Systematics of the Western Lyresnake (Trimorphodon biscutatus) complex: implications for North and Middle American aridland biogeography

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SYSTEMATICS OF THE WESTERN LYRESNAKE
(\textit{Trimorphodon biscutatus}) COMPLEX: IMPLICATIONS FOR
NORTH AND MIDDLE AMERICAN ARIDLAND BIOGEOGRAPHY

A Thesis

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in

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Thomas James Devitt
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ABSTRACT

The Western Lyresnake (Trimorphodon biscutatus) is found generally from the desert southwestern United States southward along the pacific lowland versant of Mexico to northwestern Costa Rica. This species exhibits substantial geographic variation in size, squamation, and color pattern across its range, and as such has had an unstable taxonomic history. I investigated populations of T. biscutatus representing currently and formerly recognized forms using both morphological and molecular methods to infer the evolutionary history of this widespread, polytypic taxon.

Multivariate statistical analyses (principal components and discriminant analysis) of morphological data (432 specimens, 33 characters) yielded six statistically significantly different groups, consistent with currently or formerly recognized taxa. Molecular phylogenetic analyses using parsimony and Bayesian methods (71 samples, 821 base pairs of the mitochondrial ND4 gene) recovered five clades with strong support, largely concordant with groups identified in multivariate analyses, with one exception. One clade consisted of samples representing two geographically proximate, morphologically distinct forms, Trimorphodon biscutatus lambda of the Sonoran Desert and T. b. vilkinsonii of the Chihuahuan Desert, with very low sequence divergence across large geographic distances.

These results suggest very rapid and recent morphological evolution, or, alternatively, recent introgressive hybridization. Nested clade analysis of mitochondrial haplotypes from these two forms was implemented in an attempt to identify putative historical events that may have shaped spatial patterns of diversification. These analyses revealed a pattern consistent with recent population range expansion. However, recent
introgressive hybridization is expected to leave the same genetic signature.

Based on these results, I conclude that *Trimorphodon biscutatus* (sensu lato) actually represents at least five, and possibly six independent evolutionary lineages (i.e., species). This hypothesis is tenable in light of the geological and climatic history of arid North and Middle America, and concordant with the evolutionary history of other codistributed organisms. Taxonomic changes are proposed in order to provide a better estimate of the evolutionary history of this species complex.
INTRODUCTION

The fundamental goal of systematic biology is to discover, describe, organize, and interpret biological diversity. An understanding of recurrent and historical evolutionary processes responsible for patterns of biological diversification is of paramount importance in the face of today’s threats to the global environment. Recent advances in molecular genetic techniques and robust methods of phylogenetic and biogeographic analysis have resulted in the discovery of countless cryptic species hidden within widespread lineages and afforded novel insight into evolutionary processes.

Snakes of the genus *Trimorphodon*, commonly known as lyresnakes, owing to the chevron or lyre-shaped marking present on the head of most forms, are long, slender, nocturnal snakes with broad heads and vertical pupils. They inhabit arid regions of the southwestern U.S., Mexico, and Central America. The generic name ("three types of teeth") refers to the opisthoglyphous (rear-fanged) dentition, which, coupled with a venom delivery system, enables these snakes to immobilize and extract prey such as lizards, rodents, birds, and bats from the rocky crevices and tree hollows inhabited by these snakes. Although lyresnakes superficially resemble a number of other nocturnal, rear-fanged snakes, their closest relative remains unknown. They are, however, considered members of the clade Colubrinae, a large cosmopolitan group comprised of a variety of taxa found mainly in the northern hemisphere and the largest of four clades within the non-monophyletic family Colubridae.

Two species are currently recognized within the genus *Trimorphodon*, the Mexican Lyresnake, *T. tau*, and the Western Lyresnake, *T. biscutatus*. *Trimorphodon tau* is widely distributed in upland regions of Mexico north of the Isthmus of Tehuantepec, as well as on the coastal plain, where it is sympatric with *T. biscutatus* (Scott and McDiarmid, 1984; Fig. 1). This
species inhabits areas of rocky relief from 100 to 2600 m elevation (Scott and McDiarmid, 1984). *Trimorphodon tau* differs from *T. biscutatus* in several features, including: the presence of a broad, light band with an even or slightly indented posterior edge across the nape of the neck; dorsal blotches in contact with dark ventral markings; a smaller overall size (usually less than 1 m in total length); a lower average number of scale counts for ventrals (201-231 in males, 210-243 in females); subcaudals (61-85 in males, 55-80 in females); supralabials (7-10); infralabials (9-14) and midbody scale rows (17-25) (Scott and McDiarmid, 1984; Fig. 2).

*Trimorphodon tau* has been divided into two subspecies, *T. t. tau* and *T. t. latifascia*, based on differences in the color pattern of the head (McDiarmid and Scott, 1970; Fig. 1).

![Figure 1. Distribution of the Mexican lyresnake, *Trimorphodon tau*.](image-url)
*Trimorphodon biscutatus* is distinguished from *T. tau* by several features, including: a variable head pattern, but never a broad, light band with an even posterior margin across the nape; a larger overall size (up to 1.7 m in total length in southern populations, where the species are sympatric); dorsal blotches usually not in contact with ventral markings; and a higher average number of scale counts for ventrals (222-267 in males; 221-263 in females), subcaudals (72-99 in males, 65-85 in females), supralabials (7-10), infralabials (11-14), and midbody scale rows (20-28), although overlap between the two species exists in all of these characters (Scott and McDiarmid, 1984; Fig. 3).

Figure 2. *Trimorphodon tau*, UTA R 12536, 5.6 km south-southwest of Zapotitlán Salinas, Puebla, Mexico, (reproduced with permission, from Campbell and Lamar, 1989).

*Trimorphodon biscutatus* inhabits a variety of arid habitats (Fig. 3) from the desert southwestern United States southward along the Pacific lowland versant of Mexico to northwestern Costa Rica (Fig. 4). Populations in the deserts of northern Mexico and the southwestern U.S. are found in rocky areas of relief up to 2400 meters in elevation. These
individuals from the northern part of the range rarely exceed one meter in total length and feed mainly on lizards, although bats and rodents are also taken. In contrast, individuals from south of Sonora, Mexico inhabit semiarid tropical deciduous or thornscrub forest where they are restricted to elevations below 1200m (Scott and McDiarmid, 1984). Snakes from these populations attain larger sizes (up to 1.7 m total length in populations representing *T. b. biscutatus* and *T. b. quadruplex*), and, in addition to preying on terrestrial mammals and lizards, often forage arboreally for birds and spiny-tailed iguanas (*Ctenosaura*), spending daylight hours in tree hollows (Scott and McDiarmid, 1984).

Due to substantial geographic variation in size, squamation, and color pattern, several workers have suggested that *Trimorphodon biscutatus* may actually represent more than one species. Five subspecies are currently recognized: *T. b. biscutatus*, *T. b. lambda*, *T. b. lyrophanes*, *T. b. quadruplex*, and *T. b. vilkinsonii* (Fig. 5). Although recent taxonomic revisions have provided some resolution (e.g., Grismer et al., 1994; LaDuc and Johnson, in press) a comprehensive investigation of all forms of *T. biscutatus* using both morphological and molecular data is warranted.

A combined, complementary approach to systematics using both morphology and molecules is desirable, because each type of data may provide resolution where the other cannot. The relative strengths of using morphology versus molecules in systematics have been discussed at length (summarized by Hillis and Wiens, 2000). Multivariate statistical analyses of morphological data have proven particularly useful in species delimitation of widespread, polytypic taxa (e.g., Wüster and Thorpe, 1992; Slowinski and Wüster, 2000; Brown et al., 2000; Burbrik, 2001).
Figure 3. Habitat of *Trimorphodon bicutatus*. Top: Chihuahuan desert, Chinati Mountains, Presidio County, Texas. Bottom: Tropical dry forest, Palo Verde National Park, Guanacaste Province, Costa Rica. Photos by the author.
Molecular data, particularly mitochondrial DNA, are another effective tool in species delimitation (e.g., Zamudio et al., 1997; Rodriguez-Robles and de Jesus-Escobar, 2000; Burbrink et al., 2000; Leaché and Reeder, 2002; Wiens and Penkrot, 2002) and have been used widely in phylogeographic studies to infer relationships among closely related species (Avise, 2000; Stone, 2000).

In addition to inferring intraspecific phylogenetic relationships, phylogeographic studies use information about the geographical association of genealogical lineages to provide insight into the historical processes that have shaped evolutionary history (Avise, 2000). Recent
analytical advances in phylogeography based on coalescent theory, such as nested clade analysis (NCA), attempt to assess the underlying causes of geographical associations of haplotypes (Templeton, 1995). This method examines current genetic patterns in order to distinguish between recurrent forces of population structure such as gene flow and genetic drift versus historical events such as vicariance or population range expansion. The use of NCA to infer the patterns and processes that have shaped genetic variation within species has gained popularity in recent years (e.g., Althoff and Pellmyr, 2002; Brown et al., 2002; Alexandrino et al., 2002; Pfenniger and Posada, 2002; but see Knowles and Maddison, 2002).

The objectives of this work are to gain insight into the evolutionary history of species inhabiting North and Middle American aridlands, by examining patterns of genetic differentiation within a widespread, polytypic species, *Trimorphodon biscutatus*. The results of this work may serve as a testable biogeographic hypothesis other investigations of species with similar ecological affinities that may have been influenced by the same historical forces that have shaped the evolution of *Trimorphodon biscutatus*. The conservation implications of this research should not be overlooked, as the deserts of the southwestern U.S. and Mexico are suffering from the same adverse anthropogenic effects (e.g., habitat loss and the invasion of non-native species) that have affected the rest of the earth. The loss of biodiversity in this region is potentially great, and underscores the need for basic research investigating the evolution of North America’s arid-adapted flora and fauna.
Figure 5. Forms of *Trimorphodon biscutatus*. Left to right, from top: *T. b. biscutatus*: Michoacán, México; photo by J. A. Diaz, used with permission; *T. b. lambda*: Cochise Co., Arizona; *T. b. lyrophanes*: San Diego Co., California; *T. b. quadruplex*: Palo Verde National Park, Guanacaste, Costa Rica; *T. b. vilkinsonii*: Chinati Mountains, Presidio Co., Texas; *T. paucimaculatus*: Vicinity of Chamela, Jalisco, México; photo by E. Smith, used with permission. All photos by the author except where noted.
**TAXONOMIC RESUMÉ**

The taxonomy of *Trimorphodon* has been historically unstable due to the high degree of geographic variation exhibited by this taxon. The first specimen representing *T. biscutatus* was described in 1854 from “Mexique” (Duméril, Bibron, and Duméril, 1854; locality subsequently narrowed to Tehuantepec, Oaxaca by Smith and Taylor, 1950). The taxonomy has continued to change as gaps in the distribution of this species have been filled over the last century, particularly in relatively inaccessible parts of western Mexico. In total, six species have been described from specimens that are now considered to be *T. biscutatus*.

Cope described four species of *Trimorphodon* from Mexican specimens representing *T. biscutatus*: *T. major* from “near Tehuantepec”, México (1875; which he later synonymized with *T. biscutatus*, 1887), *T. vilkinsonii* from “City of Chihuahua, México” (1886), *T. lambda* from “Guaymas, Sonora” México, and *T. lyrophanes* from “Cape St. Lucas, Lower California” México (1886; localities from Scott and McDiarmid, 1984). Klauber (1924) described *T. vandenburghi* from a specimen collected in San Diego County, California, and later investigated subspecific relationships of members of the genus (1928). Taylor (1938) described a new species, *T. paucimaculatus* from Mazatlán, Sinaloa, Mexico, and also recognized *T. biscutatus*, *T. lambda*, *T. vilkinsonii*, *T. lyrophanes*, and *T. vandenburghi*. Klauber (1940) formally synonymized *T. lambda* and *T. lyrophanes*.

Smith (1941) rejected Klauber’s (1940) proposed change, citing differences in hemipenial morphology and head pattern when he reviewed the genus. He recognized thirteen different taxa in two distinct species groups. He defined members of the *biscutatus* group by the presence of a chevron or lyre-shaped mark on the head, which included the nominate *Trimorphodon biscutatus biscutatus*, as well as *T. lambda*, *T. lyrophanes*, *T. paucimaculatus*, *T.
vandenburghi, and a new subspecies, *T. b. quadruplex* from “Esteli, Nicaragua”. Smith (1941) characterized the *upsilon* group by the presence of a light nuchal collar that members of the *biscutatus* group lacked, including *T. collaris, T. fasciolata, T. latifascia, T. tau, T. upsilon, T. forbesi, and T. vilkinsonii*. Within Smith’s *upsilon* group, all but *T. vilkinsonii* are forms that are currently recognized as *T. tau*. Smith (1942) elevated *T. b. quadruplex* to full species level, and later recognized another subspecies, *T. b. semirutus*, from Guerrero, Michoacán, and Colima, based on differences in ventral and subcaudal scale counts (1943).

