes are statistical support values for ML (bootstrap proportions in percentage)/ BI (posterior probabilities). Bayesian posterior probability values (BPP) >95% and Maximum Likelihood bootstraps (BP) >60 are shown at nodes [Colour figure can be viewed at wileyonlinelibrary.com]

recovered as a sister group of the remaining analysed genera. The sister group of *Notocochlis* was found organized into two clades. One of the clades consists of members of the Naticinae, with *Cryptonatica* being a sister group to *Nati carius* + *Paratectonatica* + Tanea. The other clade contains members of the Polinicinae, where *Neverita* + *Glossaulax* were recovered as a sister group of *Euspira*, and this clade was then clustered with *Mammilla* + *Polinices*. The reconstructed phylogeny supports monophyly of the Polinicinae, but paraphyly of the Naticinae due to the placement of the genus *Notocochlis*.

3.3 | Divergence times

The divergence times within the Naticidae were dated using an uncorrelated relaxed molecular clock model, which was calibrated based on the fossil record. Divergence times and 95% confidence intervals for each node are given in Figure 3. Our estimation shows that the origin of the Naticidae is dated at a mean of 227 MYA, although with a relatively large credible interval (95% highest posterior density: 140–360 MYA). According to the chronogram, the burst of cladogenetic events within the family Naticidae occurred successively during the Cretaceous and the early Paleogene (35–106 MYA). The branching of *Glossaulax* was dated about 82 (65–120) MYA, and the splitting off of *Euspira* is estimated to have occurred around 65 (20–130) MYA. The radiation of the analysed congeneric species (*Euspira, Neverita, Cryptonatica, Notocochlis*) is estimated to have occurred from the Paleogene to the Neogene (6–65 MYA).

3.4 | Ancestral character state reconstruction

The ancestral character state reconstruction analysis suggests that the naticids may have originated from an ancestor with a calcareous operculum (Figure 4). This analysis also suggests that only one instance of operculum modification occurred and gave rise to species that possess a corneous operculum.

4 | DISCUSSION

4.1 | Genome features

Mitochondrial genomes of gastropods usually show high rates of gene rearrangement between major lineages. However, within each major lineage, genome organizations are relatively stable, with rearrangements limited to tRNA genes (Grande, Templado, & Zardoya, 2008). The newly sequenced Naticidae mt genomes have consistent gene orders including tRNAs and conform to the consensus gene order shared by most caenogastropod mt genomes (Osca et al., 2015). All of PCGs analysed in the present study used conventional

