Deep genealogies and the mid-peninsular seaway of Baja California

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ABSTRACT

Geological forces and long-term climate changes can have profound effects on species. Such effects may be manifested in the pattern and magnitude of genealogical diversity, as revealed by mitochondrial DNA (mtDNA) lineages. The relative importance of the different forces on a regional biota must be evaluated along with a good understanding of geological and climatological history. The peninsula of Baja California of north-western Mexico is one area where both geology and climate have affected the historical biogeography of the regional biota. Molecular studies based on the genealogical relationships among mtDNA lineages have contributed greatly towards elucidating the historical biogeography of Baja California. Perhaps most noticeably, numerous concordant breaks in mtDNA genealogies half-way along the peninsula suggest a vicariant history in which the mid-peninsula was temporarily submerged. This vicariant explanation has recently been criticized, as no conclusive geological evidence exists for a continuous submergence of the mid-peninsula. As an alternative, a scenario based on climatological factors has been suggested. Here we discuss the validity of the hypothesized mid-peninsular vicariance event and the climate-based alternative in explaining the concordant genealogical breaks. We argue that, despite the significant changes in climate brought about by the glacial cycles throughout the Quaternary, a vicariant history involving a mid-peninsular seaway remains the most parsimonious explanation of the observed patterns in mtDNA genealogies.

Keywords
Baja California, climate, genealogical anchors, genealogies, geology, Gulf of California, historical biogeography, mid-peninsular seaway, mitochondrial DNA, vicariance.

INTRODUCTION

The effects of geological history versus long-term climate changes on genealogical diversity remain a highly debated topic (Hewitt, 2004a,b). The relative importance of the different forces may be evaluated only in a geologically highly active region where species cross various climate regimes. The peninsula of Baja California in north-western Mexico, a narrow tract of land c. 1300 km long, lends itself to testing the alternative hypotheses. Its geological evolution follows a complex history of tectonism, orogenesis and palaeostratigraphy (Hausback, 1984; Lonsdale, 1989; Helenes & Carreño, 1999; Carreño & Helenes, 2002). Additionally, changes to the palaeogeography of the peninsula are greatly augmented by wide-scale fluctuations in sea level associated with the glacial cycles during the Quaternary (Ortlieb, 1979, 1991; Lambeck & Chappell, 2001). Undoubtedly, the regional biota has been strongly affected by the complicated history of Baja California.

Molecular studies, particularly those investigating the genealogical relationships among mtDNA lineages, have made great contributions towards elucidating the historical biogeography of Baja California (Riddle et al., 2000; Murphy & Aguirre-León, 2002). Based on the genealogy of mtDNA lineages in *Uta stansburiana* (side-blotched lizard), Upton & Murphy (1997) suggested that the mid-peninsular region was submerged c. 1 Ma, resulting in a temporary connection between the Gulf of California and the Pacific Ocean (Fig. 1). Importantly, geographically concordant divergences have been found in the mid-peninsular region for numerous additional mtDNA genealogies, including other lizards, snakes, mammals, birds and spiders (Zink et al., 1997; Riddle et al., 2000; Rodriguez-Robles & De Jesús-Escobar, 2000; Lawlor et al., 2006).
breaks, the existence of a mid-peninsular seaway has been challenged. Indeed, marine sediments that completely transverse the mid-peninsular region have not been found to date (Hafner & Riddle, 2005). Grismer (2002), reflecting on differences among individual genealogies used to support the mid-peninsular seaway (in particular geographical location and percentage sequence divergence), deemed the molecular evidence for a 1-Ma mid-peninsular seaway equivocal. Rather, he suggested that other forces might have generated the geographical congruence among the mtDNA lineages. Specifically, he advocated that abrupt changes in phytogeography, geology and weather patterns in central Baja California might have contributed to the observed genetic divergences (Grismer, 2002).

