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# Effects of a Plio-Pleistocene Barrier on Chihuahuan Desert Herpetofauna

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**ABSTRACT**—Lake Cabeza de Vaca existed in the northern portion of the Chihuahuan Desert during the late Pliocene and possibly until the mid-Pleistocene, limiting taxon ranges and driving diversification of taxa by sundering once continuous populations occurring across this region. We re-evaluate phylogenetic studies in light of evidence of Lake Cabeza de Vaca and present molecular data that addresses the biogeographical influence of the lake. We locate deep mtDNA sequence divergence within several reptile species drawn from populations on either side of the paleolake. We propose one explanation explaining that divergence may be the molecular signature left by Lake Cabeza de Vaca upon herpetofaunal taxa occurring on the eastern and western bounds of the northern Chihuahuan Desert. These findings suggest that the influence of the ancient lake on the biogeography of the region has been too long overlooked.

The incorporation of phylogenetic methods into population and species level biogeographic studies (termed phylogeography) resulted in a greater understanding of how local and regional paleogeographical events shaped the lineages of extant taxa (Avice 2000). The conclusions reached with these methods changed the way biogeographers view the impacts of vicariance and dispersal in shaping not only species' distributions, but also phylogenetic and taxonomic relationships (Riddle et al. 2000; Knowles 2004). Phylogeographic analyses produced over the last 15 years resulted in both the resurrection of previously challenged biogeographic hypotheses as well as the generation of novel theories that account for the diversity within a given taxon (e.g., Avice and Walker 1998; Riddle et al. 2000). Here we provide preliminary molecular evidence that supports the role of the Late Pliocene pluvial lake, Lake Cabeza de Vaca, in shaping the contemporary biota of the Chihuahuan Desert.

Previous biogeographic analyses of Chihuahuan Desert biota invoked both ancient (Miocene and Pliocene) orogenic mechanisms as well as more recent (Holocene) events (desertification) in explaining both the distribution and phylogenetic relationships of flora and fauna of the region (Findley 1969; Morafka 1977; Axtell 1977; Riddle et al. 1993; Riddle 1995). While transient climatic events during the Pliocene and Pleistocene are recognized as influential in the history of the desert, rarely have specific phenomena been invoked to account for the patterns of the contemporary biota. At the first

Chihuahuan Desert Symposium in 1974 Axtell presented just such a novel hypothesis that provided a compelling explanation for the number of sister taxa whose ranges meet in the northern portion of the Chihuahuan Desert (Axtell, 1977).

Geological activity during the early Cenozoic that included volcanic activity, block faulting, and tectonic uplifting occurred at the convergence of what is now the Texas, New Mexico, and Mexican borders, creating a basin and range topography (Strain 1970). Strain (1966) identified Lake Cabeza de Vaca as a pluvial lake that formed as the series of basins filled with runoff during cycles of heavy precipitation in the early Pleistocene. Reeves (1965, 1969) identified later, lower stages of the lake, which he called Pluvial Lake Palomas. These authors suggest the lake system began to drain during the mid-Pleistocene, flowing south into a large basin in the northern Chihuahuan Desert, and, when finally breached, created the modern channel of the Rio Grande. Subsequent work by Gustavson (1991) found evidence that the Rio Grande began its current southern drainage as early as 2.25 million years ago, at the end of the Pliocene, which suggests that the lake existed prior to this event.

At its maximum, the lake covered an area of 23,000 to 26,000 km<sup>2</sup>—at such a size its effect on terrestrial organismal distributions would have been immense (Fig. 1). Evidence of the lake comes primarily from examination of ancient beach lines and the presence of lakebed depositions and evaporite basins in the area (Reeves 1965, 1969; Strain 1966, 1970). Axtell (1977) found multiple vertebrate taxon pairs whose current range boundaries converge at the lake site and thus may be remnants of a period of allopatry during the existence of Lake Cabeza de Vaca (e.g., Fig. 2 through 5). Additionally, the ranges of many other vertebrates that occur in the area may have been influenced by the presence of this ancient lake (Fig. 6 through 10).



FIG. 1—Lake Cabeza de Vaca covered an area of 23,000 to 26,000 km<sup>2</sup> during peak lake levels, and may have had a hand in shaping the genetic structure of populations in its vicinity. Adapted from Axtell 1977.