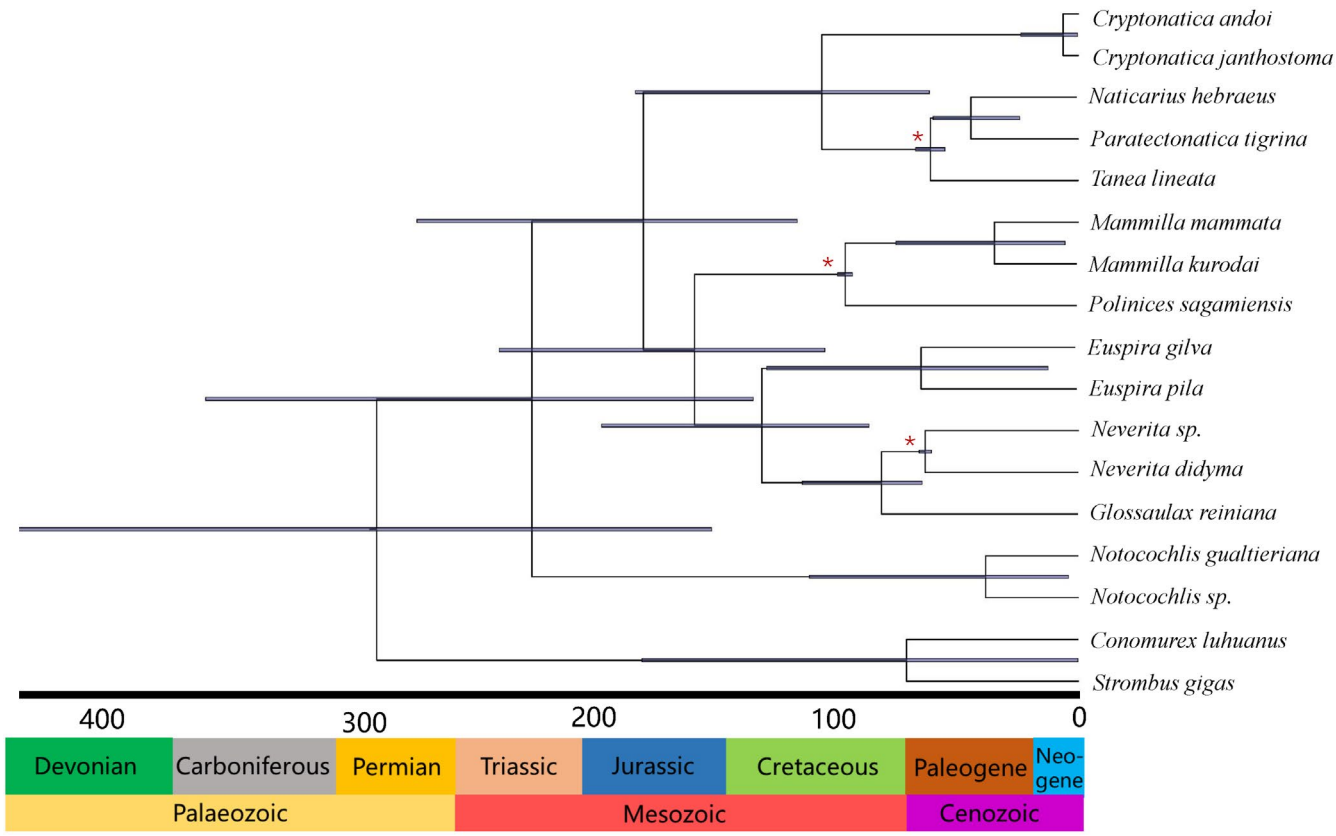
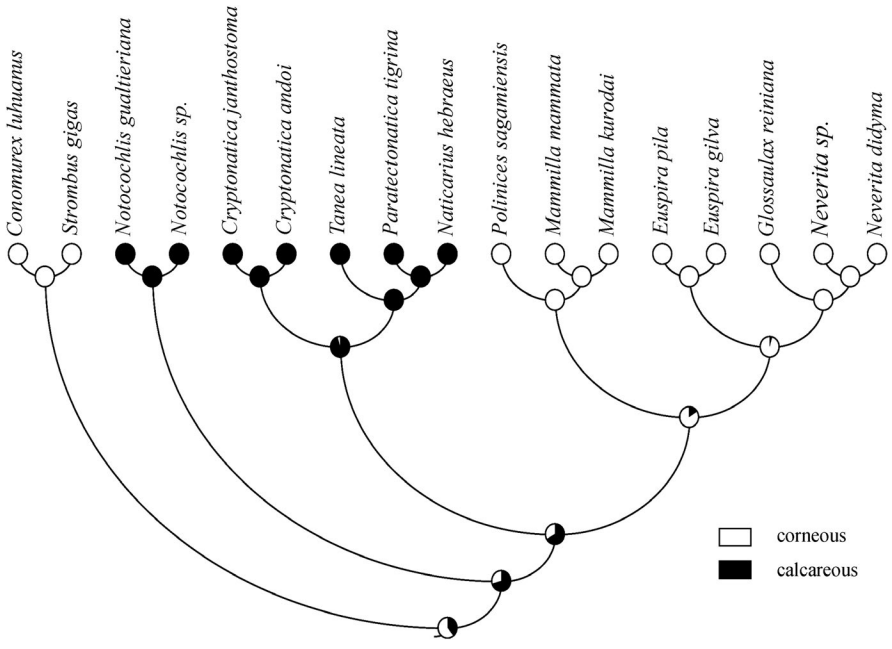


FIGURE 3 Chronogram of the Naticidae based on complete mt genomes (protein-coding genes analysed at the amino acid level). Horizontal bars represent 95% credibility intervals of time estimates. A Bayesian uncorrelated relaxed lognormal clock with three fossil-based calibration priors (indicated with an asterisk) was applied in BEAST. Dates (and credibility intervals) are in millions of years (MYA) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Ancestral character state reconstruction of naticid opercula using the maximum likelihood model Mk1 in Mesquite. Pie charts represent the degree of support at every node



initiation codons. Both ATG and GTG have been reported in many mollusc groups (Marquez, Castro, & Alzate, 2016; Osca et al., 2015; White et al., 2011; Xu, Wu, & Yu, 2012). TAA and TAG are the most common termination codons in the Naticidae, whereas the *nad6* genes of *Notocochlis* end with a single T. The incomplete stop codons presumably become functional by subsequent polyadenylation of the transcribed messenger RNAs (Lopez Sanchez et al., 2011).

The comparative mitogenomic analysis showed that the distance between *E. gilva* and *E. pila* is relatively large compared to other congeneric species, which supports the hypothesis that *E. gilva* could be a junior synonym of *Laguncula pulchella* (Benson, 1842), in which *E. gilva* and *E. pila* are probably not congeneric species, thus explaining the large distance we found in this study. The mt genomes of *Notocochlis* exhibit relatively large differences compared to the remaining members of the Naticidae, and the *nad2* deletion found in other taxa might reflect unusual constraints on the protein in these taxa (Sevigny et al., 2015; Yang, Li, Kong, & Yu, 2018). The large genetic distance between *Notocochlis* and other analysed species revealed by pairwise genetic distance analysis may provide implications for future revisions on naticid taxonomy, for instance, the paraphyly of Naticinae could be tentatively resolved by excluding the genus *Notocochlis*.

