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Global diversification of mangrove fauna: a molecular phylogeny of *Littoraria* (Gastropoda: Littorinidae)

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ABSTRACT

The genus *Littoraria* is one of very few molluscan groups that are closely associated with mangroves. We document its global evolutionary radiation and compare biogeographic patterns with those of mangrove plants, based on phylogenetic and fossil evidence. Using sequences from three genes (nuclear 28S rRNA, mitochondrial 12S rRNA and COI) we reconstruct a phylogeny of 37 of the 39 living morphospecies. Six monophyletic subgenera are defined (*Bulimilittorina*, *Lamellilitorina*, *Littoraria*, *Palustorina*, *Protolittoraria*, *Littorinopsis*) and we synonymize *L. coccinea* and *L. glabrata*. A deep division between *Palustorina* from the Indo-West Pacific and *Littoraria* from the Atlantic and Eastern Pacific is estimated by a Bayesian relaxed-clock method to be of Middle Eocene to Palaeocene age (43.2–62.7 Ma), which far predates the Early Miocene (18 Ma) closure of the Tethyan Seaway; this, as in mangrove plants, may reflect vicariance by climatic cooling, rather than tectonic processes. The age of *Littoraria angulifera* in the Atlantic is, however, consistent with Early Miocene vicariance of a Tethyan ancestor. We infer that speciation events are mainly of Miocene or older age, and that diversification has not been driven by depletion of mangrove habitats during recent glacial intervals. Parsimonious reconstruction of ancestral habitats suggests that the genus has inhabited mangrove or wood substrates since its origin, while the rock-dwelling habit of the four members of *Protolittoraria* is derived. Three species span the Eastern Pacific Barrier, and one is amphi-Atlantic, consistent with a long larval phase of up to 10 weeks. Allopatric speciation is inferred, but usually with subsequent range overlap. Ovoviviparity (interpreted as an adaptation to life in mangroves) has arisen twice.

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1. Introduction

Mangrove forests dominate about one quarter of tropical coastlines (Spalding et al., 1997). However, they are among the "most threatened major environments on earth", global loss through human activity having been estimated at 35% (Valiela et al., 2001), while some of the remaining forests are vulnerable to rising sea-levels (Ellison, 1994). These marine forests support a distinctive fauna, and the macroinvertebrates are dominated by molluscs and crabs (Macnae, 1968). For some animals, particularly those inhabiting only the seaward fringes of mangroves, the trees simply provide a hard substrate on otherwise sedimentary shores. However, the forest as a whole presents a unique and challenging habitat, characterized by shade from the leaf canopy, a three-dimensional structure of trunks and roots, a rich supply of decaying plant material, acidic and anoxic soil, variable salinity and intermittent tidal inundation, and strong predation by crabs and vertebrates. There is a small group of animals, mainly molluscs, that show an obligate association with the mangrove habitat (Plaziat et al., 2001) and these display a corresponding suite of adaptations (Vermeij, 1973; Reid, 1992).

The existence of species and groups of animals that are strongly associated with mangroves raises at least three evolutionary questions. Did the shift to the mangrove habitat initiate an adaptive radiation? Do the animals show patterns of global biogeographic history that are similar to those of the mangrove plants? Does the nature of the mangrove environment dictate the tempo and mode of speciation of its inhabitants? So far, some of these questions have been considered in a molecular phylogenetic context only for one family of gastropod molluscs, the Potamididae (Reid et al., 2008) and two families of grapsoid crabs (Gillikin and Schubart, 2004; Fratini et al., 2005; Ragionieri et al., 2009), although a few mangrove-associated species have also been included within larger radiations of gastropods on rocky shores (Littorinidae, Williams et al., 2003; *Nerita*, Frey and Vermeij, 2008).

