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Molecular phylogeny of Arcoidea with emphasis on Arcidae species (Bivalvia: Pteriomorphia) along the coast of China: Challenges to current classification of arcoids

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ABSTRACT

The current classifications of arcoids are based on phenetic similarity, which display considerable convergence in several shell and anatomical characters, challenging phylogenetic analysis. Independent molecular analysis of DNA sequences is often necessary for accurate taxonomic assignments of arcoids, especially when morphological characters are equivocal. Here we present molecular evidence of the phylogenetic relationships among arcoid species based on Bayesian inference and Maximum Likelihood analyses of three nuclear genes (18S rRNA, 28S rRNA, and histone H3) and two mitochondrial genes (COI and 12S). Tree topologies are discussed by considering traditional arrangements of taxonomic units and previous molecular studies. The results confirm the monophyly of the order Arcoidea, the family Noetiidae, and the subfamilies Anadarinae and Striarcinae, with support for the inclusion of the Glycymerididae in the Arcoidea. The subfamily Arcinae and the genera *Arca*, *Barbatia*, *Scapharca*, *Anadara*, and *Glycymeris* are non-monophyletic, suggesting that taxonomic issues still remain. The families Noetiidae, Cucullaeidae, and Glycymerididae appear as subgroups within, rather than sister groups to, the Arcidae. This study strongly suggests the need to carry out a taxonomic revision of the Arcoidea, especially the Arcidae, through combined analysis of morphological, paleontological, and molecular data.

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1.1 Introduction

Arcoid bivalves (Bivalvia: Pteriomorphia: Arcoidea) are abundant and diverse in modern seawater across all latitudes and depths, ranging from the low water mark up to 5000 m offshore. Living and extinct arcoids are (or were) epibyssate endobyssate, or shallow burrowers with a wide range of shell forms, which reflect adaptations to their life habits (Thomas, 1978).

Primitive arcoid bivalves have a long geological history stemming from the early Paleozoic era (Waller, 1978). Phenetic characters form a basis for the present classification of arcoids and it remains so for the analysis of extensive fossil records (Oliver and Holmes, 2006). Extant arcoid bivalves comprise two superfamilies, Arcoidea and Limopsoidea. The former superfamily contains five families: Arcidae, Noetiidae, Parallelodontidae, Cucullaeidae, and Glycymerididae; the latter superfamily embraces two families, Limopsidae and Philobryidae. There are a number of conflicting classifications at the superfamily level, especially with respect to

the position of the family Glycymerididae (Oliver and Holmes, 2006).

Different classification systems of the most diverse family being Arcidae are proposed on the basis of shell characters. Because most taxonomic studies are limited to a certain region, one is forced to select those aspects of each system to best fit local fauna until a consensus is reached (Kilburn, 1983). Arcidae species are divided into two subfamilies, Arcinae and Anadarinae, based on the strength of the byssus in the attached or free-living forms (Newell, 1969). This split corresponds to separate adaptive radiations, one epibyssate and one endobyssate (Oliver and Holmes, 2006). The generic and subgeneric divisions of the subfamily are inconsistent between authors because of different interpretations of such important morphological features as shell sculpture and inaequivalve or equivalve state.

The taxonomic status of noetid species is varying. Stewart (1930) first defined the noetiids to the subfamily Noetiinae in the family Glycymeridae, whereas Reinhart (1935), Bouchet et al. (2010) and Carter et al. (2011) later placed the Noetiinae into the Arcidae. Additionally, Frizzell (1946) and Newell (1969) gave the noetiids family rank and retained it in the Arcoidea, which is the

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Fig. 1 (continued)

List of taxa with the classification, source/locality data and GenBank accession numbers. Accession numbers in bold were previously published (Marko, 2002; Matsumoto, 2003)