A number of authors subsequently suggested that recognized forms were subspecies of one widespread, polytypic taxon (Bogert and Oliver, 1945; Duellman, 1957; Jones and Findley, 1963; Loomis and Stephens, 1967; Hardy and McDiarmid, 1969). Duellman (1954) synonymized *semirutus* with *biscutatus*. Lowe (1964) and Tanner and Banta (1966) followed Klauber’s (1940) taxonomy. Fugler and Dixon (1961) assigned subspecific status to *paucimaculatus*, citing clinal variation in three meristic characters. Hardy and McDiarmid (1969) proposed uniting *Trimorphodon biscutatus, T. lambda, T. lyrophanes, T. paucimaculatus,* and *T. vandenburghi* under a single name.

Gehlbach (1971) was the last to provide a review of all members of the *Trimorphodon biscutatus* complex, uniting all species under one name with six subspecies: *T. b. biscutatus, T. b. lambda, T. b. lyrophanes, T. b. quadruplex, T. b. vandenburghi,* and *T. b. vilkinsonii*. He justified his change by claiming that members of the *biscutatus* complex exhibit clinal variation across both latitude and longitude in a number of meristic characters. However, it is clear from his own data that several of the characters he presents as evidence show clear demarcation between samples from different geographic regions, failing to exhibit the rank order in character values that would be expected for a species that varies clinally.

However, they offered little evidence for the proposed change. Following Gehlbach (1971), Scott and McDiarmid (1984) defined *Trimorphodon biscutatus* as one species subdivided into six subspecies. More recent taxonomic revisions have provided some resolution. Grismer et al. (1994) proposed that *Trimorphodon biscutatus vandenburghi* be considered a junior synonym of *T. b. lyrophanes*, as the alleged diagnostic characters that distinguish these two forms (e.g., whether the anal plate is divided or entire) appear to vary clinally throughout Baja California. LaDuc and Johnson (in press) used multivariate statistical methods to examine the relationship between *T. b. lambda* and *T. b. vilkinsonii* populations. They concluded that the *T. b. vilkinsonii* populations of the Chihuahuan Desert of New Mexico, Texas and northern Chihuahua are morphologically distinct from neighboring *T. b. lambda* populations, and proposed recognizing those populations as a distinct species, *Trimorphodon vilkinsonii.*
MATERIALS AND METHODS

UNIVARIATE AND MULTIVARIATE STATISTICAL ANALYSES OF MORPHOLOGICAL DATA

A suite of 38 meristic, mensural, and color-pattern characters (Appendix A) were scored from 218 *Trimorphodon biscutatus* specimens, with an emphasis on populations in California, Mexico, and Central America. These data were combined with an existing data set consisting of the same characters obtained from 210 specimens mainly from Arizona, Texas, New Mexico, and Sonora (LaDuc and Johnson, in press), resulting in a combined data set of 428 specimens from 18 museum collections (Appendix B). Combining complementary data sets resulted in a more thorough sampling regime than would otherwise have been achieved. A subsample of specimens from LaDuc and Johnson’s data set was re-examined in order to verify inter-measurer consistency (Lee, 1990). For each specimen, locality and sex (determined by dissection when necessary) were determined.

Statistical analyses were conducted using the software SYSTAT® version 8.0 Statistics (SPSS Inc., 1998). Males and females were analyzed separately in order to remove effects of sexual dimorphism and minimize bias caused by insufficient sample sizes for females of any given population. Specimens missing data were excluded from multivariate analyses.

Six groups were defined a priori largely on the basis of current and historical subspecific distributions (Fig. 6): 1) *Trimorphodon biscutatus biscutatus*, found from the vicinity of Cihuatlán, Jalisco, south to the vicinity of Huehuetenango, western Guatemala (38 males, 19 females); 2) *T. b. lambda*, found from Nye County, Nevada, and Washington County, Utah, south through Arizona to the vicinity of the Río Fuerte, near the Sonora/Sinaloa border, Mexico (113 males, 60 females); 3) *T. b. lyrophanes*, found from Inyo County, California, south
throughout the Baja California Peninsula (29 males, 22 females); 4) *T. b. quadruplex*, found from eastern Guatemala south to Puntarenas Province, Costa Rica (30 males, 13 females); 5) *T. b. vilkinsonii*, found in Doña Ana, Grant, and Sierra Counties, New Mexico, Brewster, El Paso, Hudspeth, and Presidio Counties, Texas, and east of the Sierra Madre Occidental in Chihuahua (41 males, 22 females); and *Trimorphodon paucimaculatus*, found generally from the Río Fuerte near the Sonora/Sinaloa border south to the vicinity of Barra de Navidad, Jalisco (24 males, 17 females).

Figure 6. Populations defined a priori in multivariate statistical analyses of morphological data.
To investigate whether independent, morphologically distinct lineages exist within *Trimorphodon biscutatus*, principal components analysis (PCA) and discriminant analysis were used. For both principal components and discriminant analysis to be strictly applicable, the data must meet a number of fundamental assumptions, including random sampling, independence among samples, and multivariate normality (McGarigal et al., 2000). However, as there is no objective way to evaluate the assumption of multivariate normality fully, I transformed only those characters for which individual size variation may have biased results. All morphometric characters were log-transformed, and all of these characters except snout-vent length were regressed against log-transformed snout-vent length. The residual values resulting from these regressions were used in addition to meristic characters in the multivariate analyses. It has been demonstrated that even moderate violations of the assumptions underlying principal components and discriminant analysis do not drastically alter results provided the sample size is sufficient (Harris, 1975; McGarigal et al., 2000).

Principal components analysis was implemented to explore and describe patterns of variation in the data, by organizing specimens along a meaningful gradient emphasizing variation among rather than similarity within samples (McGarigal et al., 2000). This method does so without a priori grouping (i.e., taxonomic) assumptions. Scatterplots for each pair of principal components were constructed to check for outliers.

Discriminant analysis was then used to investigate differences among prespecified groups (i.e., subspecies), and to determine which variables contribute the most variation to group dispersion (McGarigal et al., 2000). Discriminant analysis consists of two main procedures, canonical analysis of discriminance, which describes the differences among pre-determined
groups using a suite of discriminating characters, and classification, which predicts the group membership of unknown or future samples, based on the same suite of discriminating characters.

**Molecular Analyses**

Sampling Design

Seventy-one samples representing populations from across the species’ distribution were compared in molecular phylogenetic analyses (Appendix C; Fig. 7). An effort was made to sample widely, to encompass as much geographic variation as possible. Eight specimens of *Trimorphodon tau* were included in phylogenetic analyses and defined as the outgroup (Appendix C). Tissue samples were either donated or collected in the field. Samples collected in the field were frozen in liquid nitrogen, and donated samples were sent and retained in 95% ethanol. Both were maintained at –80°C in the laboratory in preparation for DNA isolation.

DNA Isolation, Amplification, and Sequencing

Genomic DNA was isolated from liver, muscle, or shed skin using phenol-chloroform methods following the protocol of Hillis et al. (1996) or with Qiagen Dneasy tissue kits following the manufacturer’s protocol (Qiagen, Valencia, CA). An 821 base pair (bp) fragment of mitochondrial DNA comprised of the nicotinamide adenine dinucleotide dehydrogenase subunit 4 (Ndh4 or ND4 gene) and three flanking transfer ribonucleic acid genes (tRNA\textsuperscript{His}, tRNA\textsuperscript{Ser}, tRNA\textsuperscript{Leu}) was amplified via the polymerase chain reaction (PCR) using the primers ND4 and Leu (Arévalo, Davis and Sites, 1994). One μL of concentrated DNA was used as template in 50 μL PCR reactions, along with 0.3 μL of Taq polymerase, 1 μL each of 10 μM primer, 5 μL 10× PCR buffer, 3 μL dNTP, 4 μL of 25μM MgCl\textsubscript{2}, and 37.7 μL of ddH\textsubscript{2}O. The PCR reaction consisted of 35 cycles of 94°C for 1 min., 48°C for 2 min., 72°C for 3 min. PCR
products were purified using sodium acetate or Qiagen kits following the manufacturer’s protocol (Qiagen, 2002). Purified templates were sequenced using dye-labeled dideoxy terminator cycle sequencing on an ABI 377 automated DNA sequencer (Applied Biosystems, Inc). DNA sequences were edited with Sequencher™ version 3 and aligned by eye.

Figure 7. Samples of *Trimorphodon biscutatus* used in molecular phylogenetic analyses (N=71). The location of 8 samples of *Trimorphodon tau* used as the outgroup are not shown.

Phylogenetic Analyses

Phylogenetic analyses were conducted using both parsimony and model-based (Bayesian and maximum likelihood) methods. The effects of the processes underlying DNA sequence evolution on phylogenetic reconstruction have been investigated (e.g., Collins et al., 1995;
Sullivan, 1996; Wakeley, 1996; Yang, 1996a) and models of sequence evolution that utilize information about these processes have been developed. Simulation studies conducted under complex conditions show that likelihood models of sequence evolution perform better than methods using overly simplified models (Huelsenbeck, 1995; Yang, 1996b). I used a likelihood ratio test (Huelsenbeck and Crandall, 1997) implemented in the program Modeltest version 3.06 (Posada and Crandall, 1998) to evaluate the best-fit model of sequence evolution. The general-time-reversible model (six substitution rate categories) with variable sites following a discrete gamma-distributed rates model (GTR + \[ \gamma \]) was chosen (Yang, 1993; see Swofford et al., 1996 for a description of the model).

Parsimony and maximum likelihood analyses were implemented in PAUP* v4.0b10 (Swofford, 2001). An initial topology was generated under parsimony using a heuristic search (simple stepwise addition of taxa and tree bisection-reconnection (TBR) branch swapping) with equal weighting of codon positions and classes of nucleotide substitutions. Next, the model parameters that maximized the likelihood under the GTR + \[ \gamma \] model were estimated under the likelihood criterion on the initial parsimony topology. These parameters were then fixed and used in a heuristic search (simple stepwise additions of taxa and TBR branch swapping) under the likelihood criterion. This process was reiterated until the same maximum likelihood score was obtained by subsequent searches (Swofford et al., 1996; Wilgenbusch and de Queiroz, 2000).

Bayesian analyses were conducted using the program MRBAYES version 3.0b4 (Huelsenbeck and Ronquist, 2001) to compare results from parsimony and likelihood analyses and assess support for clades identified in those analyses. Phylogenetic inference using Bayesian methods provides several advantages over other methods of inference, such as ease of
interpretation of results, ability to incorporate prior information, and some computational advantages (Huelsenbeck and Ronquist, 2001; Larget and Simon, 1999; Leaché and Reeder, 2002).

MRBAYES uses Markov chain Monte Carlo (MCMC) methods to sample from a posterior probability distribution of phylogenetic trees (Metropolis et al., 1953; Hastings, 1970; Green, 1995; see Huelsenbeck and Ronquist, 2001 for a description of the algorithm). A variant of this algorithm implemented in MRBAYES known as the Metropolis-coupled Markov chain Monte Carlo has been shown to dramatically improve the mixing of the chain, by using incrementally heated chains that facilitate exploration of phylogenetic tree space (Geyer, 1991; see Huelsenbeck and Ronquist, 2001 for a description).

Nucleotide substitution model parameters were estimated as part of the analyses (i.e., not defined a priori). To ensure convergence on the global optimal topology, four independent analyses were performed, each using random starting trees and run for $1 \times 10^6$ generations. In each analysis, four Markov chains (3 incrementally heated) were sampled every 500 generations. Analyses were considered to have converged if mean log-likelihood scores and posterior probability values were the same among analyses (Huelsenbeck and Bollback, 2001). Log-likelihood scores were plotted against number of generations to determine the point at which stationarity was reached, and points sampled prior to reaching stationarity were discarded as burn-in samples.

Nested Clade Analysis

I applied nested clade analysis (NCA; Templeton et al., 1995) to a clade consisting of individuals representing two morphologically distinct forms revealed in multivariate analyses, (*Trimorphodon biscutatus lambda* and *T. b. vilkinsonii*), to investigate putative causes of
geographical associations of mtDNA haplotypes. This relatively well-sampled clade consisted of 37 individuals from Arizona, New Mexico, Texas, and Sonora (Appendix D; Fig. 11). A haplotype network was constructed using the algorithm described by Templeton et al. (1992) as implemented in the program TCS 1.13 (Clement et al., 2000). This network was then used in the formation of a hierarchical nested design following the method proposed by Templeton et al. (1987) and Templeton and Sing (1993). Equally weighted parsimony was used to estimate the number of mutational steps between clades.

