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Molecular phylogenetics and historical biogeography amid shifting continents in the cockles and giant clams (Bivalvia: Cardiidae) ☆

Nathanael D. Herrera [a,*], Jan Johan ter Poorten [b,c], Rüdiger Bieler [c], Paula M. Mikkelsen [d], Ellen E. Strong [e], David Jablonski [f], Scott J. Steppan [a]

[a] Department of Biological Science, Florida State University, Tallahassee, FL 32304, United States
[b] Naturalis Biodiversity Center, P.O. Box 9517, Leiden, Netherlands
[c] Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, United States
[d] Paleontological Research Institution, and Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, NY 14850, United States
[e] Smithsonian Institution, National Museum of Natural History, Washington, DC 20013, United States
[f] Department of Geophysical Sciences, University of Chicago, Chicago, IL 60637, United States

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ABSTRACT

Reconstructing historical biogeography of the marine realm is complicated by indistinct barriers and, over deeper time scales, a dynamic landscape shaped by plate tectonics. Here we present the most extensive examination of model-based historical biogeography among marine invertebrates to date. We conducted the largest phylogenetic and molecular clock analyses to date for the bivalve family Cardiidae (cockles and giant clams) with three unlinked loci for 110 species representing 37 of the 50 genera. Ancestral ranges were reconstructed using the dispersal–extinction–cladogenesis (DEC) method with a time-stratified paleogeographic model wherein dispersal rates varied with shifting tectonics. Results were compared to previous classifications and the extensive paleontological record. Six of the eight prior subfamily groupings were found to be para- or polyphyletic. Cardiidae originated and subsequently diversified in the tropical Indo-Pacific starting in the Late Triassic. Eastern Atlantic species were mainly derived from the tropical Indo-Mediterranean region via the Tethys Sea. In contrast, the western Atlantic fauna was derived from Indo-Pacific clades. Our phylogenetic results demonstrated greater concordance with geography than did previous phylogenies based on morphology. Time-stratifying the DEC reconstruction improved the fit and was highly consistent with paleo-ocean currents and paleogeography. Lastly, combining molecular phylogenetics with a rich and well-documented fossil record allowed us to test the accuracy and precision of biogeographic range reconstructions.

1. Introduction

Understanding the historical forces shaping biodiversity is an important aspect of marine biogeography, but one that lags behind terrestrial studies. The latitudinal diversity gradient, with high species diversity in the tropics and a decrease toward the poles, is one of the fundamental patterns of biological diversity on the planet (Hillebrand, 2004), and is found in many groups from terrestrial angiosperms to marine mollusks (Crame, 2000; Willig et al., 2003; Jablonski et al., 2006, 2013). The longitudinal decline in marine species richness has also spurred much debate (Briggs, 2003; Cox and Moore, 2010) but is less well understood. Central to these issues are hypotheses describing the origin and maintenance of faunal diversity throughout the marine realm. Much of the debate has focused on whether the tropics, especially the western Pacific, are a center of origin, or sink (accumulation) of diversity (Rocha et al., 2008). Although much attention has been focused on the Indo-Pacific, there have been few attempts to explore global patterns of origination, dispersal, and accumulation between the major marine biogeographic regions (Cowman et al., 2013). Several challenges exist for these studies, such as the lack of discrete physical barriers between the major marine realms. Further, dispersal via planktonic larvae has obscured the patterns of connectivity and origin of marine species (Cowman et al., 2013). Therefore, it is evident that a detailed assessment of global patterns of dispersal and origination among the major marine

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* Corresponding author.
E-mail addresses: nherrera@bio.fsu.edu, ndh04c@gmail.com (N.D. Herrera), terpoorten@chello.nl (J.J. ter Poorten), rbieler@fieldmuseum.org (R. Bieler), pmm37@cornell.edu (P.M. Mikkelsen), StrongE@si.edu (E.E. Strong), djablons@uchicago.edu (D. Jablonski).

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biogeographic realms is needed. Under favorable circumstances one can estimate ancestral distributions, the mode and tempo of speciation, and the effects of range expansion on lineage diversification (Wiens and Donoghue, 2004; Ree et al., 2005; Ree and Smith, 2008; Sanmartín et al., 2008; Ree and Sanmartín, 2009), however, approaches based on time-calibrated, molecular phylogenies are lacking in marine systems.

In the oceans, the circum-tropical belt can be divided into five major realms: the western Indo-Pacific (most of the Indian Ocean), central Indo-Pacific (including the "Coral Triangle" diversity hotspot of the West Pacific), eastern Indo-Pacific (the central Pacific of most authors), tropical Atlantic (from the southern Gulf of Mexico to Angola), and the tropical eastern Pacific, as defined by Briggs (2003) and Spalding et al. (2007). These realms are distinguished by a taxonomic makeup influenced by evolutionary history, patterns of dispersal, and isolation (Valentine, 1973; Spalding et al., 2007). Major barriers among these realms include: (1) the East Pacific Barrier, an uninterrupted 4000 mile expanse of water with depths up to 7 miles deep which separates the Indo-Pacific from the tropical eastern Pacific (Baums et al., 2012); (2) the closing of the Indo-Mediterranean waterway during the Terminal Tethyan Event, which cut off dispersal between the Indo-Pacific and the Atlantic; and (3) the Isthmus of Panama, which separates the Atlantic from the eastern Pacific. Within the Indo-Pacific, some species have been able to maintain widespread geographic ranges spanning the entire Indo-West Pacific region to the central Pacific islands, and in rare cases, to the Pacific coast of the Americas (Bieler, 1993; Lessios et al., 1998; Hughes et al., 2002; Reece et al., 2011). This extent is primarily owing to a lack of absolute barriers (e.g., land bridges or vast expanses of open ocean), and relatively homogeneous temperatures in this large pool of tropical waters (Jablonski et al., 2013; Tomašových et al., 2015). However, the complex distribution of taxa that generally characterizes the western, central, and eastern Indo-Pacific is a result of a combination of tectonic activity and multiple semi-permeable hydrological barriers (Barber et al., 2000, 2002; Bellwood and Wainwright, 2002; Santini and Winterbottom, 2002; Cox and Moore, 2010). With such a complex history and a lack of discrete barriers, it is difficult to tease apart the factors affecting the mode and tempo of species evolution within the marine realm.

The bivalve family Cardiidae (cockles and giant clams) comprises about 265 extant species arranged in 50 genera and nine extant subfamilies (ter Poorten, 2014) with the oldest fossil representative of the family (in the extinct Tulongocardiinae) dating back to the Late Triassic Norian Stage (209.5–228.4 million years ago [mya] by the Gradstein et al., 2012 timescale) (Schneider, 1995). The family is a member of the clade Imparidentia within the euheterodont Bivalvia and was recognized as forming a sister group (with Tellinoidea) to the large clade of Neoheterodontei (Bieler et al., 2014). Cardiids inhabit tropical to temperate seas worldwide with a few species in Arctic waters and the majority of extant taxa distributed in tropical-subtropical areas. They are mainly shallowly infaunal to epifaunal in soft sand or mud in depths to 500 m, with most species restricted to depths <150 m. Typically, cardiids are suspension feeders, but some are highly specialized, such as *Tridacna* and certain Fraginae (*Corculum*, *Fragum*, *Lunulicardia*), which form endosymbioses with dinoflagellate protists (zooxanthellae) (Maruyama et al., 1998; Schneider, 1998b; Kirkendale, 2009). The family contains endemic species in most of the major regions, as well as many widespread species (Wilson and Stevenson, 1977; Vidal, 1999, 2000; Kafanov, 2001, 2002; ter Poorten, 2009, 2013; Huber, 2010).

Our taxonomic understanding of the Cardiidae is based primarily on gross morphological features of the shell and some soft anatomy (Keen, 1969, 1980; Kafanov, 1980; Voskuil and Onverwagt, 1991a,b; Schneider, 1992; Vidal, 1999, 2000; Schneider, 2002; Savazzi and Salgeback, 2004), shell microstructure (Carter and Schneider, 1997; Schneider and Carter, 2001), and phylogenetic analyses combining these characters (Schneider, 1995, 1998a,b; Nevesskaja et al., 2001; Schneider, 2002; Fig. S1). Classifications have varied among morphological systematists (e.g., Stewart, 1930; Kafanov and Popov, 1977; Keen, 1980). However, studies incorporating molecular data are few and restricted to few taxa (Maruyama et al., 1998; Schneider and Ó Foighil, 1999; Nikula and Vainola, 2003; DeBoer et al., 2008; Kirkendale, 2009). Currently there are nine extant and five extinct recognized subfamilies (Huber, 2010; ter Poorten, 2014) based primarily on the morphological classification of Schneider and Carter (2001), Schneider (2002), and Huber (2010).