Classification	Species	Authority	Museum voucher no.	Source/locality	GenBank accession no.				
					COI	12S	H3	28S	18S
	<i>domingensis</i>								
	<i>Barbatia plicata</i>	(Dillwyn, 1817)	–	–	–	–	AF416856	–	–
	<i>Barbatia gradata</i>	(Broderip and Sowerby, 1829)	–	–	–	–	AF416857	–	–
	<i>Arca navicularis</i> 1	(Bruguière, 1792)	LSGB4061401	Weizhou, Guangxi	HQ258822	JN974669	–	–	JN974517
	<i>Arca navicularis</i> 2	(Bruguière, 1792)	LSGB4061402	Beihai, Guangxi	HQ258824	JN974670	JN974618	JN974567	JN974518
	<i>Barbatia virescens</i> 1	(Reeve, 1844)	LSGB4061801	Shengsi, Zhejiang	HQ258840	JN974676	JN974624	JN974573	JN974524
	<i>Barbatia virescens</i> 2	(Reeve, 1844)	LSGB4061802	Xiapu, Fujian	HQ258840	JN974677	JN974625	JN974574	JN974525
	<i>Trisidos kiyonoi</i> 1	(Kuroda, 1930)	LSGB4062201	Wenchang, Hainan	HQ258842	JN974674	JN974622	JN974571	JN974522
	<i>Trisidos kiyonoi</i> 2	(Kuroda, 1930)	LSGB4062202	Beihai, Guangxi	HQ258843	JN974675	JN974623	JN974572	JN974523
	<i>Arca avellana</i> 1	(Lamarck, 1819)	LSGB4061501	Fangchenggang, Guangxi	–	JN974680	JN974627	JN974576	JN974527
	<i>Arca avellana</i> 2	(Lamarck, 1819)	LSGB4061502	Fangchenggang, Guangxi	–	JN974681	JN974628	–	JN974528
	<i>Arca boucardi</i> 1	(Jousseume, 1894)	LSGB4061701	Rizhao, Shandong	–	JN974682	JN974629	JN974577	JN974529
	<i>Arca boucardi</i> 2	(Jousseume, 1894)	LSGB4061702	Nanji, Zhejiang	–	–	JN974630	–	–
	<i>Arca ventricosa</i>	(Lamarck, 1819)	–	–	AB076935	–	–	–	–
	<i>Arca</i> sp.2	–	LSGB4061601	Nanji, Zhejiang	–	–	JN974631	–	–
	<i>Arca imbricata</i>	(Bruguière, 1789)	–	–	–	–	AF416851	–	–
	<i>Arca mutabilis</i>	(Sowerby, 1833)	–	–	–	–	AF416852	–	–
	<i>Arca pacifica</i>	(Sowerby, 1833)	–	–	–	–	AF416853	–	–
	<i>Arca zebra</i>	(Swainson, 1833)	–	–	–	–	AF416864	–	–
	<i>Barbatia fusca</i> 1	(Bruguière, 1789)	LSGB4061901	Lingao, Hainan	–	JN974678	JN974626	JN974575	JN974526
	<i>Barbatia fusca</i> 2	(Bruguière, 1789)	LSGB4061902	Weizhou, Guangxi	–	JN974679	–	–	–
	<i>Nipponarca bistrigata</i>	(Dunker, 1866)	–	–	AB076936	–	–	–	–
	<i>Bentharca</i> sp.	–	–	–	AB076938	–	–	–	–
Noetiidae									
Striacinae									
	<i>Arcopsis interplicata</i> 1	(Grabau and King, 1928)	LSGB4090201	Rizhao, Shandong	HQ258875	JN974672	JN974620	JN974569	JN974520
	<i>Arcopsis interplicata</i> 2	(Grabau and King, 1928)	LSGB4090202	Rizhao, Shandong	HQ258876	JN974673	JN974621	JN974570	JN974521
	<i>Arcopsis</i> sp.	–	LSGB4090301	Fangchenggang, Guangxi	HQ258872	JN974671	JN974619	JN974568	JN974519
	<i>Arcopsis adamsi</i>	(Dall, 1886)	–	–	–	–	AF416861	–	–
	<i>Arcopsis solida</i>	(Sowerby, 1833)	–	–	–	–	AF416862	–	–
	<i>Didimacar tenebrica</i> 1	(Reeve, 1844)	LSGB4090101	Fangchenggang, Guangxi	HQ258870	–	JN974616	–	JN974515
	<i>Didimacar tenebrica</i> 2	(Reeve, 1844)	LSGB4090102	Nanji, Zhejiang	HQ258871	JN974668	JN974617	JN974566	JN974516
Noetiinae									
	<i>Noetia olssoni</i>	(Sheldon and Maury, 1922)	–	–	–	–	AF416859	–	–
	<i>Noetia ponderosa</i>	(Say, 1822)	–	–	–	–	AF416860	–	–
Cucullaeidae									
	<i>Cucullaea labiata</i>	(Lightfoot, 1786)	–	–	AB050892	–	–	–	–
	<i>Cucullaea labiata</i> 1	(Lightfoot, 1786)	LSGB4080101	Beihai, Guangxi	HQ258880	JN974666	JN974614	JN974564	JN974513
	<i>Cucullaea labiata</i> 2	(Lightfoot, 1786)	LSGB4080102	Lingshui, Hainan	HQ258880	JN974667	JN974615	JN974565	JN974514
Glycymerididae									
Glycymeridinae									
	<i>Glycymeris reevei</i>	(Mayer, 1868)	–	–	AB076933	–	–	–	–
	<i>Glycymeris rotunda</i>	(Dunker, 1882)	–	–	AB076934	–	–	–	–
	<i>Glycymeris</i> sp.1	–	LSGB4110101	Beihai, Guangxi	HQ258873	–	JN974632	JN974578	JN974530
	<i>Glycymeris</i> sp.2	–	LSGB4110102	Beihai, Guangxi	HQ258874	–	–	JN974579	JN974531
	<i>Glycymeris</i> sp.	–	–	–	–	–	AF416863	–	–
Limopsidae									
	<i>Empleconia cumingii</i>	(Adams, 1863)	–	–	AB076930	–	–	–	–
Philobryidae									
	<i>Cosa waikikia</i>	(Dall, Bartsch, and Rehder, 1939)	–	–	AB084107	–	–	–	–
Outgroup									
	<i>Mimachlamys nobilis</i>	(Reeve, 1852)	LSGB4180201	Sanya, Hainan	JN974583	JN974684	JN974635	JN974581	JN974533
	<i>Pinctada martensii</i>	(Dunker, 1873)	LSGB4140101	Beihai, Guangxi	JN974582	JN974683	JN974634	JN974580	JN974532