To perform statistical tests for geographical association, two geographical distance measures were calculated: clade distance ($D_c$), which measures the geographical spread of a clade, and nested clade distance ($D_n$), which measures the distance of a clade from the geographical center of the nested clade (Templeton et al., 1995). These distances were then compared between interior and tip clades by calculating the difference between the average interior distance and the average tip distance, ($I-T)_c$ and ($I-T)_n$, respectively, within each clade. This contrast provides a temporal component to the analysis, in that tips are expected to be younger and interior clades are expected to be older under neutral coalescent theory (Templeton et al., 1995). Next, the observed $D_c$ and $D_n$ values were compared to a distribution of these values generated by 1000 random permutations in a nested contingency analysis of geographical locations against haplotypes using the program GeoDis version 2.0 (Posada et al., 2000). The inference key of Templeton et al. (1995) was used to interpret the results of this statistical test for geographical association.
RESULTS

UNIVARIATE ANALYSES OF MORPHOLOGICAL DATA

The re-examination of a subsample of LaDuc and Johnson’s (in press) dataset revealed that nearly identical measurements were taken from the same specimens by different observers, suggesting inter-measurer bias was negligible. Univariate descriptive statistics from morphometric and meristic characters are provided in Appendix E.

MULTIVARIATE STATISTICAL ANALYSES OF MORPHOLOGICAL DATA

Males

Six geographically contiguous samples representing currently or formerly recognized subspecies assorted together in the principal components analysis (Fig. 8). Nine factors were extracted from the original 36 characters, accounting for 71.2% of the total variance. However, the first two accounted for 36.3% of the total variation and were relatively more informative in detecting group structure.

Characters with factor loadings greater than 0.50 or less than −0.50 are considered significant in interpreting principal component structure (Hair et al., 1987). Characters with large loadings on the first principal component include size (log-transformed snout-vent length) scale counts (ventrals, subcaudals, and dorsal scale rows), and differences in body blotches (length, division, and count; Table 1). The majority of these significant loadings were positive, indicating a direct relationship between the variable and the component (McGarigal et al., 2000). These characters provide a division along the first principal component between northern populations (Trimorphodon biscutatus lyrophanes, T. b. lambda, and T. b. vilkinsonii) and southern populations (T. paucimaculatus, T. b. biscutatus, and T. b. quadruplex; Fig. 8A).
Characters with large loadings on the second principal component included additional body blotch characters (width, shape, and distance between blotches), providing an east-west separation among *T. b. lyrophanes*, *T. b. lambda*, and *T. b. vilkinsonii*, as well as among *T.*

Figure 8. Bivariate scattergrams for males from the principal components analysis (A) and canonical analysis of discriminance (B,C). The Wilks’ $\lambda$ test statistic and associated p values from the canonical analysis of discriminance are shown.
Table 1. Factor and canonical loadings for males. Loadings greater than 0.50 or less than -0.50 are considered significant and are shown in bold for emphasis.

<table>
<thead>
<tr>
<th>Character</th>
<th>PC 1</th>
<th>PC 2</th>
<th>CV 1</th>
<th>CV 2</th>
<th>CV 3</th>
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<tr>
<td>VNT</td>
<td><strong>0.829</strong></td>
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<td><strong>0.657</strong></td>
<td>0.170</td>
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<td>SBCDL</td>
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<td>-0.261</td>
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<td>0.325</td>
<td>-0.331</td>
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<td>SRW1</td>
<td><strong>0.850</strong></td>
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<td>0.147</td>
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<td>SWBTH1</td>
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<td>SWBTH2</td>
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<td>SWBTH3</td>
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<td>LHTSP1</td>
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<td>LHTSP2</td>
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<td>-0.296</td>
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<td>0.009</td>
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<td>-0.061</td>
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<td>-0.143</td>
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<tr>
<td>BBTH</td>
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<td>0.496</td>
<td><strong>-0.500</strong></td>
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<tr>
<td>TBTH</td>
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<td>0.398</td>
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</tr>
<tr>
<td>PBDIV</td>
<td>0.148</td>
<td>0.462</td>
<td>-0.086</td>
<td>-0.063</td>
<td>-0.035</td>
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<tr>
<td>SBDIV</td>
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<td>HSBTH</td>
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<td><strong>-0.704</strong></td>
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<td>BSQ12</td>
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<td>BSQ1314</td>
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<td>0.036</td>
<td>-0.125</td>
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<tr>
<td>BSQAN</td>
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<td><strong>-0.781</strong></td>
<td>-0.263</td>
<td>0.296</td>
<td>0.294</td>
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<tr>
<td>L10SVL</td>
<td><strong>0.583</strong></td>
<td>0.047</td>
<td>0.130</td>
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<tr>
<td>RES.L10.TL</td>
<td>0.090</td>
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<td>-0.306</td>
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<tr>
<td>RES.L10.SNL</td>
<td>0.298</td>
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<td><strong>-0.687</strong></td>
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<td>-0.379</td>
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<td>RES.L10.HDL</td>
<td>0.371</td>
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<td><strong>0.778</strong></td>
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<tr>
<td>RES.L10.DBES</td>
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<td>0.053</td>
<td>0.002</td>
<td>0.097</td>
<td>0.456</td>
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<tr>
<td>RES.L10.DBEN</td>
<td>0.305</td>
<td>0.005</td>
<td>0.024</td>
<td>0.359</td>
<td>-0.339</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Character</th>
<th>PC 1</th>
<th>PC 2</th>
<th>CV 1</th>
<th>CV 2</th>
<th>CV 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
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<td>29.773</td>
<td>7.764</td>
<td>4.102</td>
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<tr>
<td>% variance explained</td>
<td>21.4</td>
<td>14.9</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>proportion. total dispersion</td>
<td>--</td>
<td>--</td>
<td>0.668</td>
<td>0.840</td>
<td>0.932</td>
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</table>
*paucimaculatus*, *T. b. biscutatus*, and *T. b. quadruplex* (Fig. 8A). In contrast to significant loadings on the first principal component, most of these loadings were negative, indicating an inverse relationship between the characters loading on this component (Table 1).

Canonical analysis of discriminance revealed highly significant differences among the subspecies and provided further separation among prespecified groups (Wilks’ \( \lambda \) = 0.0001, df=38; approx. \( F = 17.7833, df = 190, p < 0.0001 \); Fig. 8). Canonical loadings reveal that ventral scale counts, body blotch differences (counts, width, and distance between blotches) and residual values from two morphometric measurements (snout length and head length, both log-transformed and regressed against log-transformed snout-vent length) provide the greatest relative contribution to group dispersion (Table 1). The first two canonical variate scores provided almost complete separation among the six prespecified groups (Fig. 8B). The third canonical variate score also contributed to group dispersion, resulting in six non-overlapping groups in multivariate space (Fig. 8B,C). The nonparametric resampling method of jackknifing was used to test the statistical significance of the canonical functions based on the correct classification rate (McGarigal et al., 2000). The classification matrix correctly classified unknown specimens 95% of the time (Table 2).

**Females**

Results from multivariate analysis of females were similar to those from analysis of males. The same six geographically contiguous samples assorted together in the principal components analysis (Fig. 9). Eleven factors were extracted from the original 36 characters, accounting for 79.1% of the total variance. As with males, the first two components explained almost half of the total variance (36.5%) and were relatively more meaningful in detecting group structure.

<table>
<thead>
<tr>
<th>FORM</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>% CORRECT</th>
</tr>
</thead>
<tbody>
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<td>1</td>
<td>26</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>2</td>
<td>0</td>
<td>64</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>94</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>3</td>
<td>24</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>89</td>
</tr>
<tr>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>23</td>
<td>0</td>
<td>1</td>
<td>96</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>22</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>88</td>
</tr>
<tr>
<td>Total</td>
<td>27</td>
<td>67</td>
<td>25</td>
<td>23</td>
<td>25</td>
<td>8</td>
<td>95</td>
</tr>
</tbody>
</table>

Characters with large loadings on the first principal component (absolute magnitude greater than 0.50) included scale counts (ventrals, subcaudals, and dorsal scale rows), and differences in body blotches (length, division, and count). Of these significant loadings, all except one (body blotch counts) were positive, indicating a direct relationship between the variable and the component. These characters provide the same north-south division along the first principal component as in males. Characters with large loadings on the second principal component included additional body blotch characters (width, shape, and distance between blotches; Fig. 9A). As was observed in males, most of these loadings were negative, indicating an inverse relationship between the characters loading on this component.

Similar to analysis of males, canonical analysis of discrimination in females revealed significant differences among the subspecies and provided further separation among prespecified groups (Wilks’ \( \lambda = 0.0000 \), df=38; approx. \( F = 9.6982 \), df =190, \( p<0.0000 \); Figure 9B,C). Canonical loadings reveal that scale counts (subcaudal and dorsal scale rows) and residual values from two morphometric measurements (snout length and distance between eyes, both log-transformed and regressed against log-transformed snout-vent length) provide the greatest
relative contribution to group dispersion. The first two canonical variate scores provided almost complete separation among groups (Fig. 9B). The third canonical variate score also contributed to group dispersion, resulting in six non-overlapping groups in multivariate space (Fig. 9B,C). The jackknifed classification matrix correctly classified unknown specimens 91% of the time (results not shown).

Figure 9. Bivariate scattergrams for females from the principal components analysis (A) and canonical analysis of discriminance (B,C). The Wilks’ test statistic and associated p values from the canonical analysis of discriminance are shown.
PHYLGENETIC ANALYSIS

Of the 821 nucleotide positions, 194 were variable and 172 were parsimony-informative. Parsimony analysis using equal weights for codon positions and classes of nucleotide substitution resulted in 104 most-parsimonious trees (length = 363, Consistency Index = 0.5748 excluding uninformative characters). A heuristic search using the GTR + \( \Gamma \) model parameters optimized on the initial parsimony tree resulted in the same topology. The topology did not change following successive maximum likelihood iterations. Four separate Bayesian analyses converged upon a similar log-likelihood score (average = -3470.6; Table 3) at or before 50,000 generations, suggesting stationarity was achieved (Fig 10 A,B). Thus, the first 100 of 2,000 total samples were discarded as burn-in for each analysis, and the remaining samples were combined. The low value of the estimated gamma shape parameter alpha suggests that most sites evolve very slowly, but a few sites have moderate to high rates (Fig. 10 F; Table 3). The GTR + \( \Gamma \) model parameter estimates (post burn-in) averaged across the four analyses are shown in Table 3. The same tree topology from maximum likelihood analyses was also recovered using Bayesian methods (average length across four independent analyses = 307.5; Fig. 11).

Phylogenetic Relationships

Phylogenetic analyses strongly support the monophyly of *Trimorphodon biscutatus* (posterior probability = 100%). Significant phylogeographic structure was detected, with analyses supporting monophyly of taxa traditionally ranked as subspecies, with one exception: *T. b. lambda* and *T. b. vilkinsonii* were recovered together in the same clade (posterior probabilities =100%; Fig. 11).

Individuals from western Guatemala, Oaxaca, and Guerrero representing the nominate form *Trimorphodon biscutatus biscutatus* formed one clade, sister to individuals from eastern
Table 3. The GTR + $\Gamma$ model parameters estimated from four independent Bayesian analyses and averaged. The G\textsuperscript{T} T transformation rate is fixed at 1.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>Standard Dev.</th>
<th>Minimum</th>
<th>Maximum</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>lnL</td>
<td>-3470.589</td>
<td>11.588</td>
<td>-3512.619</td>
<td>-3431.687</td>
<td>7360</td>
</tr>
<tr>
<td>$r_{GT}$</td>
<td>1.000</td>
<td>0.000</td>
<td>1.000</td>
<td>1.000</td>
<td>7360</td>
</tr>
<tr>
<td>$r_{CT}$</td>
<td>19.790</td>
<td>5.809</td>
<td>6.127</td>
<td>38.482</td>
<td>7360</td>
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<tr>
<td>$r_{CG}$</td>
<td>0.356</td>
<td>0.384</td>
<td>5.9 $\times$ 10^{-5}</td>
<td>4.128</td>
<td>7360</td>
</tr>
<tr>
<td>$r_{AT}$</td>
<td>2.671</td>
<td>0.912</td>
<td>0.595</td>
<td>7.340</td>
<td>7360</td>
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<tr>
<td>$r_{AG}$</td>
<td>37.438</td>
<td>9.083</td>
<td>11.685</td>
<td>50</td>
<td>7360</td>
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<td>$r_{AC}$</td>
<td>2.306</td>
<td>0.784</td>
<td>0.536</td>
<td>6.050</td>
<td>7360</td>
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<tr>
<td>$\Delta_a$</td>
<td>0.366</td>
<td>0.016</td>
<td>0.311</td>
<td>0.424</td>
<td>7360</td>
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<tr>
<td>$\Delta_c$</td>
<td>0.286</td>
<td>0.014</td>
<td>0.232</td>
<td>0.350</td>
<td>7360</td>
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<tr>
<td>$\Delta_g$</td>
<td>0.109</td>
<td>0.010</td>
<td>0.076</td>
<td>0.154</td>
<td>7360</td>
</tr>
<tr>
<td>$\Delta_t$</td>
<td>0.238</td>
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<td>0.190</td>
<td>0.290</td>
<td>7360</td>
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<tr>
<td>$\Gamma$</td>
<td>0.051</td>
<td>4.542 $\times$ 10^{-4}</td>
<td>0.050</td>
<td>0.052</td>
<td>7360</td>
</tr>
</tbody>
</table>

Guatemala, Nicaragua, Honduras, and Costa Rica, representing the $T. b. quadruplex$ subspecies. Together, these southernmost clades are sister to a northern group consisting of the remaining three clades. Analyses support a relatively large divergence between these northern and southern clades (9-10% uncorrected pairwise sequence divergence). The northern clade consists of populations found generally north of the Transverse Volcanic Axis, including a $paucimaculatus$ clade representing samples from Jalisco and Sinaloa, a $lyrophanes$ clade representing California and Baja California peninsula populations, and a Sonoran plus Chihuahuan Desert clade, made up of individuals from Texas, New Mexico, Arizona, and Sonora, representing both $T. b. lambda$ and $T. b. vilkinsonii$. Samples from this $lambda + vilkinsonii$ clade exhibited very little genetic differentiation across large geographic distances, compared to samples from within other clades. Average pairwise distances for members of the five different clades are shown in Table 4.
Figure 10. Burn-in plots of estimated parameter values against number of generations from Bayesian analyses. A. Log-likelihood plot of four independent analyses. B. Same plot as (A) at higher resolution. Arrow indicates approximate point at which stationarity was reached (~50,000 generations). Tree length (C), substitution rates (D), base frequencies (E), and alpha value (F) from a representative analysis, consistent with the other three analyses. Tree topologies and nucleotide substitution model parameter values estimated prior to burn-in were discarded.
Figure 11. Phylogenetic relationships of *Trimorphodon biscutatus* based on the 50% majority rule consensus tree from Bayesian analysis under the GTR + $\Gamma$ model of sequence evolution. Posterior probability values are shown for major nodes. The same topology was recovered in the maximum likelihood analysis employing the same model.
Table 4. Uncorrected pairwise sequence divergence values for five clades of *Trimorphodon biscutatus* plus the outgroup *Trimorphodon tau* recovered in phylogenetic analyses.