Species have been affected by Quaternary glacial cycles, resulting in successive range contractions and expansions (FAUNMAP Working Group 1996; Comes & Kadereit, 1998; Hewitt, 2000). Such climate oscillations may have affected species distributions on the peninsula, as well as influencing intraspecific genetic patterns (Hafner & Riddle, 1997). Mid-peninsular genetic divergences may have formed due to temporary range fragmentation during glacial periods, followed by formation of secondary contact zones during interglacials when populations reunited (cf. Schneider et al., 1998; Hugall et al., 2002).

Genealogical splits may also form within a continuously distributed species, simply due to the hierarchical, female-restricted, and non-recombining inheritance of mitochondrial DNA, given sufficient time (Hoelzer, 2001; Irwin, 2002). Vicariance, therefore, is not required to produce deep divergences along a narrow peninsula such as Baja California.

**BEYOND THE QUATERNARY**

Recent work on the mtDNA genealogy of *Callisaurus draconoides* (zebra-tailed lizard) (Lindell et al., 2005) revealed a very deep divergence mid-way on the peninsula that was consistent with a mid-peninsular vicariance event. When evaluated with new geological evidence (Carreño & Helenes, 2002 and references therein) and genealogies of reptilian taxa of similar sampling distribution [notably including specimens from the deep-water island Isla Angel de la Guarda: *Aspidocelis* (Radtkey et al., 1997), *Sauromalus* (Petren & Case, 1997) and *Uta* (Upton & Murphy, 1997)], a significantly older time frame emerges for the events affecting the historical biogeography of Baja California. This older scenario includes a mid-peninsular vicariance event of late Miocene or early Pliocene age (cf. Rodriguez-Robles & De Jesús-Escobar, 2000). Geological and palaeontological evidence supports a mid-peninsular submergence at this time (Helenes & Carreño, 1999; Carreño & Helenes, 2002; Ledesma-Vázquez, 2002). An extensive palaeontological record of marine molluscs demonstrates that vast areas of the peninsula were submerged during the late Miocene and early Pliocene, with Pacific waters extending to the vicinity of San Ignacio (Smith, 1984, 1991). Marine incursions also have
have been recorded on the coast of the Gulf of California near Santa Rosalía, where the onset of marine sedimentation has been estimated at c. 7 Ma (Ortlieb, 1991; Holt et al., 2000). The earlier date suggested for the mid-peninsular seaway is also supported by high sequence divergences observed in additional taxa (Lindell et al., 2005), most recently spiders (Crews & Hedin, 2006).

What do we make of the absence of continuous marine sediments between the Gulf of California and the Pacific Ocean? Currently, available geological evidence would support a very narrow (e.g. 30 km) land bridge between the northern and southern halves of the peninsula close to San Ignacio (Hafner & Riddle, 2005). Such a connection would not allow any dispersal of marine species between Gulf and Pacific waters. However, multiple data sets from marine species show disjunct distributions that can be explained only by a temporary connection across the mid-peninsular region (Upton & Murphy, 1997; Bernardi et al., 2003; Hafner & Riddle, 2005; Riginos, 2005). This suggests that continuous marine deposits between the Gulf of California and the Pacific Ocean may either have been obscured by geological and geomorphological activity following closure of the mid-peninsular seaway (Hafner & Riddle, 2005), or simply have not yet been discovered.

VICARIANT LEGACY

Genealogical patterns associated with geological events, such as the formation of the deep-water island Isla Angel de la Guarda, require a date for the mid-peninsular divergence that is earlier than the estimated age of 1 Ma (Upton & Murphy, 1997; Riddle et al., 2000). This earlier date is beyond the scope of climate oscillations related to glacial cycles, which began c. 2.5 Ma (Shackleton et al., 1984). Accordingly, climate-driven habitat fragmentation cannot adequately explain the mid-peninsular genetic breaks observed for most taxa. Although a climatic change involving seasonality of rain patterns currently occurs in the mid-peninsular region (Hastings & Turner, 1965), the formation of genetic breaks due to a long-lasting abrupt change in habitat in the mid-peninsular area (sensu Grismer, 2002) also appears unlikely, simply because regional weather and vegetational regimes have repeatedly shifted following glacial cycles, not only altitudinally but also latitudinally (Van Devender, 1990). Latitudinal range changes of as much as 500 km have been reported for plants along the peninsula (Rhode, 2002).