were estimated using the heuristic search algorithm of the best-fit models with four substitution rate categories. Support for nodes was assessed by analyses of 1000 bootstrap replicates.

3. Results

3.1. DNA sequence variation

Sequences were not obtained from all the five genes for ingroup specimens. The COI and H3 alignments involved 55 and 69 specimens, 874 and 319 bp long, respectively. These alignments were compared with translated open reading frames and no insertions or deletions were found. The COI gene had 485 variable sites and 451 phylogenetically informative sites, while the H3 gene had 64 variable sites and 55 phylogenetically informative sites. Poor resolution of the H3 gene could be attributed to high sequence conservation of histone H3 in arcoids.

Sequences of ribosomal gene fragments were of variable lengths. After removal of ambiguously-aligned sites, 375 bp remained in the 12S alignment, of which 191 sites were phylogenetically informative; 679 bp remained in the 28S alignment, of which 129 sites were phylogenetically informative; and 1757 bp remained in the 18S alignment, of which 103 sites were phylogenetically informative.

Examination of genetic divergences among ingroup individuals showed that the mean and range of divergence increased with relative taxonomic rank. When compared across loci, both parameters were smallest for the 18S gene and largest for the 12S gene.

3.2. Partitioned molecular analyses

3.2.1. Single-gene datasets

The BI and ML trees obtained from each gene are shown in Supplementary Fig. 3. All the trees showed resolution to a certain degree and provided support at different taxonomic levels.

At the superfamily level, the Arcoidea was monophyletic with high support in all the trees. An exception was COI trees in which two species (*Empleconia cumingii* and *Cosa waikikia*) of the Limopsoidea appeared within the Arcoidea at low support (Supplementary Fig. 3A and F). The monophyly of the Arcidae was not supported in all the trees. The Noetiidae was monophyletic in H3 ML tree (giving low support, Supplementary Fig. 3H) as well as 28S BI and ML trees (Supplementary Fig. 3D and I). The Glycymerididae was monophyletic in the H3 trees (Supplementary Fig. 3C and H), while it was polyphyletic in COI trees with respect to the position of *Glycymeris rotunda* (Supplementary Fig. 3A and F).