4.2 | Phylogenetic analyses

In recent years, several studies have made attempts to reconstruct the phylogeny of the Naticidae using molecular data. These reconstructed phylogenies supported some morphology-based classifications (Huelsken et al., 2012), allowing to confirm several closely related genera within Naticidae, such as *Polinices* and *Mammilla*. However, a consensus is still lacking for the phylogenetic relationships within the Naticidae, due to contradicting results in previous studies (Huelsken et al., 2008, 2012; Kang et al.., 2018). The monophyly of naticid subfamilies Polinicinae and Naticinae remained equivocal because a distinct separation between members of the subfamilies Naticinae and Polinicinae had not been observed. In the present study, a considerable amount of sequence data (mt genomes) was added, aiming to achieve further resolution of Naticidae phylogeny and resolve the remaining taxonomic controversies. A total of 15 taxa from nine representative main lineages of the Naticidae were selected. Both the ML and BI trees based on the AA data set produced the same topology (Figure 2).

The monophyly of the family Naticidae was highly supported in the reconstructed phylogeny, as were relationships among its main deep lineages. *Notocochlis* was recovered as the sister group to the remaining analysed lineages, a result which was highly supported in all molecular studies to date (Huelsken et al., 2008; Kang et al.., 2018). Our analysis further corroborates these previous findings revealed by short gene fragments. The relative phylogenetic position of the genus *Notocochlis* suggests that this group represents an early offshoot within the Naticidae. As a result of the placement of *Notocochlis*, the Naticinae were recovered as a paraphyletic group. The phylogenetic relationships among the analysed genera show some noticeable differences with respect to previous studies. Here, *Mammilla* and *Polinices* were recovered as the sister group of a clade containing *Euspira* as a sister group to *Neverita* + *Glossaulax*. Thus, the monophyly of Polinicinae was supported. This grouping received high statistical support in the BI tree but moderate support in the ML tree. In previous molecular phylogenies, *Euspira* was recovered as the sister group of *Mammilla* + *Polinices* (BI = 0.97, Huelsken et al., 2012). The work of Kang et al. (2018) showed *E. gilva* (*L. pulchella*) associated more closely with *Neverita* clade, while other *Euspira* species demonstrated a close affinity to the members of the Naticinae. The *Euspira* species used in this study did not overlap with the study of Kang et al. (2018), nor with the study of Huelsken et al., 2012. Therefore, the reason for the different placement of *Euspira* in the current study compared to previous ones is likely the analysis of different *Euspira* species. Hence, the phylogenetic position of *Euspira* requires further corroboration and awaits the inclusion of more *Euspira* lineages in future molecular phylogenies and the analysis of larger sequence data sets.

The phylogeny based on nucleotide sequences were largely unresolved (not shown), one possible reason is that after discarding the 3rd codon position, the remaining positions provide inadequate phylogenetic information and were unable to resolve the phylogenetic relationships within Naticidae. For deep-time phylogenetics, nucleotides data will bring more substitutions (synonymous and non-synonymous), leading to saturation over long periods of time (Rotastabelli, Lartillot, Philippe, & Pisani, 2013). Compare to nucleotide sequences, amino acids show a better phylogenetic information/noise ratio at deeper nodes due to lower saturation levels, thus are more suitable to reconstruct the family scale phylogeny and could improve the reliability of the phylogenetic tree. Our analysis included nine major lineages from Naticinae and Polinicinae, which allows us to reach stronger conclusions about monophyly of Naticidae subfamilies. The reconstructed phylogeny is statistically robust within the Naticidae and could serve as a framework to gain further insights into how the extraordinary taxonomic and ecological diversity of naticids evolved.

4.3 | Operculum evolution

An operculum exists in many (but not all) gastropod groups. Its primary function is to seal the aperture of the shell and provide shelter for the soft parts. It is considered as an important classification feature in gastropods (Cossman, 1903, 1906), but in many groups it has been argued that the operculum is not reliable for phylogenetic reconstruction. The Amphiboloidea was traditionally regarded as a basal pulmonate mainly because of the presence of an operculum. This hypothesis was questioned by the work of White et al. (2011) who reconstructed the molecular phylogeny of