The ranges of these taxa are representative of a trend common in many southwestern reptiles and mammals. Indeed, cryptic variance has been shown in the Sonoran Desert along the Baja Peninsula for a variety of taxa (Riddle et al. 2000). In the Chihuahuan Desert, Axtell (1977) found that 47% of reptiles and 43% of nonvolant mammals presently occurring in the former Lake Cabeza de Vaca region

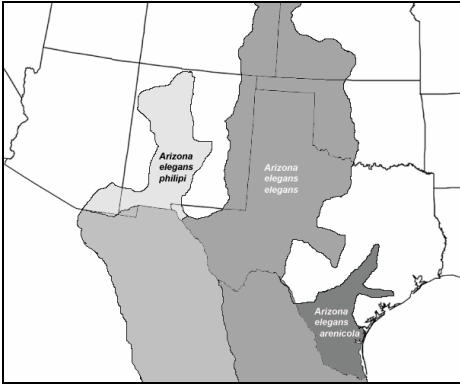


FIG. 2—Subspecies of the colubrid snake, *Arizona elegans*, converge at the site of Lake Cabeza de Vaca; a similar pattern across multiple taxa would suggest that a local event was the source.

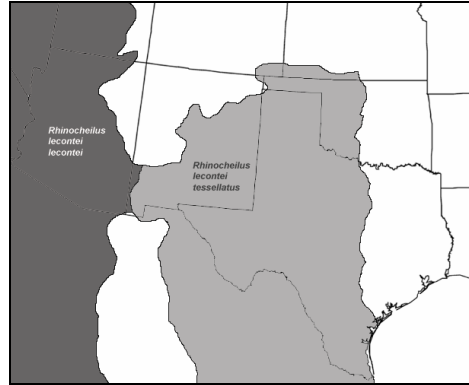


FIG. 3—Range limits of longnose snake (*Rhinocheilus lecontei*) subspecies meet in an area once occupied by Lake Cabeza de Vaca. Perhaps drainage of the lake allowed the subspecies to reconverge.

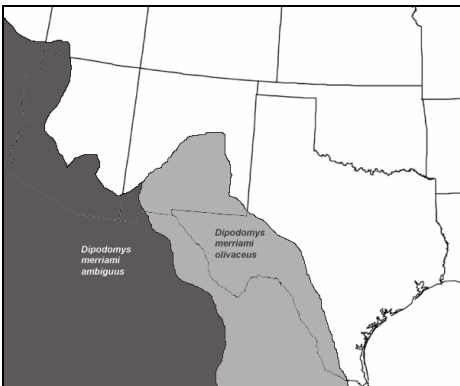


FIG. 4—Northeastern range limits of Merriam's kangaroo rat (*Dipodomys merriami*) shows subspecific differentiation in the vicinity of Lake Cabeza de Vaca. A biogeographic barrier such as the ancient lake could have been the source of such a differentiation.



FIG. 5. Eastern and western ranges of two species of banded geckos (*Coleonyx*) nearly touch in the ancient lake bed. Axtell (1977), using inductive reasoning, concluded that Lake Cabeza de Vaca likely was a biogeographic barrier.

demonstrated western or eastern range limitations in the area and approximately 46% of reptiles and 20% of mammals occurring in this region demonstrated specific or subspecific differentiation that may be associated with the lake. These findings suggest that Lake Cabeza de Vaca may have acted as a lacustrine barrier within the range of many ancestral terrestrial taxa and persisted long enough for differentiation at the species or subspecies level to occur.

Recent studies utilizing mitochondrial and nuclear DNA fragments demonstrated a similar pattern of divergence in several species from this region. Walpole et al. (1997) looked at variation in mitochondrial DNA (mtDNA) between Sonoran Desert and Chihuahuan Desert populations of the cactus mouse (*Peromyscus eremicus*) and found that mtDNA haplotypes were not shared between the populations, suggesting an absence of gene flow. They proposed that the divergence was due to a Pleistocene Epoch separation and called for taxonomic re-evaluation of the genus. Examination

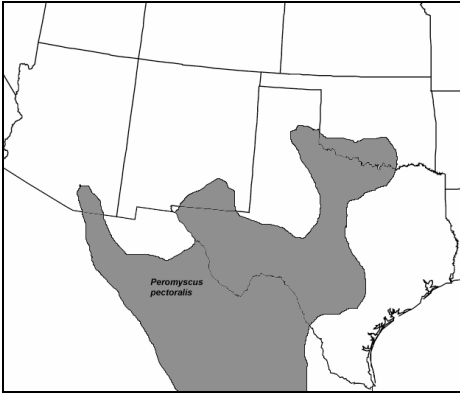


FIG. 6—The western half of the northern range limit of the white-ankled mouse, *Peromyscus pectoralis*, showing possible influence of Lake Cabeza de Vaca. A northward range expansion during the late Pliocene would have been impeded by the presence of the lake.

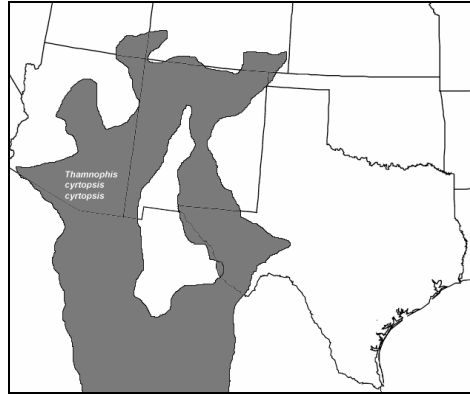


FIG. 7—The garter snake, *Thamnophis cyrtopsis*, does not occur in an area that approximates the location of Lake Cabeza de Vaca. The lake may have been a barrier to dispersal, subsequently reinforced by desertification of the region.



