

Evolutionary biogeography on Mexico's Baja California peninsula: A synthesis of molecules and historical geology

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Science progresses through a consolidation of knowledge from disparate disciplines of research. Knowledge so acquired is vital to scientific growth because it provides the underpinnings for new theories and laws that transcend disciplinary boundaries and have greater universal explanatory power. What could be more disparate than the study of DNA molecules within the mitochondria of cells, and the fluctuation of sea levels and movement of crustal plates that compose the outer layers of our planet? In this issue of PNAS, Riddle *et al.* (1) present a thought-provoking synthesis of these disciplines through a study of mitochondrial genes across major vertebrate groups in one of the most geologically dynamic areas on Earth—the Baja California peninsula.

Baja California is the second longest and most geographically isolated peninsula in the world. Over the last 4–5 million years, it has undergone a uniquely complex tectonic origin and ecological transformation. What we see today as a rugged, isolated peninsula originally was connected to the west coast of mainland Mexico but became torn away by differential movements of the Pacific and North American plates. Since then, it has rifted approximately 300 km to the northwest along what has become known as the San Andreas Fault. This separation occurred in various stages of uplift, submergence, and geographical fragmentation, leaving the peninsula an archipelago at times. This dynamic environmental history has had a profound effect on the evolution, distribution, and genetic structuring of Baja California's terrestrial vertebrates.

The first major treatment of the biogeography of terrestrial vertebrates in Baja California appeared in a 1960 symposium issue of *Systematic Zoology* (now *Systematic Biology*). There, Orr (2) presented a dispersal-based ecogeographic analysis of the land mammals and Stager (3) reviewed the works of previous authors on the distribution of the avifauna. In the same volume, Savage (4) used dispersal-based models to account for the distribu-

tion of the herpetofauna (amphibians and reptiles) (Fig. 1). These scenarios suffered because they were based on a geological history of Baja California advocated before the formulation of tectonic theory. We now know that the tectonic evolution of this peninsula played a major role in the evolution of its herpetofauna (5, 6). Subsequent works by Murphy (5), myself (6), and Upton and Murphy (7) were the first to entertain vicariant models based on plate tectonic theory to explain the evolutionary history of this region's herpetofauna. Collectively, their works hypothesized three geographic areas of vicariance within Baja California: (i) the vicinity of the head of the Gulf of California, resulting from a northern extension of the gulf during the Late Pliocene; (ii) the Isthmus of La Paz, as it was inundated during that same time; and (iii) central Baja California, resulting from a middle Pliocene mid-peninsular seaway. Riddle *et al.* (1) posit that species level analyses, such as those of Murphy (5) and myself (6), are useful, but can be insensitive to uncovering intraspecific gene phylogenies that mirror otherwise overlooked vicariant events. Therefore, some events may go undetected despite having been crucial in the regional genetic structuring of many taxa.

Riddle *et al.* (1) use mitochondrial DNA (mtDNA) sequence data from five rodents and one toad to construct intraspecific gene phylogenies (phylogenies) to test historical biogeographical scenarios proposed by previous authors (5–7). Known as phylogeography (8), this approach is a fine-grained analysis that permits the construction of intraspecific gene phylogenies (i.e., organismal relationships) as opposed to other approaches (5, 6) that produce lineage phylogenies (i.e., species relationships and higher). Riddle *et al.* (1) test both a late Pliocene through Holocene dispersal model and a late Neogene vicariance model. They correctly note that each model should have a signature phylogeography: the dispersal model should demonstrate widely distrib-



Fig. 1. Banded rock lizard from the Cape Region of Baja California, Mexico.

uted species with little or no genetic differentiation among populations from different regions whereas the vicariance model should show reciprocally monophyletic phylogroups (groups of closely related individuals) on opposite sides of a presumptive barrier, either historical or contemporary. They present their results as a series of area phylograms, which show intriguing patterns of organismal relationships, and document that all six species exhibit multiple geographically separated phylogroups. As with many seminal works with their integrative approach, Riddle *et al.* (1) raise new questions concerning vicariance biogeography in Baja California while stimulating reinterpretations of

See companion article on page 14438.

Article published online before print: *Proc. Natl. Acad. Sci. USA*, 10.1073/pnas.260509697. Article and publication date are at www.pnas.org/cgi/doi/10.1073/pnas.260509697

previous formulations. However, as is often the case during paradigmatic movements, their analyses are not fully explanatory, nor can they be with the data presently available. This will doubtless stimulate additional reanalysis and research that will be a subject discussed elsewhere.

Riddle *et al.* (1) delimit as many as five phylogroups that correlate with major physiographic features of northern Mexico, the southwestern United States, and Baja California. The significance of such correlation is the underlying hypothesis that the evolution of these phylogroups coincides with, and is a result of, the formation of these physiographic regions. This type of analysis, referred to as vicariant biogeography, has transformed the study of dispersal-based biogeography from a discipline of constructing largely untestable, unscientific scenarios to explain species' distributions, to one of rigorous testability and predictability. Combining data obtained from studies of population genetics and gene flow dynamics with allopatric speciation models, we can construct predictable hypotheses concerning the genetic structuring of widely distributed species after a period of fragmentation. In fact, this is such a powerful inference that Upton and Murphy (7) and

Riddle *et al.* (1) were able to propose a midpeninsular vicariant event in several species from central Baja California in the absence of geological evidence based solely on their genetic structuring. Understanding the relationships of these genetic mechanisms to historical geology is being applied to other taxa in other places around the world but what makes this particularly exciting in Baja California is that previously proposed hypotheses based largely on morphological analyses (6) already exist. That the genetic structuring aligns itself well with these previous hypotheses adds considerable credence to phylogeography as a reliable approach to the study of biogeography. More important, as pointed out by Riddle *et al.* (1), these analyses can uncover cryptic vicariant events that are embedded within the genetic structuring of widely distributed species that are not observable with other types of analyses. This is especially significant in areas of the world where there may be no previous hypotheses and vicariant events have gone undetected. An example of this is their proposal that some taxa show evidence of northern and southern phylogroups in Baja California, which they attribute to a mid-Pleistocene transpeninsular seaway that separated a once, continuously distributed taxon. This

initial separation resulted in the formation of two separate genetic groups, which subsequently came back together after the regression of the seaway. There are no species that unequivocally show this pattern of variation based on morphology alone and if it were not for these studies (1, 7) this important, testable hypothesis never would have been proposed.

Riddle *et al.* (1) aptly note that the ramifications of phylogeographic analyses reach beyond historical biogeography. Historical ecologists are greatly interested in the relationship between the fluctuation of species distributions over time and changes in climate (9). Conservationists need to be concerned with ranking and identifying areas of biodiversity. Current reliance on species-level distributions, however, will be prone to underestimating biodiversity because they often mask underlying patterns of genetic structuring. It is the consilience of these disciplines that will allow us to recognize hotspots of biodiversity and will ultimately aid in the preservation and financially responsible management of the species on our planet.

I thank B. Hollingsworth, B. Riddle, and R. Murphy for insightful discussions on Baja California biogeography and R. Johnson for editorial assistance.

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