At the subfamily level, the Anadarinae was monophyletic, receiving strong support in the BI and ML trees of COI, 28S and 12S, as well as the BI tree of 18S (Supplementary Fig. 3A–G and I). The Arcinae was paraphyletic or polyphyletic in all the analyses. The monophyly of the Striarcinae was only observed in 28S trees (Supplementary Fig. 3D and I), while the included Noetiinae species formed a monophyletic cluster in H3 trees (Supplementary Fig. 3C and H). The genera *Scapharca*, *Anadara*, *Tegillarca*, and *Potiarca* formed the group Anadarinae in all the single-gene trees except for H3. Among all the genera that contained more than one species, only *Tegillarca* and *Noetia* were monophyletic.

3.2.2. Combined datasets

The ILD test data showed that the combined datasets were homogeneous ($P > 0.05$). This result suggests that combining molecular partitions in a phylogenetic analysis is unlikely to reduce phylogenetic accuracy. In the present study, the combined datasets did not produce more robust phylogenetic resolution than partitioned single-gene datasets (trees not shown). The BI tree

constructed from the simultaneous dataset by excluding sequences having only the H3 gene is shown in Fig. 1.

The order Arcoidea was well supported, in which two major clades were recovered. The first Arcoidea clade (96% BPP, 84% bootstrap) was composed of anadarines and one *Barbatia* taxa, while the second (83% BPP, 76% bootstrap) contained all the remaining lineages. Within the first Arcoidea clade, Anadarinae were grouped together with high support (100%). The *Barbatia decussata* clade of Arcinae represented the Arcinae as a sister group to anadarines with high support values. *Scapharca* and *Anadara* were recovered as polyphyletic groups.

Within the second Arcoidea clade, *Arca* was not monophyletic and its major clade was well supported (96%) in ML analysis. *A. boucardi* formed a single clade and appeared as a sister group to the family Cucullaeidae. The *Barbatia trapezina*/*Trisidos kiyonoi*/*Barbatia virescens* clade of Arcinae formed a sister group to the family Noetiidae and received moderate support (91% BPP, 70% bootstrap). The Noetiidae formed an expected single cluster given the distinctive growth pattern of ligaments. The Glycymerididae was represented by the genus *Glycymeris* which did not form a monophyletic group. Although the monophyly of the Limopsoidea received a moderate support in ML analysis, it appeared within the Arcoidea and disrupted the arcoidean monophyly.

4. Discussion

4.1. Classification of the superfamily Arcoidea

The monophyly of the Arcoidea is well supported here (100% BPP, 100% bootstrap), suggesting that this order is a valid taxonomic group. The contentious problem at the superfamily level is mainly related to the position of the Glycymerididae. Vokes (1967) and Newell (1969) placed the Glycymerididae in the Limopsoidea and it is this classification that is most widely accepted. However, Amler (1999) suggested the Glycymerididae be included in the Arcoidea. Oliver and Holmes (2006) supported the view of Amler, basing their decision on shell and anatomical features, the fossil record, and published molecular studies. In the present study, two Limopsoidea taxa appeared as a subgroup within, rather than a sister group to, the Arcoidea (Fig. 1), leading to the paraphyly of the Arcoidea. Nonetheless, these two taxa formed a single clade with moderate support (ML analysis), suggesting that the Limopsoidea is a monophyletic group. If the Glycymerididae is placed in the Limopsoidea, the monophyly of the Limopsoidea would be lost. Therefore, the Arcoidea should preferably include the family Glycymerididae. It is not surprising to observe the Limopsoidea taxa within the Arcoidea, because ligament structure suggested that the former were derived from the latter (Waller, 1978).

4.2. Classification of the subfamily Arcinae

In the present study, the Arcinae was not recovered as a monophyletic group, consistent with previous finding by Marko (2002). The genus *Arca* formed three small clades, which corresponded to three morphotypes (*A. noae*, *A. avellana*, and *A. tetragona*) as identified by Oliver and Holmes (2006), and three groups (*A. zebra*, *A. imbricata*, and *A. boucardi*) as suggested by Vermeij (2013). Among those, groups *A. noae*/*A. zebra* (*A. navicularis* and *A. ventricosa*) and *A. avellana*/*A. imbricata* clustered together with high support values, whereas *A. tetragona*/*A. boucardi* formed a sister group to the family Cucullaeidae (Fig. 1). This result raises doubts about the position of the *A. tetragona*/*A. boucardi* group in *Arca*, and it supported the morphological work of Vermeij (2013). Furthermore, the *A. tetragona*/*A. boucardi* group is confined to colder temperate

334 waters (Oliver and Holmes, 2006), inconsistent with the diagnostic
335 characters of *Arca*. Although the combination of the *A. tetragona*/*A.*
336 *boucardi* group and the Cucullaeidae is surprising, these two share
337 a common morphological character with respect to the location of
338 adductor muscle on the flange structure (Oliver and Holmes, 2006).