FIG. 8—Range of the harvest mouse, *Reithrodontomys fulvescens*, showing dip in northern range limit. Lake Cabeza de Vaca may have acted as a vicariant barrier within the species' range during the late Pliocene.

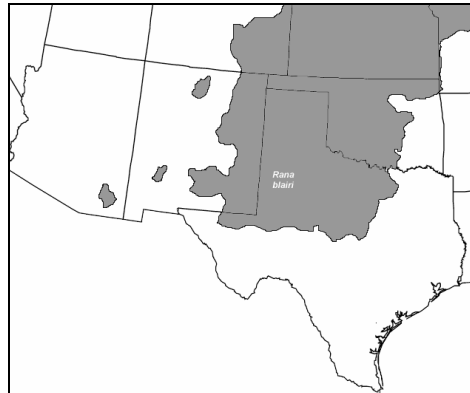


FIG. 9—Satellite populations of the leopard frog, *Rana blairi*, possibly were isolated by Lake Cabeza de Vaca in the late Pliocene. A genetic analysis of the populations may reveal their historical relationships.



FIG. 10—Range of the Mexican vole, *Microtus mexicanus*. The horseshoe shape of the southern boundary is possibly due to a dispersal limitation imposed by Lake Cabeza de Vaca

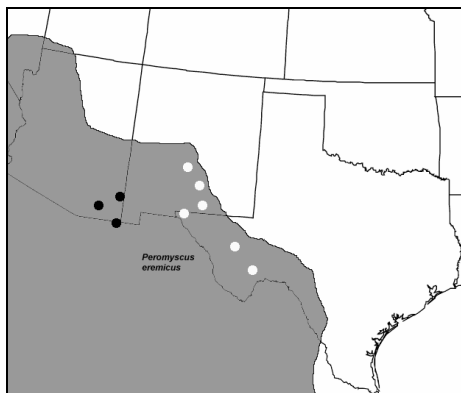


FIG. 11—Collection localities of *Peromyscus eremicus* (Walpole et al. 1997). No mtDNA haplotypes observed in the study were shared between black and white localities. Such a disparity in the midst of a continuous range could be the genetic legacy of a late Pliocene barrier.

of their data reveals that the divergence they found coincides with the vicinity of Lake Cabeza de Vaca (Fig. 11). Similar results were obtained in a study of the desert pocket mouse, *Chaetodipus penicillatus* (Lee et al. 1996), which also utilized mtDNA fragments to define the operational phylogenetic units. The authors found a significant break in haplotypes between populations from the Sonoran and Chihuahuan desert scrub biotas (Fig. 12) and thus recommended that the subspecies *C. p. eremicus* be elevated to species status.

Reptile species also show genetic breaks in the vicinity of Lake Cabeza de Vaca. Mitochondrial and nuclear analyses of the Texas horned lizard (*Phrynosoma cornutum*) from Texas to Arizona (Guerra 1998) was conducted to assess how genetic heterogeneity could inform conservation management. Guerra found a significant genetic divergence between samples taken in New Mexico and Arizona and those taken in Texas (Fig. 13). While Guerra did not incorporate samples from northern and southern portions of its range, she nevertheless attributed the divergence to Lake Cabeza de Vaca and proposed that populations in New Mexico and Arizona be recognized as a separate species.

Additionally, a recent morphological analysis of the lyre snake, *Trimorphodon biscutatus*, found significantly divergent characters between subspecies whose ranges converge in the area of the prehistoric lake (Fig. 14). Using both univariate and multivariate statistical approaches, the authors were able to assign specimens from

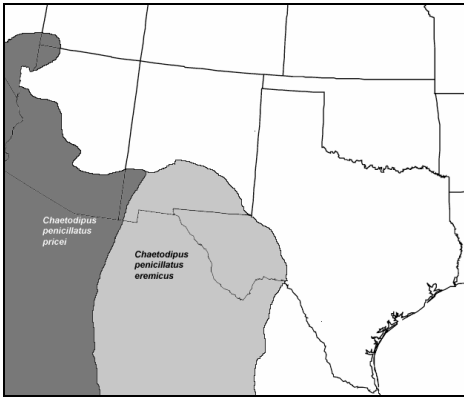


FIG. 12—Ranges of two *Chaetodipus penicillatus* subspecies. Lee et al. (1996) proposed that *C. p. eremicus* (lighter gray) be elevated to species status based on differences in mtDNA haplotypes. Further molecular phylogenies of species in this area may clarify evolutionary relationships not resolvable by morphological characters, and may thus shed light on biogeographic trends in the area.

