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Short Communication

Evolution of mitochondrial gene arrangements in Arcidae (Bivalvia: Arcida) and their phylogenetic implications

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ABSTRACT

Arcidae is a diverse group of ark shells with over 260 described species. The phylogenetic relationships and the evolution of the mitochondrial genomes in this family were poorly understood. Comparisons of mitogenomes have been widely used to explore the phylogenetic relationship among animal taxa. We described the complete mitogenomes of *Arca navicularis*, *Scapharca gubernaculum* and one nearly complete mitogenome of *Anadara consociata*. The mitogenome of *A. navicularis* (18,103 bp) is currently the smallest known Arcidae mitogenome, while the mitogenomes of *S. gubernaculum* (45,697 bp) and *A. consociata* (44,034 bp) are relatively large. The mitochondrial gene orders of the three taxa were substantially different from each other, as well as the patterns found in other ark shells. The relationships among Arcidae species recovered from different mitochondrial characters (nucleotide sequence versus gene order) were in disagreement. The phylogeny based on nucleotide sequences did not support the monophyly of Arcidae, as *Cucullaea labiata* (Cucullaeidae) appeared as a subgroup within Arcinae, rather than sister group to the family Arcidae. In addition, we presented the first time-calibrated evolutionary tree of Arcidae based on mitochondrial DNA (mtDNA) sequences, which placed the deepest divergence within Arcidae at 342.36 million years ago (Mya), around the Carboniferous (360–300 Mya).

1. Introduction

Ark shells (family Arcidae Lamarck, 1809) are amongst the oldest bivalve lineages, reaching back to the lower Ordovician (about 450 Mya; Morton et al., 1998). The species of Arcidae are globally distributed, predominantly in the tropical shallow waters and warm temperate seas, containing approximately 260 species and 31 genera (Oliver and Holmes, 2006). Several studies have explored the phylogenetic relationships of the family Arcidae using nuclear genes (e.g. 18S rRNA, 28S rRNA, and histone H3) and mitochondrial genes (e.g. COI and 12S). (Feng et al., 2015; Combosch and Giribet, 2016). It has been suggested that the subfamily Arcinae and the genera *Arca*, *Barbatia*, *Scapharca* and *Anadara* are non-monophyletic (Feng et al., 2015). Meanwhile, the family Arcidae remained a major source of inconsistency in the current system of Arcida classification, as the families Noetiidae, Cucullaeidae, and Glycymerididae appear as subgroups within, rather than sister groups to the Arcidae (Combosch and Giribet, 2016). Phylogenetic relationships based on complete mitochondrial genomes (mitogenomes) are still limited due to the paucity of arcid data relative to other bivalve groups.

In metazoans, mitogenome is typically a circular double strand DNA molecule, encoding for 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) and two ribosomal RNA (rRNA) genes (Boore, 1999). Mitogenomes have traditionally been used for molecular evolution, phylogenetic and phylogeographic analyses with many advantages, such as lacking of extensive recombination, high nucleotide substitution rates, and high copy number (Gissi et al., 2008). Variability in mitochondrial gene arrangement, length and gene content can be informative in understanding the evolution and phylogenetic relationships among metazoans (Gissi et al., 2008). The mitochondrial gene rearrangements have been suggested as sets of phylogenetically informative characters (Akasaki et al., 2006; Gissi et al., 2008; Yuan et al., 2012; Yang et al., 2016).

Thus far, six mitogenomes of Arcidae species (*Scapharca broughtonii* [GenBank accession number, AB729113], *Scapharca kagoshimensis* [KF750628], *Tegillarca granosa* [KJ607173], *Anadara vellicata* [KP954700], *Trisidos kiyoni* [KU975161], *Potiarca pilula* [KU975162]) were available in the NCBI nucleotide database. Mitogenomes of ark shells show a high variability in the aspects of genome size, gene number, gene arrangement, strand usage for transcription, repetitive and non-coding region (Sun et al., 2016). The size of Arcoidea mitogenomes are distinct from each other, ranging from 19 to 46 kb in

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length (Sun et al., 2016). The mitogenomes of Arcidae species display a high amount of gene rearrangements and seem to be equally very different from other bivalves. Like most bivalve mitogenomes, gene rearrangement in tRNAs is very common among arcid species (Sun et al., 2016).