<table>
<thead>
<tr>
<th></th>
<th>lambda + vilkinsonii</th>
<th>lyrophanes</th>
<th>paucimaculatus</th>
<th>biscutatus</th>
<th>quadruplex</th>
<th>tau</th>
</tr>
</thead>
<tbody>
<tr>
<td>lambda + vilkinsonii</td>
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<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>lyrophanes</td>
<td>5-6%</td>
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<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>paucimaculatus</td>
<td>5-6%</td>
<td>6-7%</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>biscutatus</td>
<td>9-10%</td>
<td>9-10%</td>
<td>9-10%</td>
<td>--</td>
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<td>--</td>
</tr>
<tr>
<td>quadruplex</td>
<td>9-10%</td>
<td>8-10%</td>
<td>9%</td>
<td>6-7%</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>tau</td>
<td>10-11%</td>
<td>9-10%</td>
<td>10-11%</td>
<td>8-10%</td>
<td>8-10%</td>
<td>--</td>
</tr>
</tbody>
</table>

**Nested Clade Analysis**

Twelve unique haplotypes were recovered in the nested clade analysis. The nested contingency analysis revealed significant geographical associations for 3 clades (Table 5). Inadequate sampling was found for clade 3-1, resulting in the inability to discriminate among fragmentation, range expansion, and isolation by distance. Contiguous range expansion was inferred for clades 3-3 and the total cladogram (Fig. 12).

Table 5. Significant results from the nested contingency analysis. Subscript S and L indicate that values are significantly smaller or larger, respectively, than would be expected under a random distribution.

<table>
<thead>
<tr>
<th>Clade</th>
<th>3-1</th>
<th>3-3</th>
<th>Total cladogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nested clade</td>
<td>2-1</td>
<td>2-6</td>
<td>3-3</td>
</tr>
<tr>
<td>tip (1) or interior (0)</td>
<td>1</td>
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<td>0</td>
</tr>
<tr>
<td>$D_C$</td>
<td>170.14_S</td>
<td>-</td>
<td>7.41_S</td>
</tr>
<tr>
<td>$D_N$</td>
<td>195.31_S</td>
<td>458.72_L</td>
<td>-</td>
</tr>
<tr>
<td>(I-T)$_C$</td>
<td>-</td>
<td>-200.86</td>
<td>-</td>
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<td>(I-T)$_N$</td>
<td>-</td>
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<tr>
<td>Inference</td>
<td>Inadequate sampling</td>
<td>Range expansion</td>
<td>Range expansion</td>
</tr>
</tbody>
</table>
Figure 12. Left: Haplotype network and nested design for haplotypes from 37 individual *Trimorphodon biscutatus*. Unsampled haplotypes are represented by ‘0’. Haplotypes recovered are numbered 1-12. Each branch between haplotypes represents one mutational difference. Right: Location of samples used in nested clade analysis.
DISCUSSION

CONFLICT AND CONGRUENCE

Results from multivariate statistical analyses of morphological data and molecular phylogenetic analyses are largely congruent, although some discordance was observed. Multivariate analyses revealed a number of morphological characters that reliably discriminate among six distinct forms of *Trimorphodon biscutatus*, including size (log-transformed snout-vent length), scale counts (ventrals, subcaudals, and dorsal scale rows), differences in body blotches (width, shape, division, distance between blotches and counts) and two morphometric characters (snout length and head length). In sum, six geographically contiguous, morphologically distinct groups exist, congruent with currently recognized subspecies and one formerly recognized species.

Molecular phylogenetic analyses provided strong support for five clades, four of which were concordant with groups recovered in multivariate analyses and consistent with traditional subspecific taxonomy. Interestingly, the fifth clade consists of geographically proximate samples representing two morphologically distinct taxa, *Trimorphodon biscutatus lambda* of the Sonoran Desert, and *T. b. vilkinsonii* of the Chihuahuan Desert. Individuals from this clade exhibit relatively little to no sequence divergence over large geographic distances (e.g., complete identity across > 400 miles).

At least two alternative hypotheses may be invoked to explain the high degree of genetic similarity shared among these geographically proximate, morphologically distinct forms: 1) recurrent gene flow is occurring between taxa which have experienced rapid morphological evolution, or 2) introgressive hybridization of *Trimorphodon biscutatus lambda* mitochondrial
haplotypes into *T. b. vilkinsonii* populations has occurred as a result of secondary contact. I used nested clade analysis (NCA) of mtDNA haplotypes to further investigate this hypothesis for the clade consisting of geographically proximate samples representing both taxa. The results of this analysis indicated an overall pattern of contiguous range expansion. Although results from NCA analyses are usually interpreted in terms of organismal population history, this pattern may instead reflect the history of the molecules under investigation, which do not necessarily represent true population history. That is to say that introgression of the *T. b. lambda* haplotype into *T. b. vilkinsonii* populations would also leave the genetic signature of an apparent range expansion if an introgressed haplotype swept rapidly through a population following secondary contact. This hypothesis is testable using nuclear DNA sequence data.

**Taxonomic Conclusions**

Mitochondrial DNA has proven to be a very powerful tool in phylogeographic studies, often revealing cryptic species within widespread lineages (e.g., Zamudio et al., 1997; Leaché and Reeder, 2002; Burbrink et al., 2000; Wiens and Penkrot, 2002, Rodriguez-Robles and de Jesus-Escobar, 2000). However, concern over inferring species trees from single locus gene trees is warranted (summarized in Hare, 2001). As a case in point, species delimitation based solely on the mtDNA genealogy presented herein would support five independent lineages, and may be a misinterpretation of evolutionary history if introgressive hybridization between independent lineages has confounded interpretation of the species phylogeny.

Frost and Hillis (1990) noted the dearth of examples of widespread, genetically cohesive taxa present in nature, and suggested that most broadly distributed, polytypic species likely represent multiple evolutionary species. Results presented herein support Frost and Hillis’ hypothesis, providing compelling evidence that species diversity is not accurately reflected by
current taxonomy in *Trimorphodon biscutatus*. The debate over species concepts and definitions has been argued at length, and remains a fundamental issue in evolutionary biology. de Queiroz (1998) has provided some resolution, suggesting that all modern species definitions fundamentally agree that species are population-level segments of evolutionary lineages, or, single lines of ancestry and descent. Disagreement arises with respect to the criteria used to delimit species (e.g., reproductive isolation, diagnosability, exclusive coalescence, etc.), which can be viewed as distinct time intervals along the temporally continuous process of lineage diversification (de Queiroz, 1998). I follow de Queiroz’s general lineage concept of species in concluding that *Trimorphodon biscutatus* (sensu lato) is composed of at least five and probably six evolutionary species: *T. biscutatus* (sensu stricto), *T. lambda*, *T. lyrophanes*, *T. paucimaculatus*, *T. quadruplex*, and *T. vilkinsonii*.

**GEOLOGICAL HISTORY**

In an attempt to understand spatial patterns of differentiation within *Trimorphodon biscutatus* from a historical biogeographic perspective, I investigated the geological and climatic events that may have shaped the distribution and diversification of this group. Despite the sub-optimal conditions for fossilization characterized by most arid regions, a relatively detailed reconstruction of vegetational and climatic changes in the regional deserts of the southwestern U.S. and northern Mexico has been generated using pollen records, geological studies of pluvial lakes, and particularly through studies of fossil flora found in woodrat (*Neotoma*) middens (e.g., Van Devender, 1990). The geological history of southern Mexico and Central America is not as well characterized. Although a detailed account of the geological history of North America is beyond the scope of this work, I summarize below the geological and climatic events hypothesized to have shaped the distribution and diversification of *Trimorphodon biscutatus*. 
Of particular interest are events of several distinct time periods, beginning in the early Tertiary. The insularization of the deserts of northern Mexico and the southwestern U.S., as well as other distinct arid regions of Middle America (Mexico and Central America), began with a period of intense mountain formation during the early Tertiary (McDowell and Keizer, 1977). During the mid-Tertiary, approximately 32-23 mya, the Sierra Madre Occidental of western Mexico formed as a result of volcanic activity related to a zone of subduction of the lithosphere off the west coast of Mexico (McDowell and Keizer, 1977). Beginning near the U.S. Mexico border just south of Arizona and New Mexico, the range extends southward to the Río Grande de Santiago, forming the border between Nayarit and Jalisco (Campbell, 1999). There, the range passes beneath the younger Transverse Volcanic Axis, which extends eastward roughly along latitude 19 degrees North (Campbell, 1999; Swanson and McDowell, 1984). The formation of the Sierra Madre Occidental resulted in the initial separation of what are now the Chihuahuan and Sonoran Deserts during the Miocene, probably fragmenting the ancestral distribution of what were once widespread, xeric-adapted lineages (Fig. 13).

Concurrent with the formation of the Sierra Madre Occidental in the mid-Tertiary, differential tectonic plate movements between the North American and Pacific plates tore a large margin of land from continental western Mexico and moved it northwest, forming the Baja California Peninsula (Lonsdale, 1989). Approximately 5.5 to 4 mya, the Gulf of California (Sea of Cortés) began to form, resulting from subsidence due to the separation of the peninsula (Lonsdale, 1989). During the mid-Pliocene (approximately 3 mya), the Gulf of California transgressed northward into lowland areas of California and Arizona, forming the Bouse embayment along the Colorado River (Blair, 1978; Eberly and Stanley, 1978; and Buising, 1990) and the San Gorgonio Constriction in the Salton Trough (Boehm, 1984; Ingle, 1987). The gulf
extended along the lower Colorado River as far north as Lake Mead in southern Nevada, following a 40-50 km wide shallow embayment known as the Bouse Sea (Metzger, 1968). These marine incursions effectively isolated the peninsula and much of southwestern California west of the Coachella Valley from the remainder of the continent (Metzger, 1968; Smith, 1970; Lucchitta, 1979; Winkler and Kidwell, 1986; Fig. 14).

Figure 13. Map depicting the three regional deserts of the southwestern U.S. and northern Mexico, and the Sierra Madre Occidental and Transverse Volcanic Axis.
Coincident with geologic events in northern Mexico during late Miocene and Pliocene times, a period of intense volcanic activity dramatically changed the landscape of southern Middle America (summarized in Campbell, 1999). Of particular interest to the questions at hand is the formation of the highlands of southern Guatemala, which occurred during two distinct time intervals. The extensive western plateau was formed during the late Miocene and early Pliocene, whereas a younger chain of volcanoes extending roughly parallel to the Pacific coast was formed along the western portion of the plateau during Quaternary times (Williams, 1960).