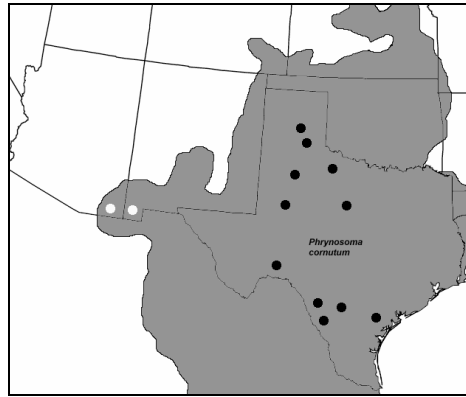


FIG. 13—Guerra (1998) found a significant break in haplotype frequencies between white and black collection localities of the Texas horned lizard and thus called for a taxonomic revision of the species. Guerra concluded that Lake Cabeza de Vaca was the likely source of the genetic divergence.

east and west of the former lake to the proper subspecies classification (LaDuc and Johnson 2003). Furthermore, the authors found that specimens collected in a putative hybrid zone (in the vicinity of Lake Cabeza de Vaca) showed no evidence of clinal variation and were consistently identified as the more western of the two subspecies,

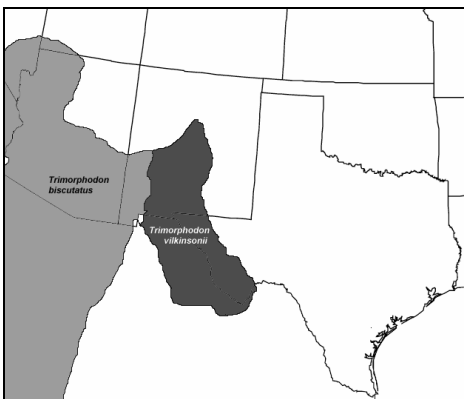


FIG. 14—Ranges of *Trimorphodon biscutatus* (lighter gray) and *T. vilkinsonii*. LaDuc and Johnson (2003) found that morphological differences justified the elevation of *T. vilkinsonii* from subspecies to species status.

*T. b. lambda*. Due to the strength of their results, the easternmost subspecies, *T. b. wilkinsonii* has now been resurrected to species status. Lack of gradation of morphological characters in the midst of a continuous range suggests that the species group may have undergone a period of allopatry in the past. These findings together provide support for the hypothetical role of Lake Cabeza de Vaca as a source of vicariance. Here we provide further evidence of the impact of Lake Cabeza de Vaca on the modern biota of the Chihuahuan Desert.

**METHODS**—We examined mitochondrial DNA sequence data of the Texas longnose snake, *Rhinocheilus lecontei*, and the Texas horned lizard, *Phrynosoma cornutum*, for evidence of early phylogenetic divergences that correspond to the geographic position of the ancient lake. *R. lecontei* was chosen due to the parapatry of two subspecies in the vicinity of the lake (Fig. 3); Axtell (1977) suggested that the morphological differentiation of these subspecies was influenced by the presence of the lake. We tested whether a molecular divergence occurred in this area, and if so, whether it corresponded to the approximate location of the lake, and whether it supported the current subspecies classification of *R. lecontei*.

*Phrynosoma cornutum* was chosen for opposing reasons. Evidence of morphological differentiation of the species is nonexistent, however, prior molecular evidence appears to strongly support both a species-level break as well as the influence of Lake Cabeza de Vaca. We sought to add to this data set by providing additional geographic sampling to determine both vicariant evidence of the lake on the species, as well as to examine whether elevation of western populations of *P. cornutum* to species status is justified. Blood and tissue samples were obtained from field-collected specimens of focal populations using standard field techniques, as well as from university and museum collections.

DNA was extracted from samples with the Qiagen DNeasy extraction kit per manufacturer's instructions. Amplification of samples was performed in 100  $\mu$ L reactions utilizing a 20  $\mu$ L Taq buffer, 0.5  $\mu$ L Taq polymerase, 1.0  $\mu$ L dNTPs, forward and reverse primers, and 75.4  $\mu$ L ddH<sub>2</sub>O. Primers appropriate for amplifying mtDNA fragments containing partial ND4, and the tRNA Histidine, Serine, and Leucine genes were used (Arevalo 1992) (see Forstner et al. 1995 for primer sequences). The area that contains these genes has been used successfully in prior reptilian (Zamudio et al. 1997; Rodriguez-Robles et al. 1999; Raxworthy et al. 2002) and mammalian (Pastorini et al. 1998) phylogenetic analyses. Forty cycles of denaturation, annealing, and extension were performed with the GeneAmp PCR System 9700 and protocol. Amplified products were cleaned using Concert Rapid PCR purification system following manufacturer's instructions. Big Dye 3.0 was used for cycle sequencing the purified PCR products and were then electrophoresed in a polyacrylamide gel on an ABI Prism 377XL DNA sequencer.