To further investigate the evolution of mitochondrial gene order in Arcidae and to make a comparison to the gene orders of other bivalves, it is crucial to include more mitogenomes from other arcid groups. In this study, we newly determined the complete mitogenomes of *Arca navicularis*, *Scapharca gubernaculum* and the nearly complete mitogenome of *Anadara consociata*. Together with the already available Arcidae mitogenomes, we investigated the evolution of gene order in arcids and assessed the phylogenetic informativeness of mitochondrial gene rearrangements. Moreover, we performed phylogenetic analyses to investigate the relationships within Arcidae using mitochondrial gene data. The results will increase the genetic information of Arcidae mitogenomes and improve the understanding of arcid mitogenome evolution.

2. Materials and methods

2.1. Taxon sampling

The specimen of *A. navicularis* was collected from the coastal water of Beihai, Guangxi Province, China (109°06′56.89″E, 21°29′0.68″N) on May 13, 2010. The specimen of *A. consociata* was collected from the coastal water of Zhanjiang, Guangdong Province, China (110°17′49.72″E, 21°09′10.87″N) on May 24, 2014. The specimen of *S. gubernaculum* was collected from the seafood market of Batangas City, Philippine (121°3′29.2″E, 13°45′25.96″N) on April 19, 2017, with the permission from the government. These samples were stored at −80 °C and deposited in Fisheries College, Ocean University of China. Total genomic DNA was extracted from adductor muscle following a modified phenol-chloroform method (Li et al., 2002). The extracted DNA was visualized on 1.0% agarose gels.

2.2. Next generation sequencing and sequence assembly

The mitogenome of *S. gubernaculum* was constructed by sequence assembly of DNA fragments generated using Illumina's next-generation sequencing (NGS). The paired-end library was prepared using NEBNext® Ultra™ DNA Library Prep Kit for Illumina (New England Biolabs, USA), which was sequenced on an Illumina HiSeq 2500 platform (by Tianjin Novogene Bioinformatics Technology Co., Ltd, China). Low-quality reads (Q values lower than 20) were removed using Trimmomatic v0.33 (Bolger et al., 2014). The mitochondrial genome sequences (clean data: 110,408,193,254 bp; reads: 225,789,273) were assembled using CLC Genomics Workbench v. 11.0.64 (http://www.clcbio.com/products/clcgenomics-workbench/). The mitogenome of *S. kagoshimensis* (KF750628) and *S. broughtonii* (AB729113) from the family Arcidae were used as initial reference for genome assembly.

2.3. PCR amplification and assembly

The complete mitogenomes of *A. navicularis* and the partial sequence of *A. consociata* were amplified with genome walking method and assembled as previously described in our study (Sun et al., 2016). The primer sequences were presented in Supplementary Tables 1 and 2.

2.4. Mitochondrial gene annotation

The mitochondrial protein coding genes (PCGs) were searched with ORF Finder (http://www.ncbi.nlm.nih.gov/gorf/gorf.html), which identifies much more open reading frames (ORFs) than the typical set of PCGs reported in mitogenomes. In order to reveal the mitochondrial PCGs, sequence homology analysis was carried out by aligning the obtained ORFs with those of other arcid species in the NCBI nucleotide database using BLASTx tool (http://www.ncbi.nlm.nih.gov/) with invertebrate mitochondrial genetic code. The positions of tRNA genes were determined by ARWEN (Laslett and Canbäck, 2008) using the mito/chloroplast or invertebrate genetic code and the default search mode based on their putative cloverleaf secondary structure. The rRNAs were identified by their similarity to published gene sequences using BLASTN searches (http://www.ncbi.nlm.nih.gov/BLAST/). The nucleotide composition was computed using MEGA 5.10 (Tamura et al., 2011). AT and GC skews were calculated according to the formulae, AT skew = (A − T)/(A + T) and GC skew = (G − C)/(G + C) (Perna and Kocher, 1995). The nucleotide skewnesses were calculated in Microsoft Excel.