There have been few attempts to estimate cardiid phylogeny using molecular data and most studies have focused on specific genera or subgroups of cardiids, especially zooxanthellate cardiids (Tridacniinae, Fraginae) and, to a lesser extent, the commercially important taxa (e.g., *Cerastoderma*). Further, most studies suffer from sparse sampling of both taxa and genetic markers. For example, Maruyama et al. (1998) analyzed the phylogenetic relationship of zooxanthellate bivalves belonging to the genera *Tridacna*, *Hippopus*, *Fragum*, and *Corculum*, as well as a few species of azooxanthellate genera (*Vasticardium* and *Fulvia*). However, they used only a single representative of each species and a single genetic marker (18S rDNA). They found the startling result that tridacnids (giant clams) are more closely related to the azooxanthellate cardiids than to *Fragum* or *Corculum*, and thus should be nested within the Cardiidae, corroborating Schneider's (1998b) morphology-based placement of the giant clams in a cardiid subfamily Tridacninae, sister to the Lymnocardiinae. Kirkendale (2009) analyzed the relationships of the Fraginae using multiple markers (4 genes; 16S, 28S, COI, CytB) and found it to be paraphyletic with respect to *Parvicardium* and *Papillicardium*, and nested within a derived European clade composed of three different cardiid subfamilies. This result contrasts greatly with previous work (Stewart, 1930; Keen, 1980; Voskuil and Onverwagt, 1991a; Schneider and Carter, 2001) based on gross morphology and illustrates the need for a reassessment of pre-cladistic analyses using more robust datasets and analyses. Consequently, the classification of cardiids remains incomplete and uncertain, especially regarding the subfamilial and generic ranking of many groups.

Like many marine bivalve clades, the Cardiidae have a rich fossil record with all 50 of the extant marine genera represented, as well as a large number of extinct lineages. These fossils, spanning >215 million years and globally distributed, offer a unique opportunity to investigate the timing of cardiid evolution incorporating multiple fossil calibrations for divergence time estimation. Additionally, ancestral ranges and patterns of origination within the marine realm can be estimated, and new methods for geographic range reconstruction can be tested employing models—e.g., the dispersal–extinction–cladogenesis (DEC) model (Ree and Smith, 2008)—that take into account the changing configuration of plates and ocean basins through time. In this study, we examine the complex geographic history of this diverse, cosmopolitan, marine bivalve clade, and evaluate possible sources of current marine biodiversity and the relationship between the major biogeographic regions over the past 135 mya. Here we (1) estimate the most comprehensive phylogeny of cardiids to date, using multiple loci, (2) calibrate a chronogram with multiple stratigraphically well-circumscribed fossils, (3) reconstruct ancestral distributions to determine historical connectivity among marine realms, and (4) evaluate the performance of the time-sliced DEC approach against a geologically static reconstruction and aspects of the rich cardiid fossil record. This study represents the most extensive examination of model-based historical biogeography among marine invertebrates.

2. Materials and methods

2.1. Taxon and character sampling

Specimens were obtained by the authors (EES, JJtP, PMM, RB) during targeted fieldwork and are vouchered in several institutions. This new material was supplemented by existing museum material (see Supplementary Material S1). One-hundred and ten species (193 individuals) representing 37 of the 50 recognized extant genera were included, yielding a broad and robust sampling of the family at the genus level (Table S1). Taxonomic coverage, based on placement in the literature at the beginning of this study, spanned eight of the nine extant subfamilies. Sequenced vouchers were examined directly when possible to ensure proper identification. Specimens were sequenced for three genes: mitochondrial large subunit ribosomal RNA 16S (~400 bp), and portions of nuclear Histone 3 (H3) (~400 bp) and 28S (~1200 bp). Each gene has been shown to resolve family-level relationships within bivalves and all are relatively easy to sequence with previously designed primers and established protocols (Giribet and Wheeler, 2002; Kappner and Bieler, 2006; Mikkelsen et al., 2006; Kirkendale, 2009). In addition to our newly sequenced material, we added 101 published sequences from GenBank to improve resolution at the species level, although with some caution as we could not verify identifications for all sequences. (Table S1). Outgroups were selected from the putative sister taxon Tellinoidea (*Scissula*) and members of the Neoheterodontei, the putative sister taxon to Cardiidae + Tellinoidea (Bieler et al., 2014).

2.2. DNA sequencing and alignment

All tissues were preserved in 70–100% ethanol, lysis buffer, or were frozen prior to DNA extraction. Total genomic DNA was extracted by either standard CTAB and phenol–chloroform extraction for molluscan tissue (Brown et al., 1996) or E.Z.N.A. mollusc DNA extraction kit (Omega Bio-Tek. Inc.) following the manufacturer's protocols. Muscle tissue from the foot or adductor was used; for specimens smaller than 1 cm in length, the entire soft body was used. PCR reactions were conducted in 25 μL volumes, including ca. 25–50 μg of DNA template, 5 μL of 10× buffer, 1.5 μL of 2.5 mM dNTPs, 1 μL of 10 μM solution of each primer (Table S2), 0.5–2 μL of 25 mM magnesium chloride solution, 0.25 μL TAQ, 0.35 μL bovine serum albumin (BSA), 3.5 μL betaine and deionized water.

Reactions were run for 35–40 cycles for all genes with the following parameters for 16S rRNA: an initial 2-min denaturation at 94 °C, further denaturation at 94 °C for 35 s, annealing 40–46 °C for 30 s (varied for problematic specimens), extension at 72 °C for 1 min. and a final extension for 10 min. at 72 °C. Nuclear genes differed in having annealing 50–58 °C for 45 s (28S) or 50–55 °C for 55 s. (Histone 3). PCR products were visualized on an agarose gel with ethidium bromide. Successful amplifications were then prepared for sequencing using enzymatic digestion with ExoSAP-IT (USP, Cleveland, USA). Complementary strands were sequenced on an ABI Prism 3100 Genetic Analyzer using big-dye terminator chemistry (Applied Biosystems).

Sequences were edited and initially aligned by eye using Sequencher 3.1.1. (Gene Codes Corp.). Protein-encoding H3 sequences were translated into amino acids and easily aligned by eye using MacClade v4.08 (Maddison and Maddison, 2003) with no indels present. Multiple sequence alignments for 28S and 16S were performed in CLUSTAL X (Larkin et al., 2007) using default pair-wise alignment parameters of gap opening and gap extension penalties. Alignments were then manually adjusted by eye in MacClade. To account for the hypervariable regions in the 16S and 28S gene alignments, we conducted two tiers of alignments. Tier 1 (T1) consisted of all data with hypervariable regions included (aligned length 2253 bp for 28S, 690 bp for 16S). For Tier 2 (T2), we removed less conserved sites using GBLOCKS v0.91b (Castresana, 2000), with the least stringent settings (aligned length 694 bp for 28S, 383 bp for 16S).

2.3. Phylogenetic analyses

All analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) approaches as implemented in RAxML (Stamatakis, 2006) and MrBayes v 3.0 (Huelsenbeck and Ronquist, 2003), respectively. All ML and BI analyses were partitioned. For H3, we ran analyses partitioned by codon position as well as the first and second position combined. For the concatenated data set, we used five partitions: one for each of two ribosomal genes and one for each of three codon positions for H3. All ML analyses were conducted on each gene individually (including T1 and T2 for 16S and 28S) and a concatenated dataset. For the concatenated dataset, we combined the three genes using T1 from 16S and 28S. We did not use the T2 alignments with the concatenated dataset because we found no significant differences between the T1 and T2 gene trees (only T1 results are shown). One hundred ML replicates were performed using a random starting tree and with the GTRGAMMA option (-m), along with 1000 bootstrap replicates with the same options. To select the best-fit model of evolution for BI analyses, we used the Akaike Information Criterion in jModelTest (Posada, 2008). Bayesian analyses were partitioned as for the ML analyses and conducted with default priors on individual genes and the concatenated data sets using the GTR + I + Γ substitution model with all parameters estimated for each partition separately. We used a random starting tree for each analysis and the Metropolis coupled Markov chain Monte Carlo lengths varied from 35 to 80 million generations for each data set depending on the time required to reach stationarity and convergence (Table S3). Convergence and stationarity were assessed by comparing the likelihood scores of the MCMC chains in the software Tracer v.1.4. In all analyses, the first 10% of the MCMC chains were excluded as burn-in. The results of BI analyses were summarized on the maximum clade credibility tree for the ML topology of the concatenated dataset with TreeAnnotator v1.6.1 (Drummond and Rambaut, 2007).