The intense period of volcanic activity that molded southwestern Guatemala during the Quaternary caused sufficient changes in the local climatic regime so as to sever a xeric corridor of habitat that once extended along the Pacific versant of Mexico from southern Sonora to Central America (Stuart, 1954). The uplift of these volcanoes resulted in mesic conditions on the southern slopes of the volcanoes along the Pacific coast of southwestern Guatemala and southeastern Chiapas, creating cooler, wetter habitat unsuitable for many xeric-adapted lineages.
Today, an abrupt turnover from xeric, subhumid vegetation to humid forest occurs around the vicinity of Tonalá, Chiapas, Mexico, and this humid forest extends southeastward along the coast to near Escuintla in Guatemala (Campbell, 1999; Fig. 15). Xeric-adapted species formerly found in this region became isolated in arid interior valleys, such as the Río Grijalva and Río Motagua Basins, that occur in the rain shadow of these coastal volcanoes (Fig. 15). These valleys show a high degree of similarity to tropical dry forests of Pacific foothills of western Mexico, and are characterized by vegetation typical of arid tropical deciduous forests, such as *Acacia*, *Bursera*, *Mimosa* spiny grasses, thornscrub, cacti such as *Pilocereus*, *Cereus*, *Opuntia*, and *Melocactus*, as

![Figure 15. Map illustrating the Guatemalan highlands (bordered by black). The humid forest existing south of these volcanoes from Tonalá, Chiapas to Escuintla, Guatemala provides a barrier to dispersal for allopatric forms of *Trimorphodon biscutatus*, which occur in drier portions along the coast and in the arid interior valleys of the Río Grijalva and Río Motagua.](image)
well as Agave. The rocky foothills bear little vegetation, whereas dense scrub and oaks (Quercus) dominate higher slopes (Campbell and Vannini, 1988).

More recent climatic changes have continued to influence the evolutionary history of xeric-adapted lineages of North America. During the Pleistocene, when cooler, more mesic conditions prevailed, arid regions contracted to lowland basins at more southerly latitudes. These isolated desert refugia were surrounded by mesic grassland at lower elevations and woodland at higher elevations, effectively restricting faunal exchange between arid islands of habitat. As a result, distinct, regional areas of endemism developed. When these “filter-barriers” to gene flow disappeared during interglacial periods such as the present, lineages either remained restricted to the region in which they adapted, or, dispersed through the filter-barrier. Dispersal across a former barrier to gene flow likely resulted in secondary contact and hybridization between some lineages.

Today, remnants of these mesic filter-barriers that persisted following the most recent (Wisconsin) glacial maximum have profoundly influenced the distribution of aridland fauna by facilitating limited dispersal of certain species, but preventing a wholesale admixture of distinct, aridland biota (Brown and Lomolino, 1998). A well-characterized example is the relatively narrow region of desert grassland in extreme southeastern Arizona, southwestern New Mexico, and adjacent Mexico, between the Chihuahuan and Sonoran deserts (Figure 17). This ecotonal transition zone known as the Deming Plains (Hafner and Riddle, in press) or the Cochise filter barrier (Morafka, 1977) has influenced the evolutionary history of a number of arid-adapted species including Trimorphodon biscutatus, and provides an opportunity for investigations into a variety of evolutionary processes.
An overlay of the results presented herein on geography suggests that the geologic and paleoclimatic events discussed above have played an important role in the diversification of the *Trimorphodon biscutatus* species group. Comparisons of congruent patterns of differentiation in other organisms provide further support for this biogeographic hypothesis.

Beginning with the deepest nodes of the tree, we can investigate the potential causal mechanisms responsible for genetic differentiation within the *Trimorphodon biscutatus* species group. The largest division (9-10% sequence divergence) supported by phylogenetic analyses (100% posterior probability) separates a northern clade (*T. b. lyrophanes*, *T. paucimaculatus*, and *T. b. lambda* + *T. b. vilkinsonii*) from a southern clade (*T. b. biscutatus* and *T. b. quadruplex*). These two assemblages meet in the general vicinity of the Transverse Volcanic Axis of southern Mexico, suggesting that the uplift of this volcanic range separated the common ancestor of the *T. biscutatus* group into northern and southern lineages. A similar biogeographic break has been reported in other taxa. A vicariant event associated with the formation of the Transverse Volcanic Axis is hypothesized to have separated ancestral populations of the toad *Bufo valliceps* (Mulcahy and Mendelson, 2000) and freshwater fish of the genus *Poeciliopsis* (Mateos et al., 2002) across this region, approximately 4.2-7.6 mya and 8-16 mya, respectively.

The Southern Clade

Within the southern clade, analyses support the monophyly of *Trimorphodon biscutatus* and *T. quadruplex*. Previous workers suggested that the break between these two forms occurred in the vicinity of the Isthmus of Tehuantepec, probably due to the fact that a marine embayment may have bisected southern Mexico during the late Tertiary (Campbell, 1999; Fig. 4).
Furthermore, there is a marked turnover in many amphibian lineages across this region (Campbell, 1999). However, results presented herein suggest that the break between *T. biscutatus* and *T. quadruplex* occurs further south along the Pacific coast of Guatemala, with *T. biscutatus* populations to the east and *T. quadruplex* populations to the west (Fig. 15, 16). A sample from the Upper Grijalva Basin of southwestern Guatemala (UTAR 42306) represented the easternmost sample of *T. b. biscutatus* in the analysis, forming a clade with samples to the west from Oaxaca and Guerrero. Samples from the Río Motagua Valley and populations south of Escuintla, Guatemala, formed a clade with other *T. quadruplex* samples from Honduras, Nicaragua, and Costa Rica. In addition to the *Trimorphodon biscutatus* species complex, a number of other xeric-adapted reptile lineages derived from the Pacific coast of Mexico are restricted to arid, interior valleys that drain to the Atlantic, including *Heloderma horridum*, *Rhinoclemmys pulcherrima*, *Sceloporus squamosus*, *Cnemidophorus deppei*, *Loxocemus bicolor*, *Sibon carri*, *Micrurus nigrocinctus*, *Crotalus durissus*, and *Porthidium ophryomegas* (Campbell and Vannini, 1988).

Figure 16. Left: *Trimorphodon biscutatus* from Guatemala: Huehuetenango, 1.9 road km N of Nenton on road to Gracias a Dios (UTA R-46489). Right: *T. quadruplex* from Guatemala: El Progreso, 8.0 km W of junction of Guat. Hwy. CA-9 and CA-14 (1.6 mi E of Río Morazan on CA-14) (KU 191125). Photos by J. A. Campbell, used with permission.
The Northern Clade

Within the northern clade, phylogenetic analyses provided strong support (100%) for *Trimorphodon lyrophanes* as the sister group of the remaining species (Fig. 11). A vicariant event resulting from the separation of the Baja California Peninsula from mainland Mexico (~5.5 mya) is likely responsible for this break.

Although traditionally considered part of the Sonoran desert, the Baja California Peninsula has recently been named as a distinct regional desert (the Peninsular Desert) based on a high degree of endemism exhibited by the region’s fauna (Riddle et al., 2000a). Using a combination of published data and their own phylogeographic work on mammals, Riddle et al. (2000b,c) conducted a comparative phylogeographic investigation of 12 arid-adapted mammalian, avian, amphibian, and reptilian lineages found on the peninsula and in nearby regional deserts of the southwestern U.S. and northern Mexico. Riddle et al. (2000a) observed relatively deep levels of divergence (7.5-8.7%) between peninsular lineages and those found in the mainland Sonoran Desert. Similarly, *Trimorphodon lyrophanes* of southern California and the Baja Peninsula show 5-6% divergence from *T. lambda* lineages of the Sonoran desert. Riddle et al. (2000a) attributed this pattern of differentiation to the northern incursion of the Gulf of California into lowland areas of southern California and Arizona during the late Pliocene (3 mya; Fig. 14), a hypothesis proposed previously by Murphy (1983) and Grismer (1994). The Bouse embayment probably restricted gene flow among ancestral, arid-adapted populations. There is a marked turnover in reptilian lineages across the Salton Trough region in southern California from Sonoran Desert forms to the east to Peninsular Desert forms to the west and south along the peninsula. In addition to *Trimorphodon lyrophanes* and *T. lambda*, other species that exhibit this pattern include *Coleonyx variegatus, Lichanura trivirgata, Crotaphytus*
vestigium, Crotaphytus bicinctores, and Pituophis catenifer (Stebbins, 2003). Lamb et al. (1989) reported a distinct genetic break in mtDNA haplotypes of desert tortoises (Gopherus agassizi) across the Colorado River, consistent with the role of the Bouse embayment as a Pliocene barrier to dispersal. However, results from phylogeographic analysis of mtDNA from desert iguanas (Dipsosaurus dorsalis) and chuckwallas (Sauromalus obesus) failed to show any significant differences across the Colorado River, suggesting that the evolutionary history of the region may be more complex (Lamb et al., 1992).

Riddle et al. (2000a) provide evidence for two additional, previously hypothesized vicariant events within the Baja California Peninsula, a Pliocene seaway across the Isthmus of La Paz, and a mid-Pleistocene midpeninsular seaway. Evidence for a seaway across the Isthmus of LaPaz is supported by a high degree of reptilian endemism in the Cape Region of the peninsula (Grismer, 1994). In contrast, Trimorphodon lyrophanes does not exhibit genetic subdivision across the Isthmus of LaPaz. However, similar to the findings of Riddle et al. (2000a) and Upton and Murphy (1997), a pattern of differentiation is exhibited by T. lyrophanes between southern and northern portions of the Baja Peninsula (2-3% sequence divergence). Upton and Murphy (1997) were the first to hypothesize that a midpeninsular seaway across the northern portion of Baja California Sur just south of the Vizcaino Peninsula during the mid-Pleistocene (1 mya) was responsible for the north-south pattern of genetic differentiation they observed in mtDNA lineages of side-blotched lizards (Uta). Riddle et al. (2000a) found levels of 2-4% sequence divergence between northern and southern peninsular lineages in all but two of the taxa analyzed, concluding that this pattern was consistent with a mid-peninsular vicariant event. There is some disagreement as to whether a mid-peninsular seaway ever existed in Baja California. Grismer (2002) reported that geologic evidence for a mid-peninsular seaway is
lacking, instead suggesting that north-south patterns of genetic differentiation may be the result of restricted gene flow due to adaptation to different local environments, which change rather abruptly midway down the Baja Peninsula. Hafner and Riddle (in press) cite the disjunct distributions of 42 species of marine fish and invertebrates on the Pacific and Gulf sides of the Vizcaíno Desert (Present, 1987) and 17 species of mammals, reptiles and birds that show genetic differentiation north and south of the Vizcaíno region (Riddle et al., 2000a) as compelling evidence for a seaway.

Phylogenetic analyses provide strong support for the separation of *Trimorphodon paucimaculatus* from a common ancestor with *T. lambda* and *T. vilkinsonii* (Fig. 11). *Trimorphodon paucimaculatus* is found north of the Transverse Volcanic Axis, from the vicinity of Barra de Navidad, Jalisco, northward along the coast to the vicinity of the Río Fuerte, just south of the border with Sonora (Fig. 7). Here, this lineage likely comes into contact with *T. lambda* of the Sonoran desert in an ecotonal transition zone between semiarid tropical deciduous forest and Sonoran Desert (Fig. 17). Lyresnakes that appear phenotypically intermediate between *T. paucimaculatus* and *T. b. lambda* have been collected in a relatively narrow portion of southern Sonora and northern Sinaloa, suggesting recent gene flow may have occurred. It seems, however, that exchange across the ecotonal transition zone of southern Sonora is restricted. *Trimorphodon lambda* of the Sonoran desert and *T. paucimaculatus* of the semiarid Pacific lowlands of Sinaloa, Nayarit, and Jalisco are characterized by approximately 5.5% sequence divergence. The southernmost limit of the Sonoran desert remains contested, based largely on the decision of whether or not to include coastal and foothill thornscrub as one of the biotic community subdivisions in the definition. Shreve (1942) concluded that the Río Fuerte in southern Sonora bounded the southern margin of the Sonoran Desert (Fig. 17). Turner and
Figure 17. Map of the southwestern U.S. and northern Mexico, illustrating location of the Chihuahuan and Sonoran Deserts, Cochise filter barrier region, and transition to coastal and foothill thornscrub south of the Sonoran Desert along the Pacific lowlands.
Brown (1982) revised Shreve’s subdivisions, and excluded thornscrub from their definition as a non-desert biome. In sharp contrast, based on phylogeographic analysis of a group of arid-adapted rodent species, Hafner and Riddle (in press) depicted a much broader definition of the Sonoran Desert, including tropical thornscrub associations extending southward throughout Sinaloa and into Nayarit. However, they noted a distinct turnover in species composition across southernmost Sonora, with some species occurring only north of the Río Yaqui, others only south of the Río Fuerte (Fig. 17), and several found only in the intervening 200-km transitional zone located between these rivers. Hafner and Riddle noted moderate levels of sequence divergence (3.5%) across the Río Fuerte region just south of the Sonoran-Sinaloan border in species that occur more widely throughout the region.