2.5. Gene order analyses

CREx (Bernt et al., 2007) was selected to conduct pairwise comparisons of the gene order. MLGO web server (http://www.geneorder.org/server.php, Hu et al., 2014) was used to infer a phylogeny from gene order data.

2.6. Phylogenetic analyses

The species used in the phylogenetic analyses were presented in Supplementary Table 3. The phylogenetic relationships were reconstructed based on nucleotide sequences of 11 PCGs (*nad2* were omitted due to missing data for *A. consociata*). The nucleotide sequences were aligned with MAFFT version 5 (Katoh et al., 2005) using default settings. Poorly aligned positions were discarded by Gblocks (Talavera and Castresana, 2007) under default conditions. The PartitionFinder v1.1.1 (Lanfear et al., 2012) was used to determine the best partitioning schemes and substitution models in phylogenetic analyses. The data blocks were predefined by genes and codon positions for nucleotide sequences of PCGs (33 partitions, PartitionFinder). The Bayesian information criterion (BIC) and the greedy heuristic search algorithm with branch lengths estimated as “unlinked” were used to identify the best-fit partition schemes. The best-fit partitioning schemes (Supplementary Table 4) were adopted in the phylogenetic analyses.

Maximum Likelihood (ML) analysis was performed using IQ-TREE Web Server (http://iqtree.cibiv.univie.ac.at/; Trifinopoulos et al., 2016) with partition models and branches evaluated by 1000 ultrafast bootstrap replicates (Minh et al., 2013). Bayesian inference (BI) was conducted with PhyloBayes MPI (Lartillot et al., 2013). To account for the potential heterogeneity of the substitution pattern among the different regions of the mitogenome, the CAT site-heterogeneous mixture model was used (Lartillot et al., 2007). Two independent MCMC chains were run. Trace plots of MCMC runs were visually inspected in Tracer v 1.7.1 (https://github.com/beast-dev/tracer/releases/latest; accessed on 15 Mar 2020) (Rambaut et al., 2018) to assess the stationarity and appropriate burn-in, which was determined to be 10000. PhyloBayes converged well when the maxdiff value was < 0.1, rel_diff value was < 0.3 and the minimum effective sample size was greater than 50 as measured by bpcomp and tracecomp (Lartillot et al., 2013), respectively.

2.7. Estimates of divergence time among species

Divergence times of major clades were estimated in BEAST 1.8.1 (Drummond et al., 2012) using the relaxed uncorrelated lognormal clocks, random starting trees and the Yule speciation model. Posterior distributions of parameters, including the tree, were approximated by sampling from two independent MCMC analyses. Partition of data and model selection were set as before. Samples from the posterior were drawn every 1000 steps over a total of 50,000,000 steps per MCMC run, following a discarded burn-in of 50% steps. The results of the two analyses were combined and checked using Tracer v 1.7.1. Using

(A)

	Sb	Sk	Sg	Tg	Av	Pp	Ac	Tk	An
Scapharca broughtonii	1184	500	508	126	140	104	122	6	2
Scapharca kagoshimensis	500	1184	500	304	374	350	190	4	2
Scapharca gubernaculum	508	500	1184	470	464	314	160	6	0
Tegillarca granosa	126	304	470	1184	808	570	68	8	4
Anadara vellicata	140	374	464	808	1184	522	68	2	4
Potiarca pilula	104	350	314	570	522	1184	54	8	2
Anadara consociata	122	190	160	68	68	54	1184	4	4
Trisidos kiyoni	6	4	6	8	2	8	4	1184	10
Arca navicularis	2	2	0	4	4	2	4	10	1184

(B)