Resultant mtDNA sequences were converted into a Nexus file format and aligned using Sequencher 4.0 (Hillis et al. 1996; Thompson et al. 1997). Subsequent refinement was completed by comparison to published reference sequences. Aligned



sequences were analyzed by the phylogenetic analysis software program, PAUP\* 4.0 (Swofford 2003). The dataset was characterized with Modeltest 3.06 (Posada and Crandall 1998) to define transition/transversion ratios, base frequencies, proportion of invariable sites, and substitution ( $\gamma$ ) distribution. After thorough examination of the dataset characteristics, it was determined that a distance-based method would provide adequate resolution of the topological relationships of focal taxa, consequently neighbor-joining was implemented as the method of phylogenetic inference. Rates of sequence divergence were calculated using uncorrected 'p' distance values in order to determine the percentage of nucleotide divergence between individuals and clades.

**RESULTS**—Tissue samples from both species representing populations found on the east and west banks of the ancient lake bed were obtained (Fig. 15).

Base pairs (912 and 850) representing the majority of the mtDNA ND4-Leucine gene region were obtained for *P. cornutum* and *R. lecontei*, respectively. Topological structure obtained for these taxa is summarized with neighbor-joining phylograms (Fig. 15), using the Jukes-Cantor distance correction method. Outgroups were not explicitly employed in analyses as geographic—not ancestral or evolutionary—relationships were sought. Hence while tree topologies (Fig. 15) are presented in the familiar diagrammatic format, they are more properly unrooted genetic distance networks allowing discrimination, when present, among populations within each taxon.

*Rhinocheilus lecontei* samples had rates of sequence divergence that ranged from 0.35 to 10.70%, while *P. cornutum* samples exhibited sequence divergence rates ranging from 0.69 to 9.77%.

**DISCUSSION**—Examination of neighbor-joining trees revealed geographic structure in both taxa (Fig. 15). Without more comprehensive sampling of the geographic area surrounding the extinct lake (southward into Mexico and its historical northern extent), final evaluation of the geographic structure of mtDNA haplotypes for these two species is not complete, however both species exhibit clear breaks that may be due to the vicariant effect of Lake Cabeza de Vaca. *Rhinocheilus lecontei* has a discernible east-west genetic break that coincides with the current morphologically-based subspecies classification, as evidenced by a 10.6% nucleotide divergence between specimens collected from either side of the geographic subspecies boundary (Figs. 3 and 15) (Conant and Collins 1998), whereas the percentage of sequence divergence within individuals of the eastern subspecies, *R. l. tessellatus*, ranges from 0.35 to 5.78. This is in direct conflict with the recent morphological assessment by Manier (2004) whose

