Heredity (2009) 102, 321–322

www.nature.com/hdy

NEWS AND COMMENTARY

Phylogeography

During the reign of frogs and toads

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Heredity (2009) **102,** 321–322; doi:10.1038/hdy.2008.123; published online 10 December 2008

Frogs and toads (anuran amphibians) have long fascinated budding naturalists and biologists because of their visible metamorphosis, associations with ponds, lakes, streams and gardens, eye-popping coloration, sensitivity to pollution, habitat degradation and climate change. Advances in analytical methods combine the low individual mobility and global (except Antarctica) distribution of anurans to make them excellent systems for testing speciation hypotheses and inferring population histories. In a recent issue of *Heredity*, Zeisset and Beebee (2008) reviewed how molecular markers provided insights into how late tertiary and quaternary (within the past 65 million years) conditions influenced biogeographical processes affecting anurans. They focused on the contrast between the northern temperate and the tropical/southern temperate zones. Although the former languished beneath the sheets of ice, the latter (except Patagonia) endured dramatic Pleistocene cycles of rainfall and aridity.

Within North America, the most refugia-rich region is the Southeastern United States, where both the Appalachian Mountains and the Mississippi Basin acted as isolated refugia, generating allopatric (geographically separated) differentiation for spring peepers, the North American bullfrog and the northern leopard frog during the Pliocene or Pleistocene (within the past 5.3 million years). Other vertebrates and even some plants share the pattern of allopatric differentiation and postglacial expansions from both Appalachian and coastal plain refugia (reviewed in Soltis *et al*., 2006).

Vicariance events, such as the uplifts of the Colorado plateau and Utah–Nevada Great Basin, and the dry, cold climate during the Miocene (23.8–5.3 million years ago) were likely forces resulting in cladogenesis in the red-spotted toad and the Columbia-spotted frog in western North America. Zeisset and Beebee (2008) find, rather unexpectedly, that Pleistocene (less than 1.8 million years ago) refugia in the Pacific northwest appear to have been forested river valleys within the cold mountain zones for tailed frogs and a host of other cold-tolerant species, including plants, mammals and reptiles.

Europe differs from North America in having more defined refugia throughout the Pleistocene; for example, the three Mediterranean peninsulae (the Balkans, Iberia and Italy), and the Caucasus, with northern expansions from them during late Pleistocene–early Holocene that explain current distributions of many plants and animals (Hewitt, 2000). As Zeisset and Beebee (2008) make clear, one of the reasons for this difference is that the main mountain ranges (Alps and Pyrenees) in Europe run eastwest, more effectively isolating the southern refugia, compared with the northsouth Rockies in North America. Another noteworthy finding is that several species (northern crested newt, moor frog and common frog) survived the last glacial maximum both in northern, relatively unknown refugia, as well as in the Mediterranean peninsulae, and that the thermophilic natterjack toad survived somewhere in western Europe, despite its requirement for warm, ephemeral pools to reproduce. Considerable research on anurans has been undertaken in Europe in the so-called suture zones where colonists from the expansions came into secondary contact.

In South America, the Amazon Basin received tremendous attention from early explorers and naturalists such as Darwin, Wallace, Spruce (all British), von Humboldt (German) and Rodrigues Ferreira (Brazilian) in part because of its remarkable diversity. Various hypotheses for the biogeographical patterns observed are still debated: the influence of the Amazonian rivers; the effects of tectonic movements and sea level fluctuations; refugia during the proposed Pleistocene arid cycles and competitive interactions between species during Pleistocene cool periods. Zeisset and Beebee (2008) suggest that there may be a primary distinction between the more recent quaternary events (such as temperature fluctuation) acting on upland anurans, for example, harlequin toads, and earlier paleogeographic events, such as the Andean uplift and marine incursions that altered the direction of the Amazon, having a greater influence on lowland species, that is, poison frogs. Several recent studies have determined that the lineage divergence across several animal groups in the geologically complex Amazon Basin is best understood by the combination of two or more of these hypotheses (Aleixo, 2004; Noonan and Wray, 2006; Conn and Mirabello, 2007).

Although few anuran phylogeographic studies from Africa exist, new work from Stock *et al*. (2008) provides evidence for a deep connection between Sicilian and North African green toads, congruent with fossil and paleogeographic data that might spur additional anuran research on this relatively neglected continent.

Darwin (1859) was aware that anurans were rare on islands because they and their eggs are unable to tolerate prolonged immersion in seawater, and he suggested that the existence of endemic frogs in the mountains of New Zealand's North Island could be explained by glaciation. In fact, there are four primitive frog species restricted to New Zealand, and no toads. Some Baltic islands have frog species with high gene flow among them, but this unusual situation is explained by the relatively low salinity of the Baltic. The island of Madagascar was attached to Africa until approximately 150 million years ago, and the Mascarene ridged frog is one of the few species found in both places. Zeisset and Beebee (2008) highlight the fact that several Madagascar ridged frog haplotypes are absent from Africa, suggesting the natural colonization of Madagascar by transoceanic dispersal after its separation from Africa, but long before humans arrived.

Australia is the home of over 200 species of anurans, mostly clustered in the wetter eastern region. Unlike northern South America and Africa, its smaller patches of rainforest are restricted to the east, but like North and South America, its primary mountain ranges run north-to-south, although their estimated uplift, approximately 65 million years ago, is much older. There are several recognized east-to-west gaps in this range, which, during arid phases, may have acted as barriers to migration between montane rain forests. A central question about Australian frogs is whether they invaded via New Guinea along a Pleistocene land bridge or whether their structure is the result of vicariance or climatic events during early Australian history.

A review by Zeisset and Beebee's (2008) provides summaries of several studies suggesting that some cladogenesis dates to the Neogene or Pliocene, and more fine-scale differentiation is the result of Pleistocene climatic oscillations.

Looking ahead, these authors propose that future studies should combine mitochondrial DNA (that tracks earlier histories) and nuclear markers (particularly microsatellites that track more recent histories) with more complete sampling to solve some of the apparent anuran discrepancies. They also suggest that there may be a relatively small number of global phylogeographic patterns for anurans, reptiles, mammals and flightless birds.

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