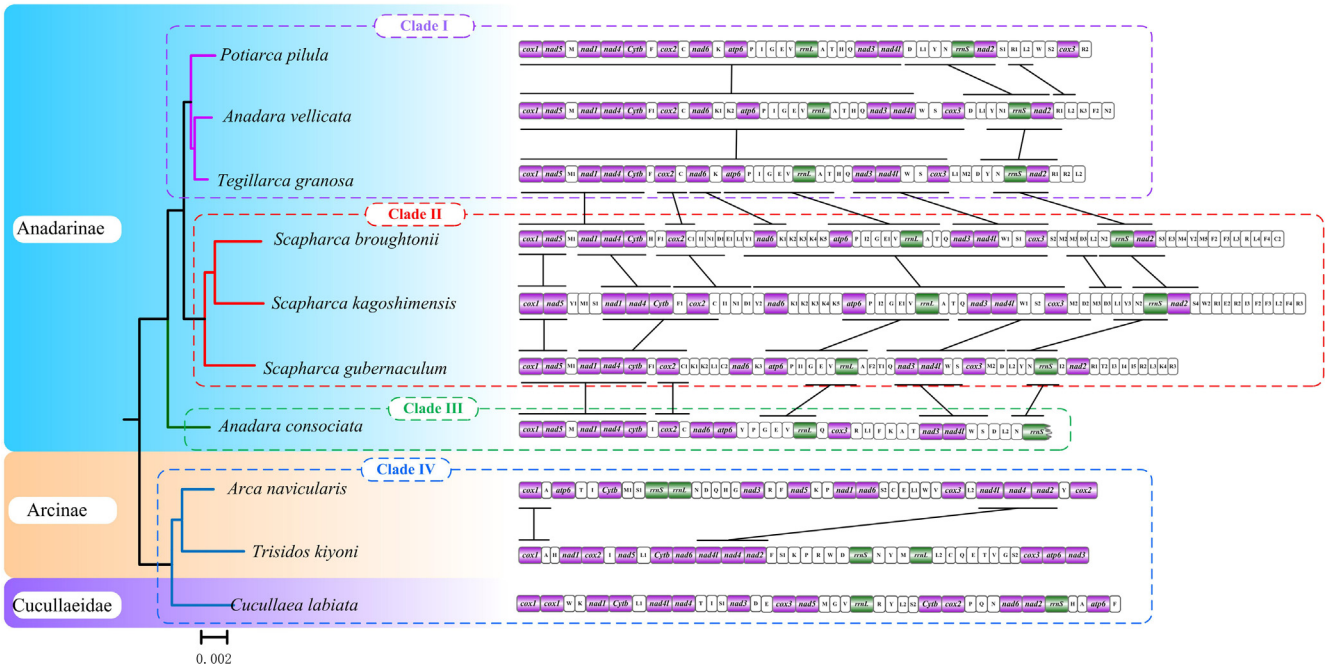

Figure 1. (A) Results of the pairwise comparisons of mitochondrial gene orders in Arcidae species obtained from CREx analysis. The numbers indicate the similarities of the compared gene orders, where 1184 is the highest number and represents identical gene order. (B) Phylogeny of the family Arcidae reconstructed using gene order data, and arrangement of mitochondrial genes in Arcidae.*Cox1* has been designated the start point for the linear representation of the gene arrangement. All genes are transcribed from left-to-right. Genes for proteins and rRNA (*rrnS* and *rrnL*) are listed under abbreviations. Transfer RNAs are represented by their one-letter amino acid code. The unassigned regions are not presented and gene segments are not drawn to scale.

TreeAnnotator (Drummond et al., 2012), the maximum-clade-credibility tree topology was identified with a burn-in of 50% and given mean node heights calculated from the posterior distribution of trees. The root age of Bivalvia was constrained between 520.5 and 530 Mya (Bieler et al., 2014). The age of Anadarinae was constrained at around 138.3 Mya, based on the geological age of *Anadara ferruginea* (Huber, 2010). Both nodes were calibrated using an exponential distribution prior, with standard deviation = 10 and 5 Mya, respectively. It has been proposed that the family Arcidae is traced back to 342.4 Mya (Combosch and Giribet, 2016), and this provided a further reference point to test against dates determined in present analysis.