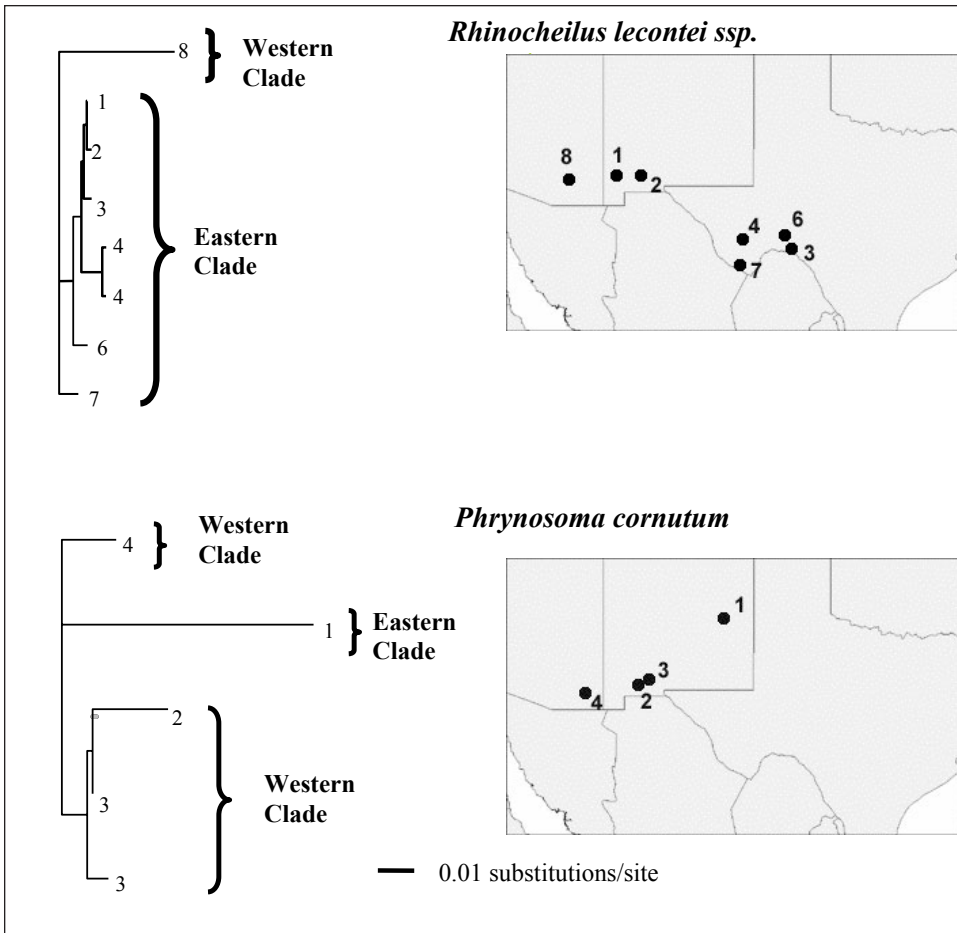


FIG. 15. Neighbor-joining phylograms for *Rhinocheilus lecontei* (top) and *Phrynosoma cornutum* (bottom), collection sites given on maps to left, with numbers corresponding to tree tips on phylograms. Bracketed tips represent putative clades originating from populations East and West of Lake Cabeza de Vaca.

results fail to support any subspecific divisions for the genus. This genetic break may be the product of the ancient lake if the eastern subspecies invaded the newly created habitat that filled the northern Chihuahuan Desert as the lake evaporated with the advent of interglacial conditions.

Results of analyses of *P. cornutum* also demonstrate a genetic divergence of the ND4-Leucine gene region between individuals collected in the northern portion of the lakebed and from a population northeast of the lakebed (Fig. 15). A minimum of 7.75 % sequence divergence exists between the northeastern population and all other population samples, while percent divergence between the individuals from the

northern portion of the lakebed and the population west of the lakebed ranges only between 2.21 and 4.64 %, suggesting that, in contrast to the hypothesized dispersal route for *R. lecontei*, western, rather than eastern, populations of *P. cornutum* dispersed into the northern desert region as the lake retreated.

Our results indicate not only the potential influence of Lake Cabeza de Vaca on these taxa, but also provide further molecular support for taxonomic revision of *P. cornutum* and demonstrate that the current morphology-based subspecies classifications of *R. lecontei* are justified on a molecular level. Clearly, further higher density sampling of these taxa is necessary to capture the degree of genetic variation present across the species' entire ranges. We present here only a starting point for research as we continue to add sample locales to our data set. Additionally, we are in the process of analyzing other taxa to further test the molecular evidence of this ancient biogeographic barrier.

The historical importance of Lake Cabeza de Vaca as a force shaping animal populations in the northern Chihuahuan Desert can no longer be overlooked. While we continue to sample taxa in this area for evidence of historical divergence, we anticipate several potential problems. Species or taxon pairs may be too recent to demonstrate a pattern of divergence (e.g., Zink 1996). Insufficient geographic sampling could also blur any differentiation (Burton 1998), as could recent gene flow (Bowen et al. 1994; Baer 1998). Lake Cabeza de Vaca may not have existed long enough to cause differentiation in some taxa, but even if differentiation is found in the area, the degree of divergence must correlate with what would be expected given the time frame of the lake's existence. For example, if the divergence is too shallow to have been caused by the ancient lake, it could be attributed to the relatively recent formation of the Chihuahuan Desert, or, if the divergence is too great, it may be due to a barrier that predated the formation of the lake, such as the mountain ranges that eventually held the prehistoric lake. Current evidence would seem to confirm a Pliocene barrier (Gustavson 1991) and other studies have placed similar levels of sequence divergence within that timeframe (Riddle et al. 2000). Employment of refined molecular clocks and population modeling may be necessary to disentangle the effects of all of these potential barriers on the population structure of taxa under study; such modeling *a priori* would add more rigor to the experimental design (Knowles and Maddison 2002; Bermingham and Moritz 1998; Templeton 1998). However, there are complicating factors in such calculations for reptiles (Bromham 2004) that will require careful calibration. Finally, comparisons among more than one DNA region will be valuable for species level taxonomy as well as assisting below the species level in evaluation of these populations (Hewitt 2001).

Regardless of the potential difficulties with interpretation of the data or with assignation of the lake as the ultimate cause of multiple phylogenetic divergences, approaches such as the one presented here, in which comparative phylogenetic analyses are implemented to address recent and regional evolutionary forces, should be encouraged (Bermingham and Moritz 1998; Hewitt 2001), rather than being restricted to larger scale or higher order relationships (Humphries and Parenti 1989). Empirical and regional biogeographic studies may also help to separate the relative roles of vicariance and dispersal in shaping the distributions, and thus evolutionary trajectories, of organisms (Zink et al. 2000).