Evidence for an adaptive radiation in the mangrove habitat comes from the age and location of fossils, and from phylogenetic reconstruction of ancestral habitats. The oldest fossil evidence for a modern mangrove genus (the palm *Nypa*) is from the Late Cretaceous, but most groups arose during the Palaeocene and diverse mangrove forests were established by the Early Eocene (Ellison

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et al., 1999; Plaziat et al., 2001). For the Potamididae, both their fossil record and ancestral habitat are consistent with the hypothesis of adaptive radiation of the extant genera in the new mangrove habitat following its appearance in the early Tertiary (Reid et al., 2008). For mangrove littorinids the fossil record is equally old, but there is conflicting phylogenetic evidence for an ancestral habitat on either rocky shores or mangroves (Reid, 1999b; Williams et al., 2003).

The mangrove plants consist of about 70 species worldwide, comprising trees, shrubs and ferns that belong to 21 family-level lineages each independently derived from non-mangrove ancestors (Ellison et al., 1999; Ricklefs et al., 2006). There has been much interest in the historical biogeography of mangroves, in particular attempting to explain why their diversity is strongly focused near the center of the Indo-West Pacific (IWP) region. (This has been called the ‘mangrove biodiversity anomaly’, e.g. Ellison et al., 1999; Ricklefs et al., 2006, although it is not anomalous in the context of the similar pattern displayed by many marine animal groups.) The limited fossil record of mangroves supports an early Tertiary origin in the Tethyan Realm, followed by pantropical distribution, disjunction when the Tethys was closed in the Miocene, and partial extinction in the Atlantic (McCoy and Heck, 1976; Ellison et al., 1999; Plaziat et al., 2001). Molecular phylogenetic evidence suggests that most mangrove lineages originated in the Old World (Ricklefs et al., 2006) and diversified within the IWP (Duke et al., 1998; Liao et al., 2007), although there have yet been no molecular phylogenetic studies at species-level of entire mangrove clades, even for the more species-rich and widespread groups such as *Avicennia* and the Rhizophoraceae. Clades of mangrove-associated animals that originated at the same time as mangroves are expected to show similar patterns (Ellison et al., 1999). So far there is only limited evidence of this in the Potamididae, which show maximum diversity in the central IWP, fossil evidence of extinction in the Atlantic, and one case of a sister-relationship between clades in the IWP and the Americas, implying possible vicariance (Reid et al., 2008).

Molecular phylogenetic studies are producing a wealth of new data on the geographical pattern and age of speciation events in the marine realm, although large and well-sampled species-level phylogenies are not yet available for mangrove molluscs. As new phylogenies accumulate, it is becoming clear that while the prevailing mode of speciation is of the classical large-scale allopatric kind, the necessary geographical disruption can be achieved by a variety of diverse mechanisms, involving vicariance by tectonic, climatic or oceanographic means, or dispersal across pre-existing barriers (Bellwood and Wainwright, 2002; Williams and Reid, 2004; Read et al., 2006; Floeter et al., 2008; Frey and Vermeij, 2008). Although the sea-level changes associated with Pleistocene glaciations were formerly considered to have driven speciation events, most estimates of sister-species divergences are older, from early Pliocene to Miocene age (Bellwood and Meyer, 2009). So far, global phylogenetic studies of species-level diversification in the tropics, with fossil calibration, have been based largely on organisms from coral reefs (Duda and Kohn, 2005; Read et al., 2006; Williams and Duda, 2008) or rocky shores (Williams and Reid, 2004; Frey and Vermeij, 2008), and it is unclear whether the same conclusions hold for other habitats. Potentially, there are several reasons why speciation processes in the mangrove habitat might display differences. The mangrove habitat is highly sensitive to sea-level change, being greatly reduced in global area during low sea-level stands (Woodroffe and Grindrod, 1991; Sun et al., 2000). The corresponding local extinctions and vicariance of associated fauna might therefore have been more severe than on reefs and rocky shores, promoting speciation in mangrove habitats during the Pleistocene glaciation cycles. Through a different mechanism, during the emergence of the Isthmus of Panama the inhabitants of shallow-sedimentary and mangrove habitats were among the last to be divided during the gradual shoaling and uplift of the barrier, again leading to relatively younger ages of sister-species in these habitats (Knowlton and Weigt, 1998; Hurt et al., 2008). Since they flourish in sedimentary environments with high nutrient status, mangroves are most well developed on continental margins, and are depauperate or absent on oceanic islands. This too may influence speciation processes, because connectivity of populations is greater on continuous coastlines and allopatry, while more difficult to achieve, is also more likely to be transient, leading to contrasting patterns on continental margins and oceanic archipelagos (Hellberg, 1998; Williams and Reid, 2004). Nevertheless, mangrove communities can also be found under oceanic conditions of low nutrient status (Woodroffe and Grindrod, 1991), and the molluscan communities associated with continental and oceanic mangroves differ in composition (Reid, 1986a). This raises the possibility of parapatric ecological speciation between continental and oceanic habitats, as recently investigated in other marine groups (Rocha et al., 2005; Reid et al., 2006). For all these reasons, the study of speciation in mangrove-associated fauna should provide a new perspective on diversification in the marine realm.