3. Results and discussion

3.1. Genome organization of the newly sequenced mitochondrial genomes

The complete mitogenomes of *A. navicularis*, *S. gubernaculum*, and the nearly complete sequence of *A. consociata* were deposited in GenBank with the Accession No. MG641752, MN061840 and MG641751, respectively. The complete mitogenomes of *A. navicularis* and *S. gubernaculum* were 18,103 bp and 45,697 bp in size, respectively, and the amplified portion of *A. consociata* mitogenome was 44,034 bp (Supplementary Fig. 1, Supplementary Table 5). Therefore, the mitogenome of *A. navicularis* was the smallest among the known Arcidae mitogenomes. However, the mitogenomes of *S. gubernaculum* and *A. consociata* were relatively large, only slightly smaller than that of *S. kagoshimensis* (46,713 bp) (Sun et al., 2014) and *S. broughtonii* (46,985 bp) (Liu et al., 2013).

The complete mtDNA sequence of *A. navicularis* consisted of 12 PCGs (lacking *atp8*), 22 tRNA genes, two ribosomal RNA genes (*rrnS* and *rrnL*) and 36 non-coding regions. On the other hand, the complete mitogenome of *S. gubernaculum* contained 12 PCGs (lacking *atp8*), 34 tRNA, two rRNA genes and 44 non-coding regions. The amplified portion of *A. consociata* mitogenome contained 11 PCGs, 20 tRNA, two rRNA genes and 30 non-coding regions. All genes in these three mitogenomes are encoded on the same strand. However, their gene orders differ from those of other Arcidae mitogenomes due to the rearrangements of both PCGs and tRNAs (Supplementary Fig. 2).

The A + T content was 62.39% in *A. navicularis*, 70.11% in *S. gubernaculum* and 61.84% in *A. consociata* (Supplementary Table 6). Among the the eight Arcidae species for which mtDNA data are available, the lowest A + T content is 60.17% in *T. granosa*, while the highest A + T content is 70.11% in *S. gubernaculum*. The AT-skew and GC-skew in the plus strands were −0.23 and 0.37 in *A. navicularis*,

−0.12 and 0.37 in *S. gubernaculum*, and −0.15 and 0.46 in *A. consociata* (Supplementary Table 6). Similar patterns of nucleotide skew have been also revealed in mitogenomes of other Arcidae taxa (Sun et al., 2015a; Sun et al., 2015b; Sun et al., 2016).

Each of the three arcid mitogenomes was characterized by its large non-coding region. A total of 3206 bp were found to be interspersed throughout the *A. navicularis* mitogenome; the corresponding values were 30,673 and 30,116 bp for *S. gubernaculum* and *A. consociata*. Among the available Arcidae mitogenomes, *A. navicularis* showed the shortest non-coding regions. The non-coding regions of *S. gubernaculum* and *A. consociata* were only slightly shorter than that of *S. kagoshimensis* and *S. broughtonii*. The size of the non-coding regions is highly variable, contributing to the overall mitogenome size variation.

3.2. Mitochondrial gene rearrangements and phylogenetic implication

The gene orders of Arcidae mitogenomes differed significantly from each other (Fig. 2). In the subfamily Anadarinae, most of the rearranged genes were tRNAs. The rearrangement of PCGs were only found in *P. pilula* mitogenome, in which the *cox3* gene transferred to the downstream of the *nad2* from the original region of *cox3-rrnS-nad2*, forming a new gene arrangement pattern. If the tRNA genes were considered, the gene order of *S. gubernaculum* was more similar to the patterns of *S. broughtonii* and *S. kagoshimensis* (Fig. 1A). They shared five identical gene blocks: *cox1-nad5*, *nad1-nad4-cytb*, *trnF-cox2-trnC*, *atp6-trnP-trnI-trnG-trnE-trnV-rrnL-trnA*, and *trnQ-nad3-nad4l-trnW-trnS-cox3* (Fig. 1B). The highest similarities were found among *P. pilula*, *A. vellicata* and *T. granosa* (Fig. 1A). A large block, *cox1-nad5-trnM-nad1-nad4-Cytb-trnF-cox-trnC-nad6-trnK-atp6-trnP-trnI-trnG-trnE-trnV-rrnL-trnA-trnT-trnH-trnQ-nad3-nad4l*, and a small block, *trnY-trnN-rrnS-nad2,* were shared, (Fig. 1B). The gene order of *A. consociata* showed more similarity with the *Scapharca* clade. In the Arcinae, gene rearrangements were more extensive, with all tRNAs, two rRNAs and 12 PCGs rearranged and only two gene blocks, *cox1-trnA* and *nad4l-nad4-nad2*, were shared by *T. kiyoni* and *A. navicularis* (Fig. 1B).