Arid-adapted lineages of reptiles and amphibians show an abrupt turnover in this region from Sonoran desert species to lineages derived from the tropical deciduous forests of the Pacific lowlands of southwestern Mexico. In addition to Trimorphodon lambda, many other endemic Sonoran reptiles and amphibians reach their southern distributional limits in the vicinity of the Río Fuerte near the Sonoran-Sinaloan border (e.g., Crotalus tigris, Heloderma suspectum, Gopherus agassizii, and Bufo alvarius; Stebbins, 2003). From the south, a variety of species from the Pacific versant of western Mexico reach their northern limits in the same region (e.g., Trimorphodon tau, Micrurus distans, Crotalus basiliscus, Agkistrodon bilineatus, and Heloderma horridum; Campbell and Lamar, 1989). Sinaloan populations of another species of nocturnal colubrid snake (Hypsiglena torquata) also show a pattern of genetic differentiation from other populations in western North America (Mulcahy, pers. comm.). Clearly, lineages inhabiting arid tropical deciduous forest and coastal and foothill thornscrub associations of the
Pacific versant of southwestern Mexico have a very different evolutionary history than the regional Sonoran Desert of Sonora, Arizona and southeastern California.

Although the uplift of the Transverse Volcanic Axis was likely responsible for the separation of the ancestor of the *Trimorphodon biscutatus* group into northern and southern lineages, it appears that secondary contact may occur today between members of these clades in southern Jalisco in the vicinity of the border with Colima. Here, *T. biscutatus* (representing the southern clade) and *T. paucimaculatus* occur either in syntopy or very close parapatry. Samples have been collected within one km of one another, but show no evidence of morphological intergradation.

*Trimorphodon lambda* and *Trimorphodon vilkinsonii*

A surprising result obtained from phylogenetic analyses is the absence of substantial phylogeographic structure distinguishing *Trimorphodon lambda* and *T. vilkinsonii*. Morphological data clearly distinguish these taxa, yet the majority of specimens exhibit almost complete sequence identity. The same haplotype was recovered in individuals from extreme southeastern Arizona (Cochise County), representing *T. lambda*, and samples to the east from the Chihuahuan Desert of New Mexico and Texas, representing *T. vilkinsonii*. Samples from west of Cochise County in other parts of Arizona, also representing *T. lambda*, were sister to the remainder of individuals in this clade (Fig. 11). Accurate estimation of the nature of gene flow across this region will require additional data in the form of recombinant, nuclear DNA, however it seems safe to say that recent gene flow has occurred between populations from extreme southeastern Arizona and populations to the east in the Chihuahuan Desert of New Mexico. This result is perhaps not as surprising given the history of recent climatic change that has greatly impacted the distribution of aridland species across this region.
Populations from the Deming Plains region of southeastern-most Cochise County, Arizona and extreme southwestern Hidalgo County, New Mexico, are associated with rocky areas of relief within a relatively narrow, desert-grassland ecotone between the Chihuahuan and Sonoran deserts (the Cochise filter-barrier; Fig. 17). This transitional region acts as a barrier to dispersal for many species endemic to the Chihuahuan and Sonoran deserts. Although both the Chihuahuan and Sonoran are warm, dry regional deserts, each has its own unique climatic regime and suite of endemic flora and fauna. However, certain widespread, xeric-adapted species appear to be less restricted by the barrier and have exchanged genes across the “filter” in the recent past.

Gehlbach (1971) was the first to note that some lyresnakes from extreme southeastern Arizona east of the Chiricahua Mountains (the Cochise filter-barrier region) appear phenotypically intermediate between Chihuahuan and Sonoran Desert forms. He concluded that these individuals represent intergrades between subspecies of one, widespread, polytypic species. However, LaDuc and Johnson (in press) showed that these intermediate individuals from southeastern Arizona consistently grouped with *T. b. lambda* populations to the west in multivariate statistical analyses of morphological data. They concluded that *T. b. vilkinsonii* is in fact an independent evolutionary lineage, and recommended recognizing it once again as a distinct species. Multivariate statistical results presented here confirm LaDuc and Johnson’s findings.

The ancestral lineage of *Trimorphodon biscutatus lambda* and *Trimorphodon biscutatus vilkinsonii* may have been widespread across arid northern Mexico prior to the formation of the Sierra Madre Occidental during the mid-Tertiary. The uplift of these mountains provided the initial division between the incipient Chihuahuan and Sonoran Deserts, and likely fragmented
widespread, xeric-adapted lineages into populations east and west of the sierra. More recently, Pleistocene climate changes resulting from pluvial-interpluvial oscillations likely caused alternate range expansions and contractions in desert lineages. During pluvial periods, deserts contracted to isolated, lowland refugia surrounded by grassland and woodland at higher elevations. These mesic regions likely proved effective barriers to dispersal for many arid-adapted lineages during the most recent pluvial period (10,000-20,000 yr. B. P.). Geologic evidence suggests that a relatively narrow band of vegetation such as this was present in the vicinity of the Deming Plains of southeastern Arizona and southwestern New Mexico during this time (Van Devender, 1990). During the hypsithermal, or period of maximum warmth since the last glacial period (8,000 yr. B. P.), aridland lineages expanded their ranges, and Chihuahuan and Sonoran lineages may have experienced secondary contact across the Cochise filter-barrier. The most recent corridor across the filter-barrier that facilitated communication between the two regional deserts formed during the late Holocene, approximately 4,500 years B.P. (Van Devender, 1990).

Given the high degree of morphological differentiation exhibited by *Trimorphodon biscutatus vulkinsonii* and *Trimorphodon biscutatus lambda*, it seems likely that Chihuahuan and Sonoran lineages of *Trimorphodon biscutatus* diverged in allopatry on the order of millions of years ago, and experienced secondary contact very recently during the Holocene, resulting in introgressive hybridization. Congruent patterns of differentiation and hybridization among co-distributed lineages across the same region provide further support for this hypothesis.

In their phylogenetic study of sand lizard relationships, Wilgenbusch and de Queiroz (2000) found that fringe-toed lizards (*Uma*) show a large separation between populations of the Mojave and Sonoran Deserts (*U. notata, U. inornata, and U. scoparia*) and those of the
Chihuahuan Desert (*U. paraphygas* and *U. exsul*) based on the mitochondrial 12S and cyt *b* genes. In the same study, they also noted that geographically proximate samples of earless lizards, *Holbrookia maculata thermophila* and *H. m. flavilenta* from Cochise County, Arizona, are characterized by much greater genetic distances from one another than from geographically more distant samples in the larger clades to which they belong. These results are in stark contrast to the phylogeographic pattern exhibited by *Trimorphodon lambda* and *T. vilkinsonii* across the same region. Similar to Wilgenbusch and de Queiroz (2000), Mulcahy (pers. comm.) found that nightsnakes (*Hypsiglena*) show a high degree of differentiation between populations of the Sonoran Desert and those from the Chihuahuan Desert across the intervening Cochise filter-barrier region.

Unlike the previous examples, other Chihuahuan and Sonoran Desert forms in addition to *Trimorphodon biscutatus* seem to have experienced recent secondary contact and hybridized across the Cochise filter-barrier. Perhaps the most well characterized example is seen in the western whiptail lizard *Cnemidophorus tigris*. Dessauer et al. (2000) investigated populations of *Cnemidophorus tigris punctilinealis* of the Sonoran Desert and *C. t. marmoratus* of the Chihuahuan Desert using a suite of both morphological and molecular characters. They identified three narrow hybrid zones located in the vicinity of the Deming Plains of extreme southwestern New Mexico characterized by steep step clines in mtDNA haplotypes and protein loci. Their estimates of gene flow indicate that these clines resulted from secondary contact during the most recent connection between the Chihuahuan and Sonoran Deserts, approximately 1,000-5,000 yr. B. P.
CONCLUSION

In conclusion, multiple lines of evidence support at least five and probably six independent evolutionary species within *Trimorphodon biscutatus* (sensu lato). Four of these, *T. biscutatus*, *T. quadruplex*, *T. lyrophanes*, and *T. paucimaculatus* are genetically and morphologically distinct. The remaining two lineages, *T. b. vilkinsonii* and *T. b. lambda*, exhibit almost no genetic differentiation at the mitochondrial level, however the hypothesis of introgressive hybridization is tenable based on geological history and congruent phylogeographic patterns in other species. I tentatively propose elevating these taxa to species level pending results from nuclear DNA phylogenetic analyses to characterize the nature of gene flow between these two lineages further. I propose the following taxonomic changes to reflect the evolutionary history of this species group more accurately.

SPECIES DIAGNOSES

(Modified from Scott and McDiarmid, 1984)

*Trimorphodon biscutatus* (Duméril, Bibron, and Duméril), 1854

Suggested common name: Western Lyresnake

*Dipsas bi-scutata* Duméril, Bibron, and Duméril, 1854:1153 (see species synonymy)


*Dipsas biscutata*: Dugés, 1884:337. Unjustified emendation.

*Trimorphodon biscutatus biscutatus*: Smith, 1941:159.

**DISTRIBUTION:** Found from the vicinity of El Cihuatlán, Jalisco south along the Pacific coast throughout Colima, Michoacan, Guerrero, extreme southern Puebla, Oaxaca and Chiapas to the vicinity of the state of Huehuetenango, southwestern Guatemala.

**DIAGNOSIS:** Up to 1.75 m total length, primary dark body blotches fewer than 30 (avg. 19), 4-12 scales wide along middorsal line at midbody, often shaped like an ‘H’, with central pale spots usually dividing primary blotches, resulting secondary blotches undivided, usually with elongate, paired markings between primary blotches; ventrals 232-279 in males, 254-286 in females; midbody scale rows 22-28; complete lyre on back of head, anal divided.

Trimorphodon lambda Cope, 1886

Suggested common name: Sonoran Lyresnake


Trimorphodon lambda lambda: Dixon et al., 1962:98.

DISTRIBUTION: Found from Nye County, Nevada and Washington County, Utah, south through Arizona, and extreme southeastern California, north and east of the Salton Sea, to southern Sonora, México.

DIAGNOSIS: Usually less than 1m total length; primary dark body blotches 18-30, 3-9 scales wide, central pale spots usually divide body blotches, resulting secondary blotches undivided; ventrals 211-240 in males, 223-249 in females; midbody scale rows 19-25; usually with a complete lyre on back of head, may be absent, especially in specimens from Cochise Co., Arizona; anal divided.

Trimorphodon lyrophanes (Cope), 1860

Suggested common name: California Lyresnake


Trimorphodon vandenburghi Klauber, 1924:17. Type locality, “Wildwood Ranch (elevation 1520 feet) near Ramona, San Diego County, California.” Holotype, California Academy of Sciences 58172, male, collected by E. B. Woodworth and Laurence M. Klauber, 4 May 1924 (not examined by author).


DISTRIBUTION: found from Inyo County, California southward through southern California west of the Salton Sea, throughout most of the Baja California Peninsula and on Cerralvo, Danzante, San José, San Marcos, and Tiburón islands.

DIAGNOSIS: Usually less than 1 m total length; primary dark body blotches 25-48, 2-7 scales wide, central pale spots divide primary blotches, resulting secondary blotches undivided; ventrals 214-237 in males, 221-250 in females; midbody scale rows 19-24; dark lyre on top of head often incomplete near the apex; anal divided or entire.

Trimorphodon paucimaculatus, Taylor, 1938

Suggested common name: Sinaloan Lyresnake


DISTRIBUTION: Found generally from extreme southern Sonora near the Sonora/Sinaloa border southward along the coast to the vicinity of Barra de Navidad, Jalisco, México.

DIAGNOSIS: May reach over 1 m total length; primary dark body blotches elongate, rectangular, numbering 17-31, light spot does not usually completely divide primary blotches; ventrals 237-258 in males, 248-265 in females; midbody scale rows 21-24; dark lyre on top of head complete; anal divided.

Trimorphodon quadruplex (Smith), 1941

Suggested common name: Central American Lyresnake


**DISTRIBUTION**: Found from southeastern Guatemala along the Pacific coast south to Puntarenas Province, Costa Rica; also present in some dry Atlantic slope valleys in Guatemala, Honduras, and Nicaragua.

**DIAGNOSIS**: Up to 1.75 m total length; primary dark body blotches 15-24, 5-15 scales wide, central light spots divide body blotches into secondary blotches, which are also further subdivided by central light markings; ventrals 249-266 in males, 250-266 in females; midbody scale rows 23-27; dark lyre on top of head complete; anal divided.

*Trimorphodon vilkinsonii*, Cope, 1886


*Trimorphodon wilkinsoni*: Cope, 1887:68. Invalid emendation.


**DISTRIBUTION**: found in Doña Ana, Grant, and Sierra Counties, New Mexico, Brewster, El Paso, Hudspeth, and Presidio Counties, Texas, and east of the Sierra Madre Occidental in Chihuahua, México.
DIAGNOSIS: Usually less than 0.7 m total length; primary dark body blotches less than 25, light central spot does not divide blotches into secondary blotches; ventrals 221-251 in males, 225-241 in females; midbody scale rows 21-25; markings on top of head variable, usually consisting only of dark spots or a very reduced chevron; anal divided.
**LITERATURE CITED**


Klauber, L. M. 1928. The Trimorphodon (lyre snakes) of California, with notes on the species of the adjacent areas. Transactions of the San Diego Society of Natural History 5: 183-194.