2.4. Divergence time estimation

Bayesian estimation of divergence times were conducted in BEAST 1.7.5 (Drummond et al., 2012) for the combined nDNA + mtDNA data set. We implemented a GTR + I + Γ model of DNA substitution with four rate categories and base frequencies estimated for all partitions. We used an uncorrelated lognormal relaxed molecular clock model to estimate substitution rates with the Yule process of speciation as the tree prior. We used the ultrametric ML phylogeny from this study as a starting tree for all runs. We ran six independent analyses, sampling every 10,000 generations. Tracer 1.5 was used to determine convergence and measure of effective sample size of each parameter. The results of the six runs were combined with LogCombiner 1.7.5, and the consensus tree was compiled with TreeAnnotator 1.7.5. The six analyses were run for 200 million generations each, with the initial 20% discarded as burn-in. We initially ran the analysis without the data to determine whether fossil calibration priors were being implemented properly and not interacting unexpectedly by checking to see if we recovered posterior distributions that were similar to the prior distributions (Drummond et al., 2006). We then rejected four calibrations that yielded a posterior distribution that strongly diverged from the prior distribution (first occurrences of *Dallocardia*,

Trachycardium, *Acrosterigma*, and *Microcardium*). The remaining 13 fossil calibrations were then used, representing the earliest occurrences of well-defined genera (Table 1, taxonomic details and sources described in Supplementary File S1; see Jablonski et al., 2013 for additional details on this genus-level database). We applied a lognormal prior distribution to all calibrations, with the means and standard deviations of the distributions set to represent the 95% estimated confidence interval for the actual origination of a taxon based on first occurrences of genera (Table S1). For the root age, we used the stem-group fossil *Tulongocardium*, the oldest known cardiid, dating from the Norian (209.4–228.4 mya) (see Schneider, 1995).

2.5. Historical biogeography

Biogeographic regions were defined following Spalding et al. (2007) with modifications based on known cardiid distributions as follows: (A) we excluded three regions from our analysis, namely the Southern Ocean, because no cardiids are known to occur there, and both temperate Australasia and temperate South America, because we did not sample any taxa from these regions. Reducing the number of regions can help mitigate computation time and reduce ambiguities in node range reconstructions, although the absence of samples from these regions precludes an understanding of their relations to other regions. (B) We further subdivided the temperate Northern and tropical Atlantic and Pacific into east and west components based on current cardiid geographic distributions, which tend to be restricted to one region or the other. (C) Within the Indo-Pacific, we combined the central Indo-Pacific and eastern Indo-Pacific into a single region. This was done because we lacked any samples that were endemic to the eastern Indo-Pacific. We thus dealt with a total of 11 biogeographic regions (Fig. 1).

Ancestral range estimation based on the time-calibrated phylogeny was implemented in RASP v. 2.1 b (Yan et al., 2012) using the DEC model of geographic range evolution with the Lagrange module (which uses source code from the C++ version of Lagrange developed by Smith, 2010). Lagrange implements a ML approach based on a stochastic model of geographic range evolution involving dispersal, extinction, and cladogenesis (DEC model; Ree et al., 2005; Ree and Smith, 2008). In the DEC model, anagenetic range evolution is governed by a Q matrix of instantaneous transition rates, the parameters of which are dispersal (range expansion) between geographic regions and local extinction (range contraction) within a region along branches of a time-calibrated phylogeny (Ree and Smith, 2008). The DEC model assumes that only one event (a single dispersal or local extinction event) can occur at any one moment in time. Therefore, transitions that imply more than one event are given a rate of zero in the Q matrix. We restricted dispersal to occur only between adjacent regions and reduced the maximum areas allowed per node reconstruction to three. Reducing the maximum areas allowed should help mitigate the tendency for DEC analyses to inaccurately infer widespread ancestors (Kodandaramaiah, 2010). Cladogenetic evolution is modeled as three alternative inheritance scenarios (Ree et al., 2005): (1) For ancestors whose ranges comprise a single area, the two daughter lineages each inherit the entire ancestral range (sympatric speciation). For widespread ancestors, lineage divergence can arise either (2) between a single area and the rest of the range, so that both lineages have different ranges from the ancestor and that are mutually exclusive from each other (vicariance or allopatric speciation), or (3) within a single area, where one descendant lineage inherits a range of only one region, whereas the other lineage inherits all regions in the entire ancestral range (peripheral isolate speciation).

Constraints can be placed on the DEC model to reflect past geological events and configurations. We stratified the phylogeny into different time slices (TS's) reflecting major changes in continental configuration over time scales that are relevant for cardiid evolution. When constructing a stratified biogeographic model, it is important not to divide it too finely so that there are multiple phylogenetic events in each TS (Ree and Sanmartín, 2009). We modeled our TS's to retain multiple phylogenetic events. We used three separate TS's: TS1 between the root age of 135 and 60 mya, TS2 between 60 and 25 mya, and TS3 between 25 and 3 mya (Fig. S2). Using TS1 as a reference, we decreased the probability of dispersal during TS2 from 1 to 0.5 between the western Indo-Pacific and eastern temperate north Atlantic (transition between Regions C ↔ I; Fig. S2) and between the eastern and western Atlantic (transitions between Regions H ↔ I; A ↔ J Fig. S2). This accounted for the slowly closing Indo-Mediterranean region (Tethys Sea) and the expanding Atlantic Ocean. For TS3, we further decreased the probability of dispersal between the central Indo-Pacific to the northeastern Atlantic from 0.5 to 0 to account for the closure of the Tethys, and across the Atlantic to 0.1 to account for its continued expansion (Fig. S2). We ran two models for each TS—an adjacency model (M0), which allows equal probability of dispersal between adjacent areas at any time, and an adjacency with constraints model (M1), in which we assigned a reduced probability of dispersal from the Indo-Pacific to the tropical eastern Pacific to 0.05 to account for the East Pacific barrier in all time slices. We treated the eastern Pacific and Caribbean as adjacent areas and did not reduce probabilities of dispersal with the formation of the Isthmus of Panama approximately 5 mya because no sister species spanning this boundary date to this later time period. To help visualize the multiple steps and analyses conducted for this research, see Supplemental Fig. S3 for a flow chart.

Table 1
Fossil calibrations used for divergence time estimates. Ages for the midpoint, lower bound and upper bound of the time bin containing fossils follow geologic time scale of Gradstein et al. (2012). All ages are in mya and nodes correspond to Fig. 3. Calibration point distributions and estimates used in BEAST analysis are given in Table S4. For taxonomic details and sources, see Supplementary File S1.