Despite the lack of attention Lake Cabeza de Vaca has received as a vicariant evolutionary influence on the biogeography of the southwestern United States (Axtell, pers. comm. to JR, 2003), it is not due to a lack of evidence, but rather very little phylogeographic analyses. In addition to the examples presented here, many other taxa demonstrate either range boundaries or subspecific differentiation at the area in which the lake occurred (see Axtell 1974 for partial list; consult Stebbins 2003; Conant and Collins 1998; and Burt and Grossenheider 1976 for further examples). With such an enormous amount of evidence, it is unfortunate that the Lake Cabeza de Vaca barrier hypothesis has been so long-neglected; we seek to encourage others to further test it.

The accomplishment of this project required the assistance of many individuals in the field and laboratory and we thank each of you for your assistance. We specifically acknowledge funding by Texas State University's REP program and Texas Parks and Wildlife Department. We would also like to express our thanks to Dr. Axtell and Dr. Scudday for their conversations with us regarding the region, its reptiles and amphibians, and the history of the study of Lake Cabeza de Vaca itself. This manuscript was reviewed by three anonymous reviewers each of whom improved both the context and content of the resulting publication.

#### LITERATURE CITED

- AREVALO, E. 1992. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of *Sceloporus grammicus* (Phrynosomatidae) in central Mexico. Unpublished PhD dissertation, Brigham Young University, Provo.
- AVISE, J.C. 2000. *Phylogeography*. Harvard University Press, Cambridge.
- AVISE, J.C., AND D. WALKER. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London B*. 1998:457–463.

- AXTELL, R.W. 1977. Ancient playas and their influence on the recent herpetofauna of the northern Chihuahuan Desert. In: R.H. Wauer and D.H. Riskind, editors. *Transactions of the Symposium on the Biological Resources of the Chihuahuan Desert Region, United States and Mexico*. National Park Service Transactions and Proceedings Series Number 3. Pages 493–512.
- BAER, C.F. 1998. Species-wide population structure in a southeastern U.S. freshwater fish, *Heterandria formosa*: Gene flow and biogeography. *Evolution* 52:183–193.
- BERMINGHAM, E. AND C. MORITZ. 1998. Comparative phylogeography: concepts and applications. *Molecular Ecology* 7:367–369.
- BOWEN, B.W., N. KAMEZAKI, C.J. LIMPUS, G.R. HUGHES, A.B. MEYLAN, AND J.C. AVISE. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution* 48:1820–1828.
- BROMHAM, L. 2004. Molecular clocks in reptiles: Life history influences rate of molecular evolution. *Molecular Biology and Evolution* 19(3):302–309.
- BURT, W.H. AND R.P. GROSSENHEIDER. 1976. *A Field Guide to the Mammals*. Houghton Mifflin, Boston.
- BURTON, R.S. 1998. Intraspecific phylogeography across the point conception boundary. *Evolution* 52:734–745.
- CONANT, R. AND J.T. COLLINS. 1998. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America*. Third Edition, expanded. Houghton Mifflin, Boston.
- FINDLEY, J.S. 1969. Biogeography of southwestern boreal and desert mammals. In: J.K. Jones, Jr., editor. *Contributions in Mammalogy*. University of Kansas Museum of Natural History Miscellaneous Publications 51:113–128.
- FORSTNER M.R.J., S.K. DAVIS, E. AREVALO. 1995. Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analyses of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 4:93–102.
- GUERRA, T.M. 1998. Genetic analysis of the Texas horned lizard (*Phrynosoma cornutum*): Implications for conservation. Unpublished Master's thesis. Texas A&M University, College Station.
- GUSTAVSON, T.C. 1991. *Arid Basin Depositional System and Paleosol: Fort Hancock and Camp Rice Formations (Pliocene-Pleistocene), Hueco Bolson, West Texas and adjacent Mexico*. Bureau of Economic Geology, Report Investigation No. 198. The University of Texas at Austin.
- HEWITT, G. 2001. Speciation, hybrid zones and phylogeography—or seeing genes in space and time. *Molecular Ecology* 10:537–549.
- HILLIS, D.M., B.K. MABLE, A. LARSON, S.K. DAVIS, AND E.A. ZIMMER. 1996. Nucleic acids IV: Sequencing and cloning. In: D.M. Hillis, C. Moritz, and B.K. Mable, editors. *Molecular Systematics*, Second Edition. Sinauer Associates, Inc., Sunderland, Massachusetts. Pages 321–381.