pulmonates based on complete mt genomes. The delimitation of naticid subfamilies Naticinae and Polinicinae was based on the material composition of the operculum (Bouchet et al., 2005; Torigoe & Inaba, 2011). Thus far, however, none of the molecular phylogenies of Naticidae has shown that the Naticinae can be unequivocally separated from the Polinicinae (Huelsken et al., 2008, 2012; Kang et al., 2018). In the present study, the robust phylogenetic tree based on complete mt genomes suggested that the Polinicinae is a monophyletic group, thus providing support for the use of the material of the operculum as a delimitation criterion for the Polinicinae and the Naticinae. Understanding the evolution of naticid opercula could expand our understanding of naticid evolution and classification. Therefore, an ancestral state reconstruction was conducted in order to further explore the evolution of the operculum in naticids (Figure 4). The results showed that naticids most likely originated from ancestors with a calcareous operculum. Operculum calcification is an important phylogenetic signal. Unlike corneous opercula, calcareous opercula usually fit snugly in the aperture and provide better resistance to environmental changes and predators, thus offering some adaptive advantages (Checa & Jimenez-Jimenez, 1998). It could be argued that ecological adaption was an evolutionary process triggering the operculum calcification, thus giving rise to the naticid species with calcareous opercula.

The phylogenetic relationship recovered in this study largely agree with morphological studies. However, the observed paraphyly of the Naticinae still raises questions about the relationship between operculum evolution and naticid classification. As a result, except for the material composition, there are other details needed to be considered to evaluate the operculum evolution. The diversity of operculum morphology best illustrates the complexity of naticid operculum evolution. For instance, the calcareous operculum varies in the number of grooves on the exterior surface (Kabat, 2000). Other than that, Pastorino (2005) argued that there is variation in the extent and thickness of the calcareous deposits over the corneous layer of the operculum. For example, *Notocochlis isabelleana* (d'Orbigny, 1840) has an operculum with a thick calcareous layer covering the basal corneous layer, while *Tectonatica impervia* (Philippi, 1845) has a thinner calcareous layer that only partially covers the corneous layer. According to the basal placement of *Notocochlis* recovered in this study and the phylogeny constructed with partial genomes (Huelsken et al., 2008; Kang et al.., 2018), the calcareous layer was probably gradually reduced in the evolutionary history of naticids, and eventually gave rise to species with completely corneous opercula. However, the current study could not cover a wide range of Naticinae species to study the morphological character evolution of the operculum. In future studies, a wider sampling that includes comprehensive data of both molecular and morphological characters will aid in reaching a deeper comprehension of this character and give further insights into the classification of naticids.

4.4 | Divergence time estimation

The reconstructed time tree based on a relaxed molecular clock model dated the origin of the family Naticidae in the late Triassic (about 227 MYA), which congruent with previous theories that this group may have originated in the late Triassic (Bouchet & Warén, 1993; Wenz, 1941). However, according to fossil records, the earliest reported fossil naticid is dated to about 388.1 MYA and was placed in the genus Natica (Ochs & Wolfart, 1961). The status of these excessively early "naticids" remains doubtful because of the frequent confusion of *Natica* with *Nerita* in earlier classifications, so that these fossils may actually refer to Neritoidea or extinct Mesozoic families (Kabat, 1991).

We assumed the divergence time should predate the fossil occurrence, yet the fossil records suggest that some of these lineages (genera) may have appeared before, such as *Glossaulax* (Clark & Durham, 1946) and *Euspira* (Böhm, 1895). This probably resulted from the confusion in the fossil record due to shell morphology convergence from unrelated groups (Bandel, 1999) and would need to be confirmed with a thorough revision of the reported fossils, especially their referrals to the different families or genera. The precision of calibration points directly depends on how complete and unbiased is the fossil record is. Also, in this study, an uncorrelated relaxed molecular clock was used to infer branch lengths and nodal ages, it has been reported that studies comparing the precision of different models have produced conflicting results (Drummond, Ho, Phillips, & Rambaut, 2006; Lepage, Bryant, Philippe, & Lartillot, 2007), as a result, the observed discordance between our results and the fossil records could be due to the choice of molecular clocks.

5 | CONCLUSION

We present here the first mitogenomic phylogeny for the Naticidae, 14 complete or nearly complete mt genomes were added to the catalogue of Naticidae mt genomes and brought about a vast improvement in the number of available mt genomes for this family. We have shown, with strong support, that the Polinicinae are a monophyletic group while the Naticinae being paraphyletic. Our results provide support for the use of the material composition of the operculum in the definition of naticid subfamilies and suggest that the evolution scenario of this character is far more intricate and more details need to be taken into account to properly evaluate the evolution process. The present work emphasizes that

complete mt genomes are a very promising tool for achieving important levels of resolution within the Naticidae. The use of complete or nearly complete mitochondrial genomes increases the number of characters and thus the phylogenetic signal, providing more accurate results than analyses of one or a few mt or nuclear genes. This phylogeny provides a robust backbone to further understand the evolutionary processes and diversification of Naticidae.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

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SUPPORTING INFORMATION

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

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