Comparative analysis of mitochondrial gene order has been proved to be a valuable phylogenetic tool the study of molluscs evolution. Akasaki et al. (2006) examined the mitochondrial gene arrangements of subclass Coleoidea, and claimed that Octopoda showed the ancestral gene order, and the gene arrangements of Oegopsida and Sepiida were derived from those of Octopoda. Based on the gene rearrangements and phylogenetic relationships of five Tellinoidea species, Yuan et al. (2012) suggested that the genus *Sinonovacula* should taxonomically be placed within the superfamily Solenoidea instead of Tellinoidea. In this study, we reconstructed the phylogenetic tree of Arcidae based on the gene order data (Fig. 1B). In the Anadarinae, *P. pilula*, *A. vellicata* and *T. granosa* were clustered together in the gene order tree (Clade I). *S. gubernaculum*, *S. broughtonii* and *S. kagoshimensis* formed a sister clade (Clade II). *A. consociata* (Clade III) was clustered with Clade I and Clade II. In the Arcinae, *A. navicularis* was supported as the sister to *T. kiyoni*. *Cucullaea labiata*, the only extant species from the family Cucullaeidae, was supported as the sister species to *A. navicularis/T. kiyoni* (Clade IV).

3.3. Phylogenetic relationships and divergence time estimation of Arcidae

ML and BI based on nucleotide sequences were performed to reconstruct phylogenetic relationships (Fig. 2A). Seven species belonging to subfamily Anadarinae, including *S. gubernaculum*, *S. broughtonii*, *S. kagoshimensis*, *T. granosa*, *A. vellicata*, *P. pilula* and *A. consociata* were clustered together, supporting the monophyly of subfamily Anadarinae. It should be noted that *A. consociata* was placed in a branch as a sister group to *T. granosa*, instead of *A. vellicata*. In the subfamily Arcinae, *T. kiyonoi* showed the closest relationship with *C. labiata*, and then clustered together with *A. navicularis*. These results supported the viewpoints of Feng et al. (2015) and Combosch and Giribet (2016) that the family Cucullaeidae appeared as subgroup within, rather than a sister group to the Arcidae. These results are also consistent with morphology, because the massive myophoric flanges that distinguished cucullaeids were also found in *B. glomerula*, *A. tetragona*, and *A. boucardi* (Oliver and Holmes, 2006). The relationships revealed by mtDNA sequences disagreed with that based on gene order. This difference may not be unexpected, because gene rearrangement in tRNAs is very common, and is not phylogenetically informative in Arcidae group, being their position is too mobile (Blanchette et al., 1999; Bernt et al., 2013).

Divergence time estimates were given in Fig. 2B. The subfamilies Arcinae and Anadarinae diverged about 342.52 million years ago (Mya) with a 95% highest posterior density intervals (HPD) of 341.16–345.21 Mya, around the Carboniferous (360–300 Mya). This age is consistent with the divergence time of Arcidae estimated in a previous study (342.4 Mya; Combosch and Giribet, 2016). According to the fossil record, the Arcidae occurred in the Jurassic (Oliver and Holmes, 2006). However, in our study, this lineage possibly originated earlier, around the Carboniferous (360–300 Mya). The Arcinae species started their divergence about 282.35 Mya (95% HPD: 217.76–328.03). The Anadarinae clade diverged 138.98 Mya (95% HPD: 130.75–150.02). These estimates indicate that, *A. navicularis* with the smallest mitogenome size originated earlier (282 Mya), while the divergence of the Arcidae species with extra large mitogenome size (> 40 kb), e.g. *A. consociata*, *S. kagoshimensis* and *S. broughtonii*, is rather recent (20–68 Mya).