339 *Nipponarca* and *Trisidos* have intermediate features between the
340 Arcinae and Anadarinae. The present study provided evidence that
341 both the genera probably should not be assigned to the Anadari-
342 nae. Newell (1969) previously included *Bentharca* in the Anadari-
343 nae, although it was earlier considered as a subgenus of the
344 Arcinae (Reinhart, 1935). Results from the present study support
345 the viewpoint of Reinhart (1935) that *Bentharca* is a member of
346 the Arcinae, but as an independent genus. Owing to the limitations
347 of sampling, the conclusions regarding the position of these taxa
348 need further examination by increasing taxon sample size. The
349 genus *Barbatia* was polyphyletic and its taxonomic status needs
350 revision.

351 4.3. Classification of the subfamily Anadarinae

352 According to data from the present study and Matsumoto and
353 Hayami (2001), the Anadarinae should be recognized as a valid
354 subfamily. However, the traditional subfamily is split into the Arci-
355 nae and Anadarinae based on the strength of byssus (Newell,
356 1969), which needs revision owing to the existence of a group with
357 an intermediate set of features between the Arcinae and Anadari-
358 nae. In order to preserve the validity of the Anadarinae, we may
359 consider to accept the new genus *Mosambicarca* as proposed by
360 Lutaenko (1994), or the new subfamily Hawaiarcinae as estab-
361 lished by Noda (1986), for species with intermediate features
362 (e.g., *Trisidos kiyonoi*, Fig. 1). The monophyly of *Scapharca* and *Ana-*
363 *dara* was not supported in the present study. This result was con-
364 tradictory to the conclusions of Matsumoto and Hayami (2001) and
365 Marko (2002), likely because of different sample sizes (number of
366 taxa). *Tegillarca* was recovered as a valid group.

367 4.4. Taxonomic status of the families Noetiidae, Cucullaeidae, and 368 Glycymerididae

369 The noetiids have been raised to the rank of family and are
370 widely accepted as members of the Arcoidea according to distinc-
371 tive growth pattern of ligaments (Frizzell, 1946; Newell, 1969).
372 However, Thomas et al. (2000) have shown that the derived char-
373 acters on which the family Noetiidae is based may not be uniquely
374 shared. Thus, it is thought that the Noetiidae can well be poly-
375 phyletic. In the present study, the Noetiidae formed its own clade
376 and received good support (Fig. 1). This result suggests that the
377 Noetiidae is a monophyletic group, although only three taxa of
378 the subfamily Striarcinae were included. The nesting of the Noeti-
379 dae within the Arcidae indicates that the former is a younger
380 group derived from the latter. This finding is supported by the fos-
381 sil record that the Arcidae has arisen by the Jurassic, while the
382 Noetiidae extends back only to the Cretaceous.

383 The Cucullaeidae is thought to be contemporary with the Arci-
384 dae, both of which have their origins in the Jurassic (Oliver and
385 Holmes, 2006). However, the Cucullaeidae formed a clade with
386 *Arca boucardi* and appeared within the Arcidae (Fig. 1), indicating
387 that it may be younger than the Arcidae. Although there are
388 numerous fossils available for the Arcooids, it is difficult to date
389 our phylogenetic tree. Our results showed that the Arcidae, the
390 Arcinae, and the *Arca*, *Barbatia*, *Scapharca*, and *Anadara* are not a
391 monophyletic group. This finding indicates that a number of prob-
392 lems exist in the current classifications of arcooids. Consequently,
393 choosing appropriate fossil calibration points is more difficult
394 when dating the phylogenetic tree. The origin of the Cucullaeidae
395 and its t88(with)731448oucard260TD(00.7(is)11)-318.125(ly)-318.7(its)dit88(her)-492(oucaudy)-3ieTJ6.54MC/P/MCID8>>B9CBT8.188006.37614.

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