Node	Taxon	Stage/substage	Midpoint	Lower bound	Upper bound
1	Root	Norian	219.0	228.4	209.4
2	*Vasticardium*	Early Bartonian	40.4	41.2	39.5
3	*Dinocardium*	Late Lutetian-Early Bartonian	42.0	44.5	39.5
4	*Fulvia*	Bartonian-Early Priabonion	38.6	41.2	35.9
5	*Europicardium*	Rupelian	31.0	28.1	33.9
6	*Clinocardium*	Late Lutetian–Early Rupelian	37.0	42.0	32.0
7	*Hippopus*	Aquitanian	21.7	23.0	20.4
8	*Lunulicardia*	Pliocene	4.0	5.3	2.6
9	*Americardia*	Chattian	25.6	28.1	23.0
10	*Acanthocardia*	Middle Rupelian	30.7	31.5	29.8
11	*Parvicardium*	Late Ypresian	49.9	51.9	47.8
12	*Afrocardium*	Late Lutetian	42.9	44.5	41.2
13	*Lophocardium*	Priabonian	35.9	37.8	33.9

3. Results

3.1. Phylogenetic results

Replicate ML inferences of the individual genes each resulted in a single tree (Figs. S4–S6). For 16S and 28S, we found no significant differences in analyses with or without hypervariable regions (T1 and T2 analyses); therefore, only T1 results are shown. A striking result of the gene trees is a lack of monophyly of the currently recognized subfamilies. Only one subfamily, Clinocardiinae, was

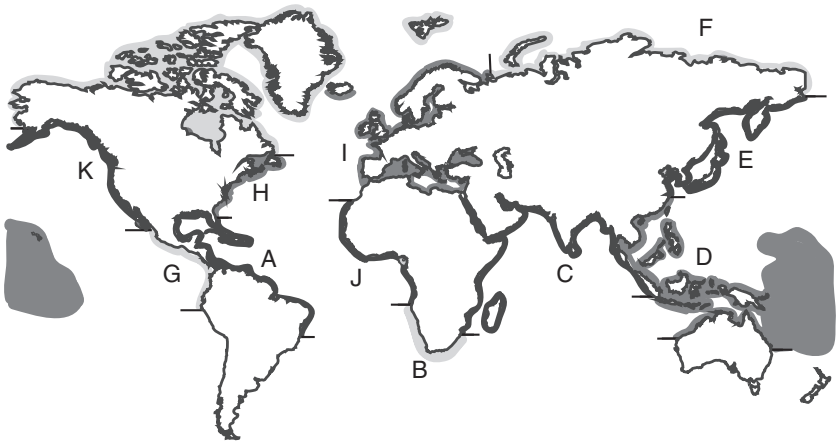

Fig. 1. Biogeographic regions used in this study. Key: A, western tropical Atlantic; B, temperate southern Africa; C, western Indo-Pacific; D, central/eastern Indo-Pacific; E, western temperate northern Pacific; F, Arctic; G, eastern tropical Pacific; H, western temperate North Atlantic; I, eastern temperate North Atlantic; J, eastern tropical Atlantic; K, eastern temperate North Pacific.

found to be monophyletic among the three gene trees. Tridacninae (giant clams) was also monophyletic but was only represented by 16S. All other cardiid subfamilies were found to be para- or polyphyletic. There was general agreement on the middle and deeper-level relationships, especially on the 16S and 28S gene trees. Of the three, the H3 gene tree had the most discordance with the other gene trees, but not with high support (compare Figs. S3–S5).

Six distinct clades of cardiids could be recognized (labeled "A" through "F" in Fig. 2) and were well supported by both ML and BI analyses for the concatenated dataset, with three of the six clades (clades A, D, F) exceeding 95% bootstrap proportions (BP) and 0.95 posterior probability (PP). One clade (B) contained members of four subfamilies and received moderate Bayesian support (PP: 0.87) but low bootstrap support (<50). The remaining two clades (C, E) were weakly supported, owing to uncertainty in the branching structure of clades C, D, and E. Clade A consisted of a Laevicardiinae group. Within this clade, *Frigidocardium* and *Lophocardium* was sister to *Microcardium* and *Trifaricardium*. Support for these two clades was weak owing to the uncertain placement of *Lophocardium* (BI analyses recovered it as sister to *Microcardium* and ML analyses recovered it as sister to *Frigidocardium*). Clade B consisted of species from five subfamilies in two subclades. Clade 1 consisted of *Freneixicardia* and *Afrocardium* (Orthocardiinae) and *Lyrocardium* (Laevicardiinae), whereas clade 2 consisted of *Monodacna* and *Cerastoderma* (Lymnocardiinae), *Papillicardium* and *Parvicardium* (Fraginae), and *Acanthocardia* (Cardiinae). All nodes in clade 1 received moderate to strong support whereas many in clade 2 were weakly supported. *Freneixicardia* was strongly supported as the first to diverge from subclade 1, with strong support for the sister group relationship between *Afrocardium* and *Lyrocardium* (BP: 66%, PP: 0.96). Within subclade 2, *Parvicardium* was found to be paraphyletic. *Parvicardium vroomi, P. scriptum,* and *P. exiguum* formed a strongly supported clade, and diverged first from the rest of subclade 2. There was also uncertainty in the branching structure of the Lymnocardiinae. ML analyses supported *Monodacna* as the first offshoot of a clade consisting of *Cerastoderma* + (*Acanthocardia* + *Papillicardium*) whereas BI analyses (tree not shown) recovered a monophyletic Lymnocardiinae as sister to *Acanthocardia* + *Papillicardium*. *Acanthocardia* was strongly supported as sister to *Papillicardium* in both BI and ML analyses (BP: 74%, PP: 0.96).

Clade C consisted entirely of Fraginae and contained two subclades (3, 4). Subclade 3 consisted of a strongly supported '*Ctenocardia*' and '*Trigoniocardia*' group, whereas clade 4 was composed of Kirkendale's (2009) '*Fragum*' group, which included all species in the genera *Fragum, Corculum,* and *Lunulicardia*. The Tridacniinae was monophyletic (clade D), with *Hippopus* and *Tridacna* reciprocally monophyletic. The placement of the Tridacniinae (clade D) was uncertain; its placement with respect to clades C and Z was unresolved in the ML analyses (Fig. 2), sister to clade C in the BI analyses (Fig. 3), and as sister to clade B in the divergence dating analysis (Fig. 4, see below).

The remaining two clades (clades E and F) were moderately to well-supported sister clades, although clade E received low BP. Within clade E, the Clinocardiinae (clade 5) diverged from clade 6, followed by a split between a clade consisting of *Fulvia lineonotata* + *Laevicardium lobulatum* and the rest of *Fulvia* + (*Europicardium* (*Bucardium* + *Cardium*)). Within clade F, the Caribbean *Laevicardium* (*L. elenense, L. pictum, L. serratum, L. pristis*), West African *L. senegalense,* and the Panamic *Dinocardium* formed a subclade, sister to clade 8, consisting of a well-supported *Vasticardium* (BP: 95%, PP: 1.0) plus a moderately-supported (BP: 75, PP: 1.0) Indo-Pacific clade of *Acrosterigma, Phlogocardium, Dallocardia, Trachycardium, Mexicardia,* and *Papyridea* and the remaining members of *Laevicardium.*

3.2. Historical biogeography

We observed large effective sample size (ESS) values (>200) and convergence for all parameters, including the prior, posterior, and date estimates for the combined runs for the Bayesian divergence time analysis. The results sampled from the posterior yielded a root age dating to the Norian, 210.1 mya (95% highest posterior density [HPD] = 209.4–216.4 mya; Fig. 3, see Table 2 for all mean node age estimates and HPD). The time-stratified DEC estimation of geographical ranges for the Cardiidae is presented in Fig. 4 (adjacency with constraints model). The adjacency with constraints model (M1) was favored over the adjacency model (M0) with significantly better log-likelihood ratios scores (M0: $-\ln L = 275.38$; M1: $-\ln L = 269.15$).

Biogeographical and dating analyses inferred that the crown group of the extant Cardiidae (node W) began to diversify in the tropical Pacific (Regions DG; Fig. 4) and date to the Early Cretaceous, ca. 131.9 mya (95% HPD = 99.4–174.6 mya). Crown group clade A is young, dating to around 34.5 mya (95% HPD = 33.7–36.5 mya) and further diversified within the Indo-Pacific/eastern tropical Pacific (D/G). Dispersal to the eastern temperate north Atlantic via the Tethys Sea was estimated in the