The fossil records showed that Cucullaeidae was contemporary with the Arcidae, both of which had their origins in the Jurassic (Oliver and Holmes, 2006). However, based on our time-calibrated phylogeny, the Cucullaeidae was younger than Arcidae. The discrepancies between molecular estimates and fossil record seemed not uncommon. In many cases, molecular clock estimation give much older divergence dates than would be expected from the fossil record (Park et al., 2012; Reis, et al., 2014), which is the most common problem of establishing accurate origin time of extant clades. The fossil record provides a definitive date by which individual lineage must have arisen, but this was not necessarily when they arose, thus it was not surprising that the fossil record indicates significantly younger ages of origination (Smith and Peterson, 2002). Another common source for discrepancies is under-representation of extant taxa. For example, Cucullaeidae was represented by only one extant species, although it has a long fossil record. Consequently, this family was biased to appear much later in our dated phylogeny than they are in the fossil record (Combosch and Giribet, 2016). A third source of discrepancies between molecular approaches and fossil record lies in the difficulty to calibrate molecular clocks. The molecular evolution rates may vary across lineages. This rate heterogeneity is an obstacle to accurate estimation of divergence times from molecular data. For example, a rate calculated for one lineage may significantly underestimate divergence times on another lineage if molecular evolution is slower there, or overestimate it if the rate is faster (Smith and Peterson, 2002).

The divergence time estimates indicated the diversification time of the Anadarinae clade to be 138.98 Mya (95% HPD: 130.75–150.02). This result supports a previous study, which showed that Anadarinae was a major driver of the observed increase in Arcidae diversification during the Cretaceous (Combosch and Giribet, 2016). The Cretaceous (145–65 Mya) is widely regarded as a period of major faunal reorganization. In the marine ecosystem, this period has been described as Mesozoic Marine Revolution (Vermeij, 1977) and the predation intensity has increased substantially since the Middle Mesozoic (Vermeij, 1977). During the Cretaceous, the predator-prey arm race between new durophagous predators (e.g., teleost fishes, stomatopods, and decapod crustaceans) and corresponding prey adaptations (e.g., thicker exoskeletons of calcium phosphate and calcium carbonate in bivalves and gastropods; Vermeij, 1987) became increasingly aggressive. Bivalves adapted to this transition by growing thicker shells and adopting infaunal habitats (Vermeij, 1977). This feature was common in arcids, especially Anadarinae. The Cretaceous was also considered as a