APPENDIX A

MORPHOLOGICAL CHARACTERS

1. Nature of the anal plate, divided or entire (ANAL)
2. Number of ventral scales (VNT)
3. Number of subcaudal scales excluding the terminal spine (SBCDL)
4-5. Number of supralabials on the left (SUPRAL) and right (SUPRAR) sides of the head
6-7. Number of infralabials on the left (INFRAL) and right (INFRAR) sides of the head
8-9. Number of preoculars on the left (PREOCL) and right (PREOCR) sides of the head
10-11. Number of postoculums on the left (POSTL) and right (POSTR) sides of the head
12-13. Number of loreals on the left (LORL) and right (LORR) sides of the head
14-16. Number of dorsal scale rows at the 25th ventral (SRW1), midbody (SRW2), and 25th ventral anterior to the vent (SRW3)
17. Number of body blotches (BBTH)
18. Number of tail blotches (TBTH)
19-21. Number of scales on the midline encompassed by the blotches (including the light center) at the 25th ventral (SWBTH1), at midbody (SWBTH2), and at the 25th ventral from vent (SWBTH3)
22-24. Number of scales on the midline encompassed by the light center of the blotches at the 25th ventral (LHTSP1), at midbody (LHTSP2), and at the 25th ventral anterior to the vent (LHTSP3)
25-28. The number of scales on the midline in the interspace between blotches between the 1st and 2nd bands (BSQ12), 7th and 8th bands (BSQ78), 13th and 14th bands (BSQ1314), and last set of bands anterior to vent (BSQAN).
29. Log-transformed snout-vent length (L10SVL)
30. Residual of log-transformed tail length regressed against log-transformed snout-vent length (RES.L10.TL)
31. Residual of log-transformed snout length regressed against log-transformed snout-vent length (RES.L10.SNL)
32. Residual of log-transformed head length regressed against log-transformed snout-vent length (RES.L10.HDL)
33. Residual of log-transformed distance between eyes regressed against log-transformed snout-vent length (RES.L10.DBES)
34. Residual of log-transformed distance between eye and nostril regressed against log-transformed snout-vent length (RES.L10.DBEN)
35. Completeness of the lyre-shaped head marking (LYRE; 0 = no markings, 1 = only spots, 2 = lyre mostly incomplete, 3 = lyre mostly complete, 4 = complete lyre present)
36. Number of "H"-shaped blotches (HSBTH; 0 = no H-shaped blotches, 1 = first blotch H-shaped, 2 = 1-5 blotches H-shaped, 3 = 6-10 blotches H-shaped, 4 = 11-15 blotches H-shaped)
37-38. Nature (divided or entire) of the primary (PBDIV) and secondary (SBDIV) blotches.
APPENDIX B

SPECIMENS EXAMINED

Museum acronyms follow Leviton et al. (1985), except EAL (private collection of Ernie A. Liner)

Trimorphodon biscutatus biscutatus (57): MEXICO: Chiapas (CAS 140948, 163754, LACM 38210, 122900-1); Colima (KU 67731, LACM 37335, 59135, 130115, MVZ 72194, 76716, 161563, UMMZ 80200-1, 114567); Guerrero (KU 87474, LACM 58136, MVZ 161565-7, UMMZ 85768); Jalisco (KU 95787, 95970, 106288, 37336, 136970-1, LACM 37337); Michoacan (KU 29492, MVZ 170791, UMMZ 104606, 105154, 112517, 112519-21, 121529, 114565-6, 118953); Oaxaca (CAS 143898, KU 137675, LACM 7103, 8480, 38207-9, 58137-8, 65245, 103370, 103372, 114146, 128455).

Trimorphodon biscutatus lambda (174): MEXICO: Sonora (BYU 36809, 37202, 37174, 41159, 41196, CAS-SU 24047, 24051, EAL 115, KU 67732, LACM 122903, SRSU 1484, UAZ 9633-4, 9637-41, 27062-63, 28065-66, 30737, 39750, 44011-12, 45603, 45902, 46462, 46781). UNITED STATES: Arizona: Cochise Co. (AMNH 80160, 85043-45, 94858-59, 99334-35, 111209, 115624, 126747, BYU 16744, 32086, CAS 190689-90, CM 69729, NMSU 2384, SWRS 158-59, UAZ 26931, 26958, 26966, 37760, 37762, 39595, 39756-57, 40059, 41560-61, 41563, 41576, 43601, 46851, UF 53466, 84195, UMMZ 120313, UNM 25235, 49754, 50227, 50449, 51682, 53654, 53910, 53939, UTEP 5477, 11409); Gila Co. (CAS 80656, CM 53753, FMNH 74970); Graham Co. (UAZ 26955); Greenlee Co. (CAS 190691); La Paz Co.: UTEP 15989); Maricopa Co. (CM 48621, 48669, 51418); Pima Co. (CAS 33846, 129202, 152522, 158220, 190686, FMNH 74971, LSUMZ 28649, SRSU 1485, 5662, UAZ 26929, 26934, 26947, 26951, 26959, 26965, 35788, 37767-68, 37840, 37849, 39593, 46270, 46495, 47321, 48894, 49428, 50086, 50197, UTEP 2771, 11021, 11199, 15326); Pinal Co: (UAZ 26927, 37764-65); Santa Cruz Co. (LSUMZ 32895, UAZ 26927, 26939-41, 26962, UMMZ 75785, 75809, 170823, UTEP 15916); Yavapai Co. UAZ 37850, 46285); Yuma Co. (UNM 41641, 55161); New Mexico: Catron Co. (NMSU 2959, UNM 48105); Hidalgo Co. (AMNH 80380, MVZ 67228, NMSU 4958, UAZ 35952, UNM 4200). Nevada: Clark Co. (CAS-SU 19921); Nye Co. (BYU 17939, 23727). Utah: Washington Co. (BYU 501-2, 653, 1798, 23801).

Trimorphodon biscutatus lyrophanes (51): MEXICO: Baja Norte (KU 185657-8, LACM 126261, 134001); Baja Sur (LACM 103399, MVZ 11903-4, 57931, 104219-20, 117313-4, 117372, 128495, 140881, 142046, 161562). UNITED STATES: California: Imperial Co. (LACM 27920, 67280); Inyo Co. (CAS 65496, 143731); Kern Co. (KU 62902, LACM 132249); Orange Co. (LACM 103402); Riverside Co. (LACM 103404-11, 103413-6); San Bernadino (LACM 2711); San Diego Co. (KU 8497, 74366-8, LACM 2710, 27924, 28700, 103412, 103433, 103434-8, 103439); Nevada: Nye Co. (CAS-SU 19922).

Trimorphodon biscutatus quadruplex (43): COSTA RICA: Guanacaste (KU 35513, 63894-5, 102532-4, LACM 113916-8, 114144, MVZ 170797, 80026, UMMZ 123332, 123588, 131292-3); Puntarenas (KU 63896, 86586). EL SALVADOR: (KU 183972), La Libertad (KU 116968, 183971), Sonsonate (LACM 114145). GUATEMALA: (UMMZ 131294-5), El Progreso (KU 191125, MVZ 146984-5), Santa Rosa (UMMZ 107347-8). HONDURAS: Choluteca (KU 140081), Valle (KU 116967), (MVZ 78764). MEXICO: Chiapas (UMMZ 113770); Oaxaca.
NICARAGUA: Chinandega (KU 125012), Chontales (KU 63897), Managua (KU 86259, 174425-8), Matagalpa (KU 42307-10, 86260) Rivas (KU 101925, 125011).

*Trimorphodon biscutatus vilkinsonii* (63): MEXICO: Chihuahua (AMNH 96653, CM 60117-9, UNM 34382-4 USNM 14268). UNITED STATES: New Mexico: Dona Ana Co. (NMSU 3615, 5095, 6944); Luna Co. (UTEP 11273); Sierra Co. (NMSU 5489-90, UNM 16264-6, UNM 17799, UNM 25668, UTEP 15597). Texas: Brewster Co. (BYU 40886, SRSU 2550, 3713, 4043, 6228, 6231, UTEP 10724-25, 11200, 12146); El Paso Co. (AMNH 28862, CAS 139998, UTEP 1752, 1754, 1979, 2328, 2329, 2452, 2458, 2482, 2484, 2491, 2492, 2526, 2532, 2533, 2694, 4017, 6227, 12104, 12330, 13671-72); Jeff Davis Co. (LSUMZ 34726); Presidio Co. (FMNH 201039, SRSU 1689, 4595, 4767, TNHC 3332, 28404, UTEP 10762, 11358).

*Trimorphodon paucimaculatus* (41): MEXICO: Jalisco (KU 67734, 187744, LACM 25932); Nayarit (LACM 103374-6, 103378-82, MVZ 70278, 71334); Sinaloa (CAS-SU 24052, KU 73636, 78931, 80765, LACM 7089-93, 7095, 7097-8, 7100, 28716, 103379, 103381, 103383-9, 122377, 122902, ROM 14959, UAZ 37770, 37708)

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APPENDIX C

LOCALITY OF SAMPLES USED IN MOLECULAR ANALYSES


*Trimorphodon biscutatus* samples.

*T. b. biscutatus* (N=5): (1) Guatemala: Huehuetenango: 14.5 km S Nenton (UTA R 42306); (2) Mexico: Oaxaca: 2.3 mi. S Tehuantepec on road to Salinas Cruz (MVZ 143524); (3) Mexico: Oaxaca: Carretera El Camaron, San Carlos Yautpe (ENEPI 6749); (4) Mexico: Oaxaca: 13.7 mi. N on Hwy. 185 from junction with Hwy. 190 (MVZ 164979); (5) Mexico: Guerrero: Rio Chilta Bridge (LSUMZ 39531).

*T. b. lambda* (N=31): (6) USA: Arizona: Cochise Co.: Chiricahua Mts., Portal Rd. at 1.1. mi. (rd) N Herb Martyr Rd (UAZ 54126); (7) USA: Arizona: Cochise Co.: Perilla Mts., Hwy. 80, ~ 8 mi. N of Douglas (LSUMZ 84797); (8) USA: Arizona: Cochise Co.: Hwy. 80, 27.1 mi. S of Price Canyon Road (CLS 430); (9) USA: Arizona: Cochise Co.: Hwy. 80, 1.0 mi. N. Hwy. 90 (DGM 774); (10) USA: Arizona: Cochise Co.: Mule Mts., Hwy. 80, 3.2 mi. E of AZ 92 (UAZ 53614); (11) USA: Arizona: Cochise Co.: Mule Mts., Hwy. 90, 0.6 mi. W of AZ 80 (UAZ 53615); (12) USA: Arizona: Cochise Co., Mule Mts., 3.0 mi. E of jct. AZ 80/AZ 92 (UAZ 53616); (13) USA: Arizona: Cochise Co.: Mule Mts., Hwy. 80, 4.0 mi. E of jct. AZ 80/AZ 92 (UAZ 53617); (14) USA: Cochise Co.: Chiricahua Mts., Cave Creek Canyon Rd., 0.9 mi. E of Southwestern Research Station (LSUMZ 83684); (15) USA: Cochise Co.: Chiricahua Mts., Cave Creek Canyon Rd., 1.2 mi. E of Southwestern Research Station (UTEP 11409); (16) USA: Cochise Co.: Chiricahua Mts., 2.7 mi. E of Southwestern Research Station (LSUMZ 83685); (17) USA: Arizona: Cochise Co.: 16.5 mi. E of Douglas (AZ 80 E and N intersection) (LSUMZ 83695); (18) USA: Cochise Co.: Portal Rd., 1. mi. E of Portal (MVZ 229993); (19) USA: Arizona: Gila Co.: AZ 288, 3.0 mi. N jet. with AZ 88 (LACM 131374); (20) USA: Arizona: Gila Co.: 13.9 mi. NW (by Hwy. 88) Claypool (MVZ 232612); (21) USA: Arizona: Graham Co.: Hwy. 266, 2.7 mi. W of Hwy. 191, Pinaleño Mts. (DGM 1079); (22) USA: Arizona: La Paz Co.: Harcuvar Mts., Alamo Dam Rd., 10 mi. N Wenden, Cunningham Pass (UTEP 15989); (23) USA: Arizona: Maricopa Co.: 0.5 mi. (rd) W Eagle Eye Rd. on Hwy. 60 (UAZ 54127); (24) USA: Arizona: Maricopa Co.: 9 mi. N of I-10 on Wickenburg-Hassayampa Rd. at Coyote Wash (TJD 084); (25) USA: Arizona: Mohave Co.: Black Mts., 4.5 mi. E of Oatman Road/US Rte. 66 (UTA-R 50702); (26) USA: Arizona: Pima Co., Tucson Mts. (TJL 770); (27) USA: Arizona: Santa Cruz Co.: Santa Rita Mts., Mt. Hopkins, 0.3 mi. N of Whipple Observatory picnic area on observatory road (UAZ 54125); (28) USA: Arizona: Santa Cruz Co.: AZ Hwy. 82 at 0.7 mi. (rd.) S Patagonia Lake State Park entrance (UAZ 54128); (29) USA: Arizona: Santa Cruz Co.: jct. of E Three R Rd. and Hwy. 82, Patagonia Mts. (DGM 767); (30) USA: Arizona: Yavapai Co., 13 mi. SE Bagdad on Hwy. 96 (MVZ 232829); (31) USA: Arizona: Yavapai Co., 8 mi. SE Bagdad on Hwy. 96 (MVZ 232830); (32) USA: Arizona: Yuma Co., Old Hwy. 80, 0.4 mi. W of Mohawk.
Exit (no. 54), I-8 (DGM 847); (33-34) Mexico: Sonora: Alamos, Río Cuehujaki (ROM 14897, 14945); (35) Mexico: Sonora: 7.8 mi. NE of Ures on Hwy. 14 (TWR 1342); Mexico: Sonora: Hwy. 1, 18 km. ENE Navojoa (JRO 683).