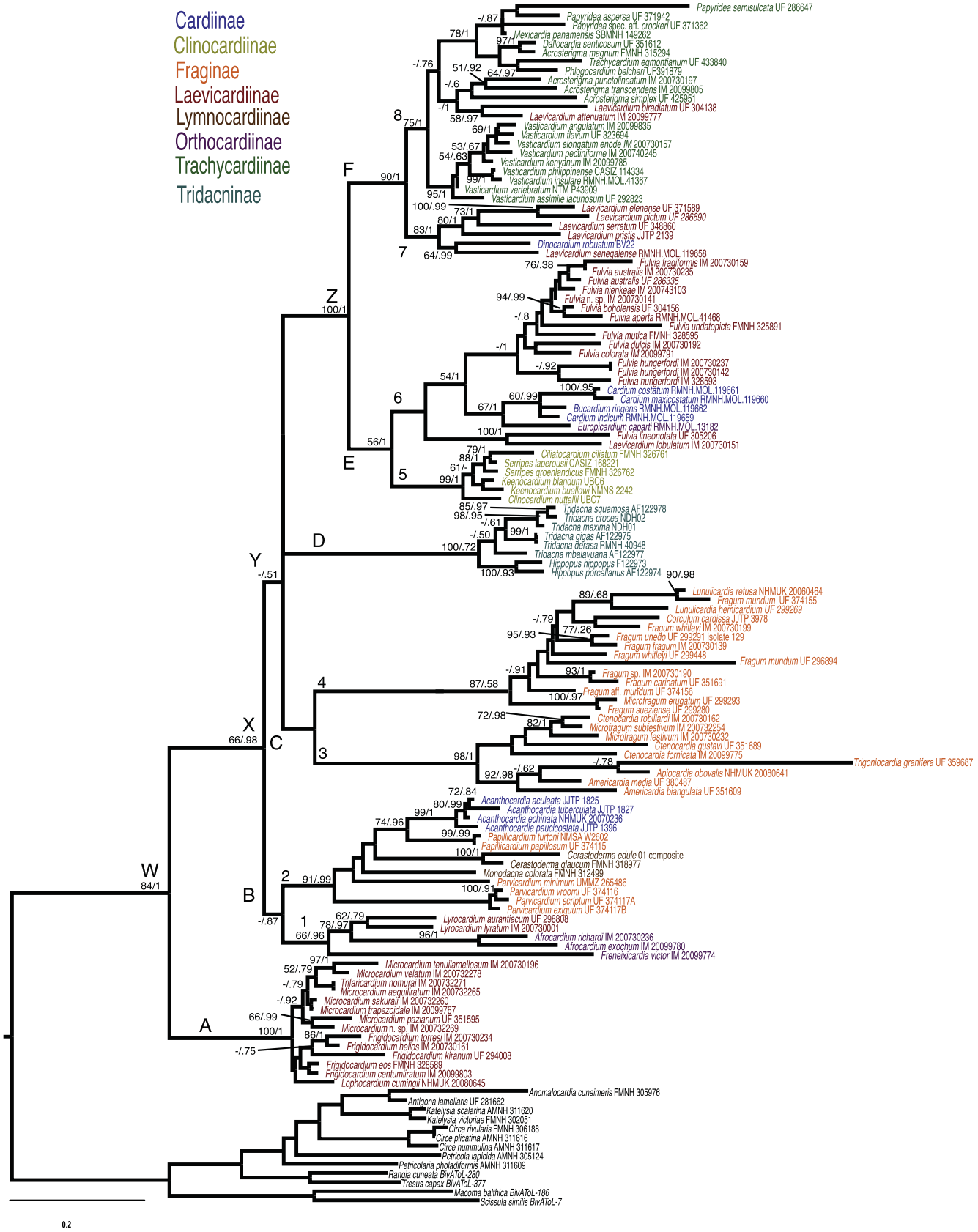

Fig. 2. Maximum-likelihood phylogram of concatenated dataset for three genes (H3, 16S, 28S). Numbers above branches indicate ML bootstrap and Bayesian posterior probabilities, respectively. Colors indicate recognized subfamilies. Labeled nodes correspond to discussion in the text.

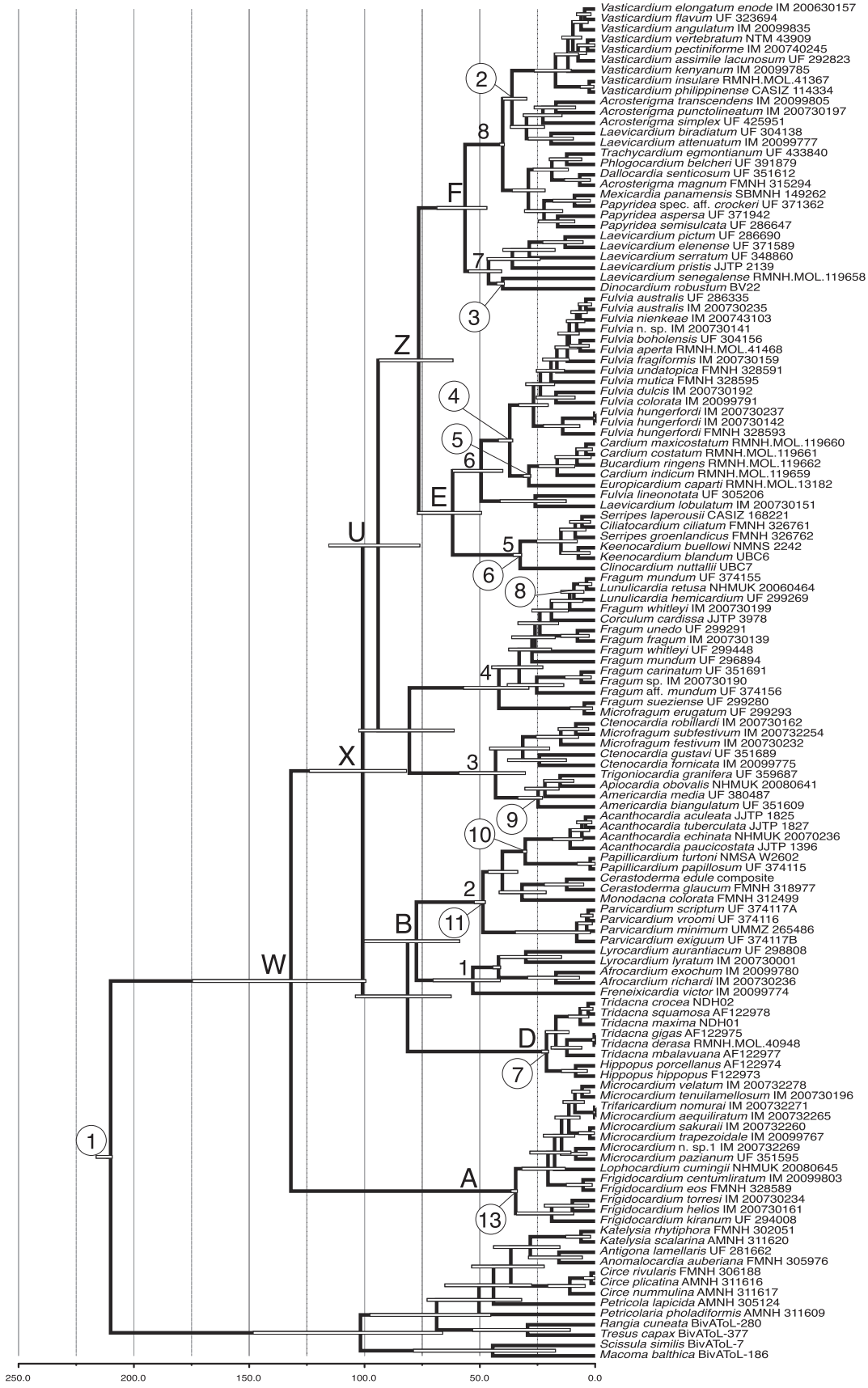

Fig. 3. Chronogram of Cardiidae produced from the BEAST analysis. Maximum clade credibility tree with mean nodal ages and 95% highest posterior density (HPD) intervals indicated by bars. The time-scale in mya and geological time periods are shown at the bottom. Numbered circles indicate the 13 fossil calibrations listed in Table 1.