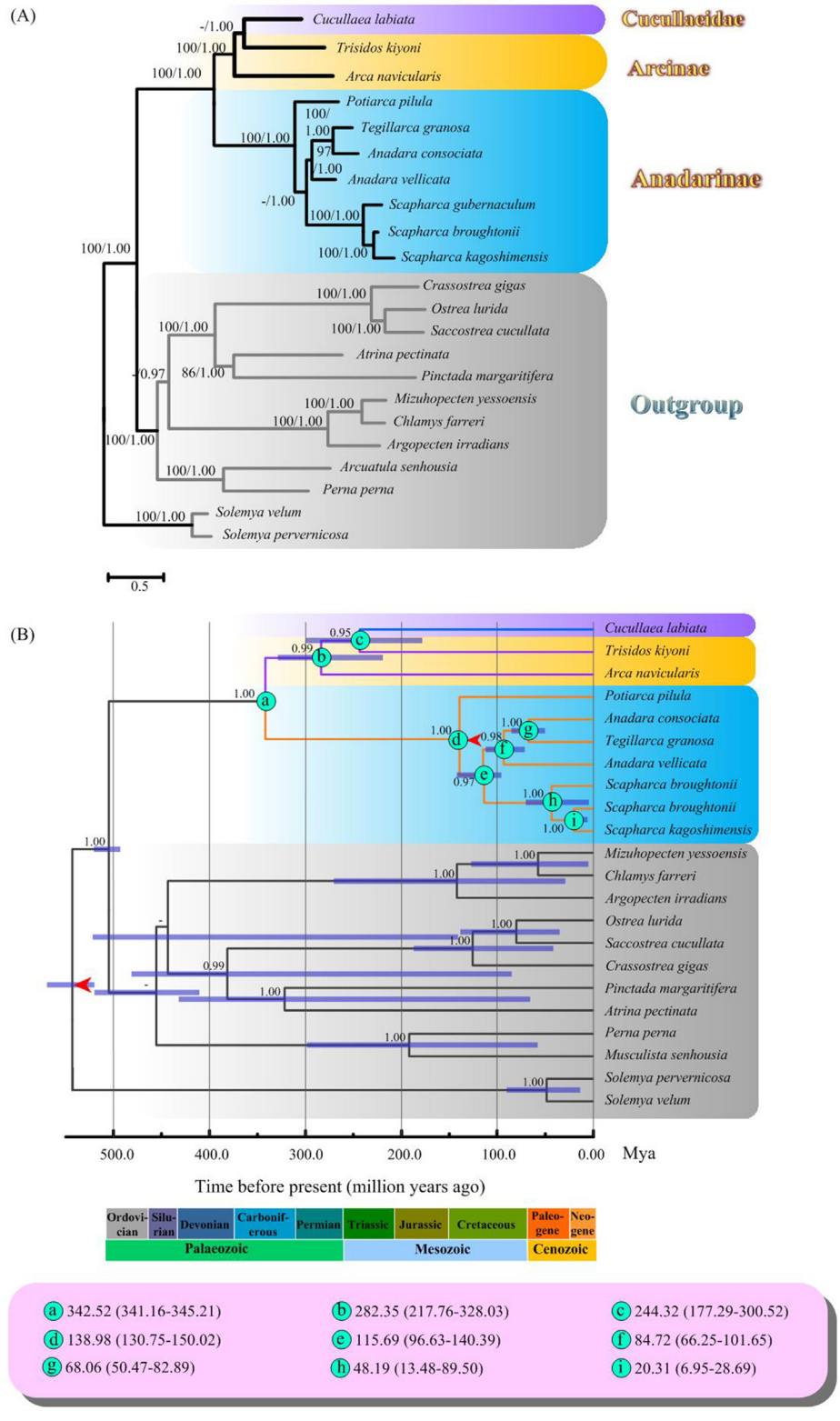

Figure 2. (A) Phylogenetic relationships derived from Maximum likelihood (ML) and Bayesian Inference (BI) based on nucleotide sequences. Numbers in the nodes correspond to ML bootstrap proportions and BI. Dashes ("-") indicate a bootstrap support < 85 and posterior probabilities < 0.95. (B) Evolutionary time tree of Arcidae inferred from Bayesian inference analyses with BEAST. Blue bars indicate 95% highest posterior density intervals (HPD) for nodes of interest. Numbers in the nodes correspond to posterior probabilities for nodes. Dashes indicate the posterior probabilities < 0.95. The notes under the figure indicates median ages and 95% HPD for nodes of interest. Colors correspond to the currently accepted family/subfamilies. Calibrated nodes are indicated by arrows. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

greenhouse period with warm and constant climates, and consistently increased sea level, which led to the inundation of continental shelves, opening of seaways, and reunion of marginal seas, providing new habitats for shallow water marine taxa like arcids (Combosch and Giribet, 2016; Vermeij, 1977).

CRediT authorship contribution statement

Shao'e Sun: Conceptualization, Conceptualization, Formal analysis, Writing - original draft. **Qi Li:** Funding acquisition, Supervision, Resources, Writing - review & editing. **Lingfeng Kong:** Supervision, Resources, Writing - review & editing. **Hong Yu:** Supervision, Resources, Writing - review & editing.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106879.

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