The molluscs that inhabit mangrove forests are not diverse. In a worldwide survey of gastropods associated with mangrove biotopes, Cantera et al. (1983) listed 277 species. This, however, is misleading, because more than half are from adjacent mudflats or rocky shores, or are micromolluscs from brackish landward areas, and have no obligate association with mangroves. The true mangrove associates are mostly marine snails, found predominantly or exclusively in this environment, variously dependent on the trees for substrate, food, shade or protection from predators (Vermeij, 1973; Plaziat, 1984; Reid, 1986a; Plaziat et al., 2001; Lozouet and Plaziat, 2008; Reid et al., 2008). These mangrove gastropods include less than 20 species of *Nerita*, *Cerithium* and Muricidae, and an indeterminate number of the more diverse but poorly studied Ellobiidae. The most conspicuous and abundant of mangrove gastropods belong to the families Potamididae (29 species, mostly associated with mangroves, Reid et al., 2008) and Littorinidae.

Our study group is the littorinid genus *Littoraria*. Most other members of the family Littorinidae are inhabitants of rocky shores, and several have already been the subject of studies of global biogeography and speciation (e.g. *Littorina*, Reid, 1996; Reid et al., 1996; *Austrolittorina*, Williams et al., 2003; *Echinolittorina*, Williams and Reid, 2004; Williams and Duda, 2008). Only two littorinid clades have a strong association with mangroves: *Mainwaringia* with just two species, both in Southeast Asia (Reid, 1986b), and *Littoraria*. The morphological taxonomy, habitat and geographical distributions of *Littoraria* species are well known (Reid, 1986a; Reid, 1999a,b, 2001; Stuckey and Reid, 2002). All of the 39 recognized species are of tropical or subtropical distribution, and the great majority occur mainly on mangrove trees or other halophytic plants, in salt marshes and on driftwood, although at least five species are found most frequently on rocky shores and others can occasionally occupy rocks in sheltered inlets. Adaptations to this habitat shown by *Littoraria* species include shell architecture (Reid, 1992), shell color polymorphism (Reid, 1987; McKillup and McKillup, 2008), ovoviviparous development (Reid, 1989), activity rhythms (Ohgaki, 1992; Lee and Williams, 2002), plasticity of radular teeth (Reid and Mak, 1999) and other dietary innovations (Lee et al., 2001; Silliman and Newell, 2003). Diversity is highest in the IWP with 28 species, while six inhabit the eastern Pacific and a further six the Atlantic Ocean (Table 1). Development is planktotrophic in all but one of the species, with a larval duration estimated at 3–10 weeks (Reid, 1986a, 1989). The fossil record of littorinids is scant, but that of *Littoraria* is richer than most and has been briefly reviewed (Reid, 1999b).

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