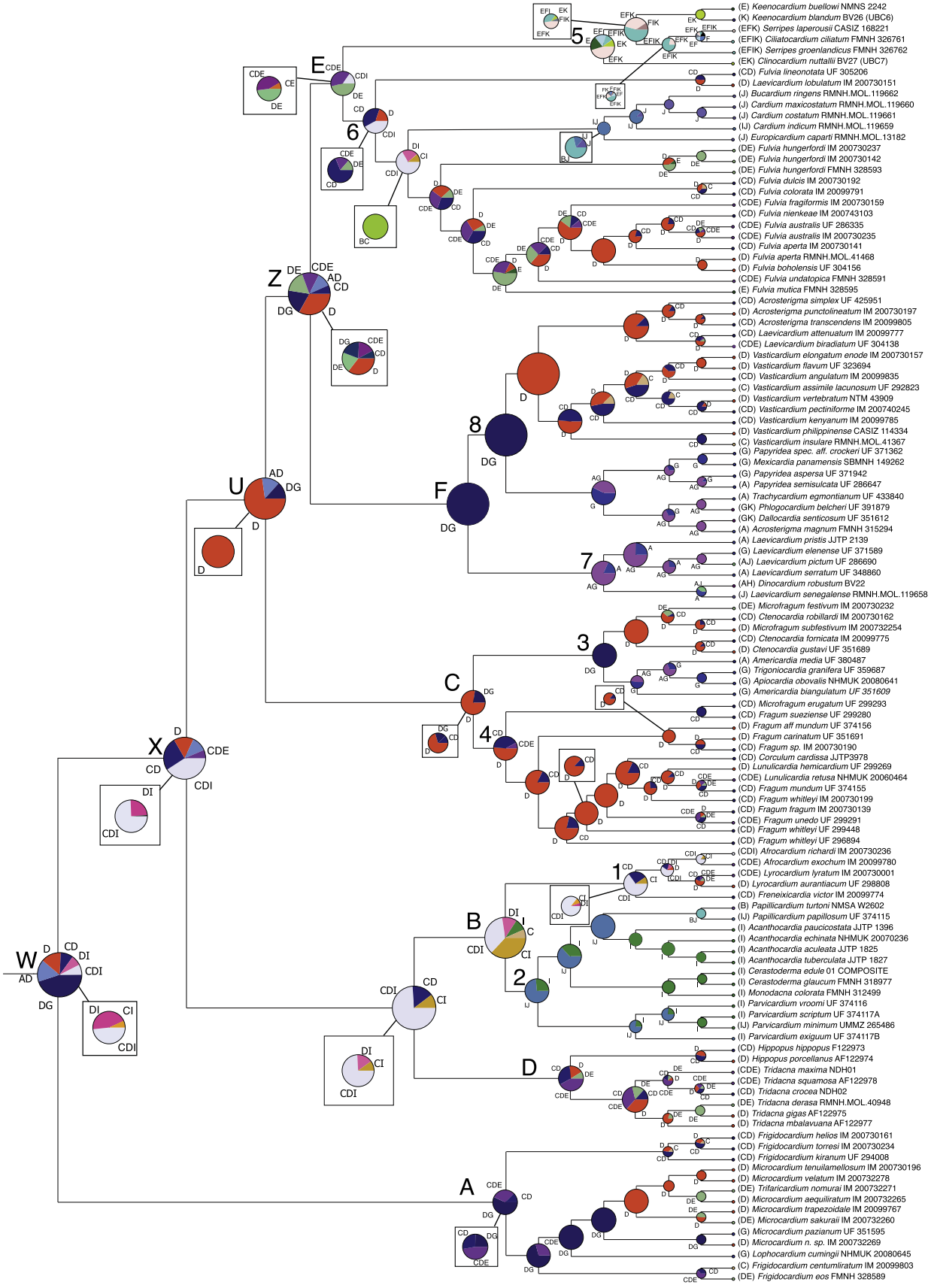

Fig. 4. Biogeographical reconstruction of ancestral ranges in the Cardiidae using DEC with time-slicing. Pie charts and letters at nodes represent the probabilities of the most likely ancestral ranges. Letters to the left of the species names indicate current biogeographical distributions and correspond to the distribution map (Fig. 1). Boxed pie-charts are those from reconstruction without time-slicing, using current tectonic configurations, when those reconstructions differed from the time-sliced reconstruction.

Table 2
Median clade ages with upper and lower 95% highest posterior density estimated by Beast for 19 focal nodes. Node labels correspond to Figs. 1–3.

Node	Age estimate
Root	210.1 (209.4–216.4)
A	34.5 (33.7–36.5)
B	77. 5(58.7–100.2)
B 1	53.1 (41.1–70.3)
B 2	48.7 (47.6–52.4)
C	80.6 (61.1–102.5)
C 3	43.2 (30.2–59.0)
C 4	41.8 (28.7–57.1)
D	21.1 (20.2–23.2)
E	61.8 (49.3–77.2)
E5	32.5 (31.5–35.6)
E6	49.5 (40.0–61.9)
F	56.4 (46.9–68.6)
F7	46.2 (40.5.9–54.9)
F8	40.1 (39.3–41.4)
W	131.9 (99.4–174.6)
X	100.9 (81.8–123.9)
U	94.1 (78.0–115.5)
Z	76.5 (61.6–9)

lineage leading to clade X around the Early/Late Cretaceous boundary (~100.9 mya; 95% HPD = 81.8–123.9 mya). Two major lineages diverged from clade X, clades Y and a clade containing B + D. clade Y was estimated as being found in only the central Indo-Pacific (Region D; as the most likely state) but with some support for being widespread between the central Indo-Pacific and the eastern tropical Pacific or western tropical Atlantic (Fig. 4). Clade B inherited the widespread ancestor from clade X, and clade B + D. Within clade B, the major split resulted in the formation of a European clade (clade 2) around the Early Eocene (48.7 mya; 95% HPD = 47.6–52.4 mya. The Tridacninae (clade D) was estimated as being widespread throughout the Indo-Pacific regions and diverged around the Late Cretaceous. It is also notable that the BEAST analysis recovered the tridacnids as sister to clade B as opposed to the other Indo-Pacific derived cardiids (clade C) as in the concatenated dataset (Fig. 2).

The split between clades E and F occurred approximately 76.5 mya (95% HPD = 61.6–93.8) with a most likely central Indo-Pacific distribution (clade Z). Clade E consists of the widespread temperate derived Clinocardiinae (clade 5), which diverged from clade 6 during the Paleocene (~61.8 mya; 95% HPD: 49.3–77.2 mya; clade E). The split between the two main lineages in clade F occurred in the Early Eocene approximately 56.4 mya (95% HPD: 46.9–68.6 mya). Clade F-8 was estimated as being widespread throughout the tropical Pacific whereas clade F-7 is primarily restricted to the tropical Atlantic.

Comparing the time-stratified reconstruction with the unstratified (i.e., geologically constant) reconstruction revealed only a few nodes that differed (boxed pie-charts, Fig. 4). The only region of the tree with significant conflict between reconstructions involved the nodes descendant from ancestor 6 leading to the *Cardium/Europicardium* clade. In the unstratified reconstructions, the highest likelihoods were associated with ancestral ranges including Region B, Southern Africa (Regions BJ for the immediate ancestor of the *Europicardium* clade) and BC for the next more-basal ancestor). These are in contrast to the stratified reconstruction, where the highest likelihoods all include Region I, eastern temperate Atlantic (IJ and CDI, respectively), and Region B receives effectively 0 likelihood. In other words, the time-stratified analysis reconstructs the Atlantic and Indo-Pacific connection through the Tethyan seaway, whereas the unstratified analysis connects them around Southern Africa. With the time-stratified reconstruction, five nodes were less uncertain/complex, three were more so (*X*, *Y*, and *Z*), and four were slightly different (Fig. 4). The nodes with reduced uncertainty were generally in the middle of the tree, whereas those with greater uncertainty were clustered in deep nodes.

4. Discussion

4.1. Taxonomic implications

Our study represents the most comprehensive phylogenetic analysis of the Cardiidae to date and indicates the need for major taxonomic revisions at the subfamilial and generic levels. We found little agreement with previous cardiid classifications (Kafanov and Popov, 1977; Keen, 1980; Schneider, 1998b, 2002; Schneider and Carter, 2001). General agreement was found with the more limited taxonomic sampling in the molecular study of Kirkendale (2009). Of the eight subfamilies of Schneider and Carter (2001) and Schneider (2002), only two (the North Pacific cold- water Clinocardiinae and the giant clams Tridacninae) were recovered here as monophyletic (Fig. 2). With the majority of cardiid systematics based on morphological characters, it is not unexpected to find some discordance owing to convergence of characters, especially in response to similar selective pressures (i.e., predation, habitat preference, thermal tolerances) and is often observed in bivalves (Vermeij, 1980; Schneider and Carter, 2001). However, the high degree of conflict between our results and previous work is surprisingly extensive for such a well-studied group.