The older scenario for the mid-peninsular seaway of Baja California may better explain the spread in geographical location among breaks of individual genealogies. The mtDNA lineages isolated on opposite sides of a seaway form a secondary contact zone once the barrier disappears. The original location of such secondary contact zones would be very similar across species affected by the isolation event. However, the location of a contact zone is not stagnant (Barton & Hewitt, 1981, 1989), and well documented examples exist of moving contact zones (Dasmahapatra et al., 2002; Secondi et al., 2003). Hence a geographical spread among secondary contact zones established millions of years ago following a common vicariance event should be expected. Geographically separated breaks can also be produced by the process documented by Hoelzer (2001) and Irwin (2002). However, such a process would produce a much more random distribution of genetic breaks along the peninsula, rather than the apparent congregation of contact zones seen in the mid-peninsula. A more pertinent issue is the nature of the individual contact zones, given the older suggested date: Why do the secondary contact zones in mtDNA along Baja California remain so narrow, despite the millions of generations that have passed after they were established (J.L. and R.W.M., unpublished data)?

So, what about the molecular clock? Among taxa, substantial variation occurs in the percentage sequence divergence (Murphy & Aguirre-León, 2002; Lindell et al., 2005). Unfortunately, despite alleged advances in molecular clock theory, divergence estimates from sequence data for the mid-peninsular seaway vary, to the extent of being useless (Ayala, 1999; Edwards & Beerli, 2000). They are too inaccurate to help us pinpoint the timing of events. The complex history of Baja California illustrates the necessity of evaluating geographically detailed genealogies with known, dated geological events (Murphy & Crabtree, 1985; Upton & Murphy, 1997). Such ‘genealogical anchors’ include the formation of deep-water islands (Lindell et al., 2005). This approach is more likely to provide the temporal detail necessary to compare genealogies in a historical biogeographical analysis. It is of particular importance for regions of complex biogeographical history, such as that harboured in the ‘peninsular archipelago’ of Baja California (Murphy & Aguirre-León, 2002), where the possibility of temporally nested events – the fact that seemingly concordant events may, in fact, represent distinct histories – exists (Hafner & Riddle, 2005).

CONCLUSIONS

The historical biogeography of Baja California has been strongly affected by geological and palaeogeographical forces. These forces have left a genetic imprint, particularly evident in the mid-peninsular region, where deeply divergent genealogies show a striking level of congruence. It is possible that forces other than an ancient seaway have significantly affected individual genealogies among those harbouring deep genetic splits in the mid-peninsular region; however, the alternative explanations have no support and are countered by strong evidence. Consequently, a vicariance event affecting all species similarly remains the most parsimonious explanation for the congruent genealogical breaks around the mid-peninsular region. Future analyses based on geographically and temporally detailed genealogies will help elucidate the historical biogeography of the peninsular archipelago of Baja California and may suggest the occurrence of additional vicariance events, including the possibility of recurring mid-peninsular seaways.
ACKNOWLEDGEMENTS

This work was supported by the Theodore Roosevelt Foundation of the American Museum of Natural History (J.L., R.W.M.), the Royal Swedish Academy of Sciences (J.L.), Sigma-Xi’s Grants-In-Aid program (J.L.), Natural Sciences and Engineering Research Council (NSERC) Discovery Grant A3148 (R.W.M.), and the ROM Foundation (R.W.M.). J.L. is also sincerely grateful for scholarships from the Sweden–America Foundation (Borgrättsfonderna) and the Ontario Graduate Scholarship in support of his doctoral degree, of which this work is part. We also thank Ana Luisa Carreño and one anonymous reviewer, who provided valuable comments that significantly improved the manuscript.

REFERENCES


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**BIOSKETCHES**

**Johan Lindell** is an evolutionary biologist currently completing his doctoral thesis at the University of Toronto. His work focuses on intraspecific patterns in Baja Californian lizards in response to historical biogeographical forces, with emphasis on contrasts between maternal and biparental histories.

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