- HUMPHRIES, C.J. AND L.R. PARENTI. 1989. *Cladistic Biogeography*. Oxford University Press, Oxford.
- KNOWLES, L.L. AND W.P. MADDISON. 2002. Statistical phylogeography. *Molecular Ecology* 11:2623–2635.
- KNOWLES, L.L. 2004. The burgeoning field of statistical phylogeography. *Journal of Evolutionary Biology* 17:1–10.
- LADUC, T. AND J. JOHNSON. 2003. A Taxonomic Revision of *Trimorphodon biscutatus wilkinsonii* (Serpentes: Colubridae). *Herpetologica* 59:364–374.
- LEE, T.E., B.R. RIDDLE, AND P.B. LEE. 1996. Speciation in the desert pocket mouse (*Chaetodipus penicillatus* Woodhouse). *Journal of Mammalogy* 77:58–68.
- MANIER, M.K. 2004. Geographic variation in the long-nosed snake, *Rhinocheilus lecontei* (Colubridae): beyond the subspecies debate. *Biological Journal of the Linnean Society* 83:65–85.
- MORAFKA, D.J. 1977. *Biogeographical Analysis of the Chihuahuan Desert Through Its Herpetofauna*. Junk, Netherlands.
- POSADA, D. AND K.A. CRANDALL. 1998. Modeltest: Testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- PASTORINI, J., M.R.J. FORSTNER, R.D. MARTIN, AND D.J. MELNICK. 1998. A reexamination of the phylogenetic position of *Callimico* (Primates) incorporating new mitochondrial DNA sequence data. *Journal of Molecular Evolution* 47:32–41.
- RAXWORTHY, C.J., M.R.J. FORSTNER, AND R.A. NUSSBAUM. 2002. Chameleon radiation by oceanic dispersal. *Nature* 415:784–787.
- REEVES, C. 1965. Pluvial Lake Palomas, northwestern Chihuahua, Mexico and Pleistocene geologic history of south-central New Mexico. In: J.P. Fitzimmons and C.L. Balk, editors. *Guidebook 16: Southwestern New Mexico II*. New Mexico Geological Society, Socorro. Pages 199–203.
- REEVES, C. 1969. Pluvial Lake Palomas northwestern Chihuahua, Mexico. In: D.A. Cordoba, S.A. Wengerd, and J.W. Shomaker, editors. *Guidebook 20: The Border Region (Chihuahua, Mexico, & USA)*. New Mexico Geological Society, Socorro. Pages 143–154.
- RIDDLE, B.R. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): The Late Cenozoic development of a North American aridlands rodent guild. *Journal of Mammalogy* 76:283–301.
- RIDDLE, B.R., D.J. HAFNER, L.F. ALEXANDER, AND J.R. JAEGER. 2000. Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. *Proceedings of the National Academy of Science* 97:14338–14443.

- RIDDLE, B.R., R.L. HONEYCUTT, AND P.L. LEE. 1993. Mitochondrial DNA phylogeography in northern grasshopper mice (*Onychomys leucogaster*)—the influence of Quaternary climatic oscillations on population dispersion and divergence. *Molecular Ecology* 2:183–193.
- RODRIGUEZ-ROBLES, J.A., D.F. DENARDO, AND R.E. STAUB. 1999. Phylogeography of the California mountain kingsnake, *Lampropeltis zonata* (Colubridae). *Molecular Ecology* 8:1923–1934.
- STEBBINS, R.C. 1985. *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin, Boston.
- STRAIN, W.S. 1966. *Blancan Mammalian Fauna and Pleistocene Formations, Hudspeth County, Texas*. Texas Memorial Museum Bulletin 10, Austin.
- STRAIN, W.S. 1970. Bolson integration in the Texas-Chihuahuan border region. In: *Geology of the Southern Quitman Mountains Area, Trans-Pecos, Texas; Symposium and Guidebook, 1970 Biennial Field Trip*. Permian Basin Section, Society of Economic Paleontologists and Mineralogists, Midland, Texas. Pages 88–90.
- SWOFFORD, D.L. 2003. PAUP\*: Phylogenetic Analysis Using Parsimony and Other Methods (software). Sinauer Associates, Inc., Sunderland, Massachusetts.
- TEMPLETON, A.R. 1998. Nested clade analyses of phylogeographic data: Testing hypotheses about gene flow and population history. *Molecular Ecology* 7:381–397.
- THOMPSON, J.D., T.J. GIBSON, F. PLEWNIAK, F. JEANMOUGIN, AND D.G. HIGGINS. 1997. The ClustalX-Windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 22:4673–4680.
- WALPOLE, D.K., S.K. DAVIS, AND I.F. GREENBAUM. 1997. Variation in mitochondrial DNA in populations of *Peromyscus eremicus* from the Chihuahuan and Sonoran deserts. *Journal of Mammalogy* 78:397–404.
- ZAMUDIO, K.R., K.B. JONES, AND R.H. WARD. 1997. Molecular systematics of short-horned lizards: Biogeography and taxonomy of a widespread species complex. *Systematic Biology* 46:284–305.
- ZINK, R.M. 1996. Comparative phylogeography in North American birds. *Evolution* 50:308–317.
- ZINK, R.M., R.C. BLACKWELL-RAGO, AND F. RONQUIST. 2000. The shifting roles of dispersal and vicariance in biogeography. *Proceedings of the Royal Society of London B* 267:497–503.