The Laevicardiinae *s.l.* is polyphyletic with the majority of genera distributed across three significant clades: clade A (a "*Frigidocardium* group"), part of clade E-6 (*Fulvia*), and clade F-7 (Fig. 2). Schneider (1995) placed *Fulvia, Frigidocardium, Keenaea, Laevicardium, Lophocardium*, *Lyrocardium*, *Microcardium*, *Pratulum, Trifaricardium* and *Nemocardium* in Laevicardiinae and recovered Laevicardiinae as sister to the rest of the Cardiidae. *Fulvia* is paraphyletic and forms a large subclade within clade E-6. *Fulvia lineonotata* is sister to *Laevicardium lobulatum*, and together they are sister to the core *Fulvia* group+ a clade consisting of *Europicardium*, *Bucardium*, and *Cardium*, a result anticipated in part by ter Poorten (2009). *Laevicardium*, the type genus of the subfamily, is also polyphyletic. The Caribbean members of *Laevicardium* form clade F-7 that includes *Dinocardium robustum*, previously a member of Laevicardiinae (Keen, 1969, 1980) that was moved to the Cardiinae (Schneider, 1992; Schneider and Carter, 2001) they share a superficial resemblance with the Atlantic *Laevicardium* in having smooth shells (that facilitate rapid burrowing; Stanley, 1970), but that hypothesis of relationship fails to be supported even by other morphological characters.

There has been much contention around the placement of the derived Indo-Pacific taxa assigned to *Laevicardium* (clade F-8, Fig. 2). Based on gross morphology, they share a resemblance with the Atlantic *Laevicardium.* However, analyses of microstructural characters suggest otherwise (Wilson and Stevenson, 1977; ter Poorten, 2009). ter Poorten (2009) considered their inclusion in *Laevicardium* doubtful and more likely a case of morphological convergence but made no formal recommendations. We found *L. attenuatum* and *L. biradiatum* nested inside the Trachycardiinae (clade F-8, Fig. 2). Our results indicate that Vidal (1999) was correct in placing both *L. attenuatum* and *L. biradiatum* in *Acrosterigma*. Further, *Lyrocardium* is not closely related to any other genus belonging to Laevicardiinae but is nested within a clade with *Afrocardium* and *Freneixicardia* (Orthocardiinae; Fig. 2, clade B-1).

Keen (1980) and Kafanov and Popov (1977) considered *Europicardium* as a subgenus of *Acanthocardia* or a genus in the tribe Vepricardiini, respectively, both in the Cardiinae. However, Schneider (2002) elevated *Europicardium* to full generic rank and

placed it in Orthocardiinae with the newly erected *Freneixicardia* and *Afrocardium* and found this clade sister to *Cardium* and *Bucardium*. It is evident that *Europicardium* should be moved to the subfamily Cardiinae, because it is sister to *Cardium* + *Bucardium* and not closely related to any member of Orthocardiinae (Fig. 2). *Afrocardium*, which has been little studied and a source of confusion was historically thought to be a member of the Fraginae. Our results confirm the findings of Schneider (2002) that *Afrocardium* is closely related to *Freneixicardia*, which is sister to *Lyrocardium* + *Afrocardium*. Fraginae is not supported as monophyletic, and our data confirm the general findings of Kirkendale's (2009) molecular study. We recovered a core '*Fragum*' group, which includes all species in the genera *Fragum*, *Corculum*, and *Lunulicardia* (clade C-4) as well as a *Ctenocardia* + *Trigoniocardia* group (clade C-3, also including *Americardia, Apiocardia,* and *Microfragum*), that are sister to the core '*Fragum*' group. Of the remaining fragines, there has been disagreement over the placement of the earliest diverging genera, *Parvicardium* and *Papillicardium*. Kirkendale (2009) showed both genera to be part of a clade that included other derived European cardiids, which included species from three different subfamilies (Cardiinae, Fraginae, and Lymnocardiinae). Our analyses consistently recovered a well-supported European clade comprising the "fragines" *Parvicardium* and *Papillicardium* plus *Acanthocardia* (Cardiinae), *Cerastoderma,* and *Monodacna* (both Lymnocardiinae, clade B-2). Clade B-2 also appears to include the remaining two genera of the Lymnocardiinae of which most are found in the Mediterranean-Caspian region (Albrecht et al., 2014). However, *Cerastoderma edule* is an Atlantic species, not occurring in the Mediterranean-Caspian region and *Papillicardium turtoni* is a South African species. Our results show that Albrecht et al.'s (2014) recommendation to move *Cerastoderma* to Cardiinae was premature; the only cardiines that study included are members of *Acanthocardia* that we show clearly are not in Cardiinae.

Membership in Trachycardiinae has long been disputed and there is no consensus about the placement of *Vasticardium* and *Acrosterigma*. Both genera were assigned to Cardiinae by Schneider (1992) and Vidal (1999), however Keen (1969, 1980) and Schneider and Carter (2001) placed both genera in Trachycardiinae based on shell morphology and microstructure. Later, Schneider (2002) excluded both genera from the Cardiinae and considered Trachycardiinae to be the sister group to all other living eucardiids: Cardiinae, Clinocardiinae, Fraginae, Trachycardiinae, and Lymnocardiinae (but see ter Poorten, 2009). Trachycardiinae is paraphyletic with respect to the Indo-Pacific derived *Laevicardium*, which is a subclade sister to all *Acrosterigma* excluding *A. magnum*.

Formal subfamilial and generic taxonomic revisions will be dealt with elsewhere, but we can identify likely taxonomic changes. Clade C contains the type genus (including the type species *Fragum fragum*) of Fraginae and would retain that name. Clade D is the Tridacninae and if clade E-5 is retained as the Clinocardiinae (type species *Clinocardium nuttallii*), Cardiinae is available for clade E-6 (type species *Cardium costatum*). Both the names Trachycardiinae and Laevicardiinae would be available for clade F, but this analysis lacked the type species for both and the constituent taxa are intermingled, leaving us to delay decisions until after further review of the morphology in light of these phylogenetic relationships.

The results of this study shed some light onto the origin and evolution of photosymbiosis in the Cardiidae; the only known marine bivalves to have evolved an obligate symbiotic association with photosynthetic dinoflagellate algae (Schneider and Ó Foighil, 1999). Photosymbiosis in the Cardiidae has evolved independently twice, once in the monophyletic Tridacninae at ~21.1 mya (20.2–23.3) and a second time in a clade recognized by Kirkendale (2009), which includes the genera *Fragum*, *Lunulicardia*, and *Corculum* (Clade C-4, Fig. 2) at ~41.8 mya (28.7–57.1). Both clades consist of members found almost exclusively on clear, coral reef flats or shallow lagoons of the tropical Indo-Pacific.

4.2. Historical biogeography

Our results indicate that, following the origin of the Cardiidae in the Late Triassic, their Mesozoic diversification and end-Cretaceous bottleneck (which can be roughly estimated as ~80% extinction at the genus level, see also Schneider, 1995), the crown group initially diversified in the Indo-West Pacific. From the Indo-West Pacific, there were three expansions into the north Atlantic, which was adjacent to a tropical Indo-Mediterranean region that existed between Africa and Eurasia within the Tethys Sea until the Oligocene (~35 mya) (Kauffman, 1973; Briggs, 2006). Our results suggest that the Indo-Mediterranean region acted as a source and not a sink for much of the present-day cardiid diversity in the eastern Atlantic and Arctic regions, evidenced by expansions that subsequently led to vicariant events that gave rise to four cardiid clades (Fig. 4: eastern tropical Atlantic Clade B, North temperate Pacific Clades E-5 and E-6). This region may also have been a source of broader Indo-Pacific diversity, if the fossil record of coral reef fishes can be taken literally (Bellwood and Wainwright, 2002; Bellwood and Meyer, 2009), and several other groups, including the giant clams (Tridacninae) of this study, may have originated in this area (see Harzhauser et al., 2008; Renema et al., 2008).

The unidirectional expansion from the Indo-Mediterranean suggested by our results is also concordant with paleoceanographic reconstructions, which suggest a westerly transport of warm Indian Ocean water into the Atlantic via the Tethys during the Middle Eocene (Stille et al., 1996; Bush, 1997; Thomas et al., 2003; von der Heydt and Dijkstra, 2006; Allen and Armstrong, 2008). One colonization of the temperate North Atlantic led to a largely unexpected European clade (although anticipated by Kirkendale, 2009, based on more limited sampling). This is the strongest of several examples in which molecule-based phylogenetic hypotheses are more concordant with geographic distribution patterns than are morphology-derived ones. We therefore conclude that there are more localized diversification and much more morphological convergence amongst clades that occupy different geographic regions than previously anticipated.

