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

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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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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.

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