A striking pattern in our results is the lack of influence of the Indo-Mediterranean region on the western Atlantic, even under a model of high connectivity in TS1 (Mesozoic). It is evident that the present cardiid diversity in the western Atlantic, or more particularly the Caribbean, is more closely tied to the Indo-Pacific via connection to the tropical eastern Pacific through the former Panamanian Seaway. This interpretation contrasts with the recent works of Rocha et al. (2005), Joyeux et al. (2001), and Floeter et al. (2008), who found that the eastern tropical Pacific and Atlantic have been largely isolated from the Indo-Pacific for some time. In contrast, Anker and Baeza (2012) also find a similar pattern to ours in hooded shrimps of the genus *Betaeus* and *Betaeopsis* where much of the current diversity in the western Atlantic stems from the eastern Pacific. This is a pattern also detected by Malay and Paulay (2009) in *Calcinus* hermit crabs. Peak diversification of extant lineages in the western tropical Atlantic (Caribbean) does not occur until the Miocene. We recovered three dispersals into the Caribbean from the tropical eastern Pacific (Fig. 4: *Americardia* clade C-3 [oldest known fossils of this genus in the Oligocene or Miocene of Ecuador]; *Dinocardium/Laevicardium* group clade F-7 [oldest known fossils of these genera in the Eocene of western Atlantic and Caribbean]; *Papyridea/Trachycardium* group clade F-8 [oldest known fossils of these genera in the Miocene of Florida and the Caribbean]) all

between 25 and 40 mya. During the Eocene and into the Miocene, warm tropical water flowed in an easterly direction from the tropical eastern Pacific into the Atlantic prior to the Pliocene closure of the Panamanian isthmus (Stille et al., 1996; Bush, 1997; Thomas et al., 2003; von der Heydt and Dijkstra, 2006). Our reconstruction matches the directionality of paleoceanographic reconstructions, and is consistent with source-sink biogeographic models for the region (e.g., Woodring, 1966; Landau et al., 2009). This reconstruction also gives support to the Vortex model (Jokiel and Martinelli, 1992) where we can infer dispersals from the centers of origin followed by subsequent episodes of vicariance occurring upstream of the dispersals. In this case, as new species are generated in the highly diverse Indo-Pacific and disperse in an eastward direction following the currents, the diversity tails off.

Our reconstruction showed most of the major lineages originating in the Indo-Pacific (composed of the eastern, central, and western Indo-Pacific). The central Indo-Pacific is a major source of regional cardiid diversity, with the western Indo-Pacific and western temperate northern Pacific serving primarily as recipients of species originating in the central Indo-Pacific, rather than as donors. Our reconstruction shows prolonged movement from the central Indo Pacific (i.e. the Coral Triangle and adjacent regions) into the western Indo-Pacific and western temperate northern Pacific beginning in the Miocene and escalating during the Pliocene to Recent.

5. Conclusions

5.1. Utility of DEC approach

Our results show both the strengths and the limitations of DEC approaches. On one hand, DEC allowed us to infer that the western Atlantic was largely a recipient of cardiid diversity rather than a generator of new clades (i.e., we have been able to exclude a western Atlantic origin for most clades). It supported tropical western Pacific origins, and it did so with increased confidence by applying a model that favored the rejected eastern source. On the other hand, many of the nodes cannot be resolved beyond that point, so that we cannot test, for example, tropical versus temperate origins of clades within the Angola-Mediterranean-Norway expanse, or confidently pinpoint origins within the space between Norway and Hawaii. Even here, however, it is encouraging that these broad areas are consistent with the paleontological data for the relevant genera.

The strongest discordance between the time-stratified and unstratified reconstructions involved the nodes descendant from ancestor E-6 leading to the *Cardium/Europicardium* clade. Unstratified reconstructions along this lineage were associated with Region B, temperate southern Africa, whereas stratified reconstructions were predominantly associated with Region I, temperate eastern Atlantic. Notably, Region B is not occupied by any member of this clade or its sister group, although several species, living and fossil, occur in region J, the tropical eastern Atlantic. Constrained by modern geography and the adjacency criterion, the unstratified reconstruction is forced to reconstruct ancestors in a region that currently links the Atlantic with the central Indo-Pacific, and leads to a faulty conclusion. In contrast, the time-stratified analysis allows a Tethyan connection. In this instance, the stratified DEC approach appears more biologically realistic. The oldest fossils assigned to the basal extant member of this clade, *Europicardium*, are in region I, just 5–10 myr older than our reconstructed age for the node.

The great value of cardiids as a model clade is their extensive fossil record that can be used to test geographic and temporal reconstructions. A few of the biogeographic reconstructions are actively misleading, in giving strong support for regions of origin that do not include the oldest known fossils of the clade. Thus, *Vasticardium* is inferred unambiguously to have originated within the central Indo-Pacific (D/DG), but the oldest known fossils are in Egypt (Oppenheim, 1903). Additionally, the giant clams (Tridacninae, clade D) are found to be unambiguously western Pacific in origin, whereas the oldest known fossils are in the western Indian Ocean (Harzhauser et al., 2008). These results underscore the value of integrating fossil and present-day distributions, particularly given the enormous regions estimated as ancestral by phylogenetic approaches alone. For example, the ancestral area of *Lophocardium* is reconstructed as a region potentially encompassing both the western and eastern tropical Pacific; the oldest fossil is in Colombia, localizing the origin in the east. The origin of *Clinocardium* is only resolved phylogenetically to a region encompassing the Arctic, eastern and western temperate Pacific, and eastern temperate Atlantic, and the fossil record localizes that origin to the northwest Pacific (notably the one region common to all reconstructions). Although we cannot rule out fossil discoveries in the less-explored regions, the absence of these clades from the well-characterized fossil record of North America, Europe, and northern Asia is likely to be meaningful (see Jablonski et al., 2006; Valentine et al., 2013 on spatial variation in the robustness of negative paleontological evidence).

Regional extinctions, which are especially difficult for phylogenetic approaches to detect, are well-documented in the fossil record of marine invertebrates for the Mediterranean-Indian Ocean region and for both poles in the mid-Cenozoic (Renema et al., 2008; Krug et al., 2010). Indeed, regional extinction is a general problem in evolutionary biogeography, as attested by fossils, for example, of North American horses, camels, rhinoceratoids, and proboscidians, European ratites, *Arcopora* reef corals in southern Britain, and many other examples (Webb, 1977; Mayr, 2005; Wallace and Rosen, 2006; Tomiya, 2013); few believe that the presence of the most basal living angiosperm in New Caledonia need indicate the early biogeography of the clade (e.g., Friis et al., 2011). But the fossil record is also imperfect and so must also be approached cautiously. For example, the Cenozoic marine fossil record is better sampled in temperate zones than in the tropics (Valentine et al., 2013 and references therein), so that a model inferring a tropical origin of a clade might not be falsified by fossil occurrence in the temperate zone. For example, *Papillicardium*'s oldest fossil is from northwestern Europe whereas our DEC analysis reconstructs the genus as tropical western Africa plus southern Africa. The fossil record of western Africa is the poorest of all regions, so the reconstruction from extant distributions is more convincing than the fossil occurrence. Similarly, the DEC analysis reconstructs the origin of *Afrocardium* possibly in a region extending from Norway to Hawaii via the Mediterranean and Indian Ocean (with highest likelihood in the Indo-Pacific, Regions C and D), and thus its first fossil occurrence in the heavily sampled record of western Europe should be viewed with some caution.

By incorporating both molecular and paleontological data, we are better able to assess the accuracy of reconstructions and divergence times. As is evidenced here, in some cases, DEC reconstructions afford very low-resolution inferences or are misleading due to extinction. In other cases, especially with the addition of time-stratified analyses that take into account changing paleogeography, reconstructions appear to be more biologically and geographically realistic than without. We note that misleading reconstructions are a problem with all methods that seek to estimate ancestral attributes (phenotypic or geographic) from extant data and phylogenies and we are not claiming that DEC is particularly prone to them. However, having a rich fossil record to compare mitigates the number of inaccurate reconstructions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.07.013.

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