*T. b. lyrophanes* (N=17): (36-37) Mexico: Baja California Norte: El Rosario (ROM 14484, JRO 266); (38) Mexico: Baja California Norte: 15.0 mi. (rd.) W of Bahía de los Ángeles (BYU 34638); (39) Mexico: Baja California Sur: 5 mi. NW Santa Rosalia (ROM 14482); (40) Mexico: Baja California Sur: Hwy. 1, 1.5 km E San Ignacio (JRO 531); (41) Mexico: Baja California Sur: Hwy. 1, 4 km E San Ignacio (JRO 536); (42) Mexico: Baja California Sur: 0.5 mi. S “El Trinco” (probably El Triunfo; ROM 34073); (43) Mexico: Baja California Sur: 3 mi. from San Dionysius (ROM 34074); (44) Mexico: Baja California Sur: Isla San Marcos (RWM 1920); (45) Mexico: Baja California Sur: Hwy. 1, 5.4 mi. W San Ignacio (13580); (46) Mexico: Baja California Sur: Hwy. 1, 29.2 mi. W Ciudad Constitución (13608); (47) Mexico: Baja California Sur: 3.1 mi. N (by Mex. Hwy. 1) San Ignacio (MVZ 233299); (48) USA: California: Inyo Co.: Trona-Wildrose Rd. crossing Slate Range N of Trona (TJD 085); (49) USA: California: San Bernardino Co.: Joshua Tree National Park (4/24/2000); (50) USA: California: San Diego Co.: Hwy. 78, Sentenac Canyon (5/6/1999); (51) USA: California: San Diego Co.: 1.0 mi. SW of Borrego Springs, on S22 Montezuma Valley Road; distance measured from Palm Canyon Road intersection (TJD 088); (52) USA: California: San Diego Co.: off Hwy. 94 on Barrell Lake Rd..

*T. b. vilkinsonii* (N=7): (53) USA: Texas: Presidio Co.: TX 170, 11.5 mi. NW Lajitas (UETP 10762); (54) USA: Texas: Brewster Co.: TX 118, 8 mi. N jct. with TX 170, foot of South Luna Vista Hill (UETP 12146); (55) USA: Texas: Brewster Co., about 30 mi. S of Alpine (TJL 883); (56) USA: Texas: El Paso Co.: Franklin Mts. (TJL 882); (57) USA: Texas: Presidio Co.: Chinati Mts. (TJL 338); (58) USA: New Mexico: Sierra Co.: NM 51, 2.7 rd. mi. ESE Rio Grande bridge in Truth or Consequences (UETP 15597); (59) USA: New Mexico: Grant Co.: off Tyrone-Redrock Rd. (TJD 086).

*T. b. quadruplex* (N=9): (60) Costa Rica (MVZ 164854); (61) Guatemala: Santa Rosa: Carretera Escuintla-Taxisco (UTA R 44717); (62-63) Guatemala: Zacapa: Cabañas, Aldea El Arenal, ca. 1.0 km. NNE from El Arenal Quebrada Seca (UTA R 42221, 42222); (64) Guatemala: El Progreso: Carretera Guatemala-Cob n (UTA R 42299); (65-66) Honduras: Comayagua: Comayagua, Aldea Las Mesas (MSM 450, UTA R 41247); (67-68) Nicaragua: Isla de Ometepe, San Ramón, Volcán Madera (AEH 021, 026).

*T. paucimaculatus* (N=2): (69) Mexico: Sinaloa: playa N of Mazatlán on road to Alamos (ROM 14959); (70) Mexico: Jalisco: Municipio La Huerta, Arroyo Colorado, 6 km. NE Estación de Biología, Reserva Chamele-Cuixmala (ENS 10594).

### APPENDIX D

**Latitude and Longitude Coordinates for Samples Used in Nested Clade Analysis**

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APPENDIX E

UNIVARIATE STATISTICS

Morphometric (in mm) and meristic (number of scales) variation in *Trimorphodon biscutatus biscutatus*, *T. b. lambda*, *T. b. lyrophanes*, *T. b. quadruplex*, *T. b. vilkinsonii*, and *T. paucimaculatus*. Table entries for each character include mean ± 1 standard deviation, range, and sample size. See text for Appendix A for character abbreviations.

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APPENDIX F

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CTTAGGAAATGAACTCTTTCCAACCACCAATTTATATCGACTGAACTCAG
AATATCTGACATTTTACATACGTCTTTTACTTACACCAATTTATATCGACTGAACT
CTTAGGAAATGAACTCTTTCCAACCACCAATTTATATCGACTGAACTCAG
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'AZCochise(UAZ54126)'
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GCAACATTAGCCAACCTCAAACCTTAGGCAATACAAACAGATTAAAGCCCTAATCGC
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ATGAGCTTTTACGAGCCACTTTATATGTACCTCACCGATCCACTTACGAGA
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CTTAGGAAATGAACTCTTTCCAACCACCAATTTATATCGACTGAACTCAG
AATATCTGACATTTTACATACGTCTTTTACTTACACCAATTTATATCGACTGAACT
CTTAGGAAATGAACTCTTTCCAACCACCAATTTATATCGACTGAACTCAG
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'AZCochise(UAZ54126)'
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75
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CCAAAGGATAATAGTATTC [816]
'AZSantaCruz(UAZ54128)'
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CCAAAGGATAATAGTATTC [816]
'AZMaricopa(UAZ54127)'
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CCAAAGGATAATAGTATTC [816]
'AZSantaCruz(UAZ54125)'
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CCAAAGGATAATAGTATTTCC [816]
'AZYuma(DGM847)'
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CCAAAGGATAATAGTATTTCC [816]
'AZCochise(CLS430)'
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'AZCochise(LSUMZ83685)'
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GGAATTTTCTACAACTGATATTGAAGCTAC
GAACTATCCTAGCTAGCTAGCCTAGAAACAACTGATATTGAAGCTAC
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CCAAAGGATAATAAGTATTCC [816]
'AZGila(MVZ232612)'
CTAGCCCGCAATCCTATTAAATATTAGGGGGGTACGGGATCATATTGGAATAGGCACAAAACC
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'AZMaricopa(TJD084)'
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CCAAGGATAATAATGATTCC [816]
'AZPima(TJL770)'
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'AZSantaCruz(DGM767)'
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'AZZMaricopa(DGM767)'
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'AZYavapai(MVZ232829)'
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'AZYavapai(MVZ232830)'
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'MXSonora(JRO683)'
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'MXSonora(ROM14897)'
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CCAAAGGATAAATAGTTATTCC [816]
'MXSonora(ROM14945)'
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'MXSonora(TWR1342)'
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CCAAAGGATAAATAGTTATTCC [816]
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CCCAAGGATAATAGTATTCC [816]
'MXSinaloa(ROM14959)'
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'MXBajaSur(13608)'
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CCCAAGGATAATAGTATTCC [816]
'MXBajaSur(13608)'
CTAGCCGCAATCTCTATTAAAACCTAGGGGGGTACGGTATCATTCGAATAAACACAAAC
CTTACACCAAAATACATCTGTCCTGGAATATTAATACACATCAGAGGGTATGGCATCATCCGAATAAACACAAAC
AGCAACACTAGCCAACCTAACCCTGCTACACAAACACAGATTTAAAAAGCCTTAATCGC
AGAAAGCTCAGCCACACCTAACCCTGCTACACAAACACAGATTTAAAAAGCCTTAATCGC
CTACTACATTCACTTTGAATGGCTGAATTGTGCTGCTACCCCTATGAGGGGAGTTATAAGACCTGCTAACTCTTTTTCCTGG::ATAATATA:CCAGTCCCTCTCA
CCCAAGGATAATAGTATTCC [816]
'MXSinaloa(ROM14959)'
CTAGCCGCAATCTCTATTAAAACCTAGGGGGGTACGGTATCATTCGAATAAACACAAAC
CTTACACCAAAATACATCTGTCCTGGAATATTAATACACATCAGAGGGTATGGCATCATCCGAATAAACACAAAC
AGCAACACTAGCCAACCTAACCCTGCTACACAAACACAGATTTAAAAAGCCTTAATCGC
AGAAAGCTCAGCCACACCTAACCCTGCTACACAAACACAGATTTAAAAAGCCTTAATCGC
CTACTACATTCACTTTGAATGGCTGAATTGTGCTGCTACCCCTATGAGGGGAGTTATAAGACCTGCTAACTCTTTTTCCTGG::ATAATATA:CCAGTCCCTCTCA
CCCAAGGATAATAGTATTCC [816]
CC:GAGGGGACCATAAGACCTGCTAATCTTTTTCCTGGTAAATAATTAACCAGCCCCCTCTACCAAAAGGATAAATAGTATTC [819]
'MXBajaSur(JRO536)' CTAGCCCGCAATCTTATTTAAAAACTAGGAGGGGTATGGCAGCATCTCCGAATAACACAAAC CCTACCAAATAAAAACAGACCTATTTCTACATTTATGTACTCTCCTCTTATGAGG AGCAACACTAGCCAACCTACCTGGCCTACAACAAAAAGATTTTAAAGGCGCTAAATCG CATACTCATCTATTAGCCACATAGGCCCTAGTTATCGCGACACACTATAATCCAAACAC ATATGAGTTTTTCTAGGGGCTATAGCCCTAATATCGCCCGAACTACTCCTCATCAA CATTATCTGCTCCCAACACACATAACTGCTATCCCCCCCAGCATATAATCTACAGGAGAATCTACTTATCTAC CAACATCGAGATTCTCAACTGCTATAATCTACAGGAGAACTACCAATTTACATCTGCT CCTACAAACACTTGGGTTATTTATTTCTCTGGTAAATAATTAACCAGCCCCCTCTACCAAAAGGATAAATAGTATTC [819]
'MXBajaSur(ROM14482)' CTAGCCCGCAATCTTATTTAAAAACTAGGAGGGGTATGGCAGCATCTCCGAATAACACAAAC CCTACCAAATAAAAACAGACCTATTTCTACATTTATGTACTCTCCTCTTATGAGG AGCAACACTAGCCAACCTACCTGGCCTACAACAAAAAGATTTTAAAGGCGCTAAATCG CATACTCATCTATTAGCCACATAGGCCCTAGTTATCGCGACACACTATAATCCAAACAC ATATGAGTTTTTCTAGGGGCTATAGCCCTAATATCGCCCGAACTACTCCTCATCAA CATTATCTGCTCCCAACACACATAACTGCTATCCCCCCCAGCATATAATCTACAGGAGAATCTACTTATCTAC CAACATCGAGATTCTCAACTGCTATAATCTACAGGAGAACTACCAATTTACATCTGCT CCTACAAACACTTGGGTTATTTATTTCTCTGGTAAATAATTAACCAGCCCCCTCTACCAAAAGGATAAATAGTATTC [819]
'MXBajaSur(RWM1920)' CTAGCCCGCAATCTTATTTAAAAACTAGGAGGGGTATGGCAGCATCTCCGAATAACACAAAC CCTACCAAATAAAAACAGACCTATTTCTACATTTATGTACTCTCCTCTTATGAGG AGCAACACTAGCCAACCTACCTGGCCTACAACAAAAAGATTTTAAAGGCGCTAAATCG CATACTCATCTATTAGCCACATAGGCCCTAGTTATCGCGACACACTATAATCCAAACAC ATATGAGTTTTTCTAGGGGCTATAGCCCTAATATCGCCCGAACTACTCCTCATCAA CATTATCTGCTCCCAACACACATAACTGCTATCCCCCCCAGCATATAATCTACAGGAGAATCTACTTATCTAC CAACATCGAGATTCTCAACTGCTATAATCTACAGGAGAACTACCAATTTACATCTGCT CCTACAAACACTTGGGTTATTTATTTCTCTGGTAAATAATTAACCAGCCCCCTCTACCAAAAGGATAAATAGTATTC
CACATTATACCATTATTCTAATTCTCATACTAAAACCAGAAGCTACTGCTAGTGACG
TAATTT:AAAAAAAAATATCAAGCTGTGACCATGACAATAGGAGCCACTCCTGCACA
CC:GAGGGGGCTCATAAGACCTGCTAACTCCTTTTCTCTGGTAAATATAATTACCAGCCCA
CTCTACAAAGGATAATAGTATTC [819]
'MXBajaNorte(BYU34638)'
CTAGCCGCAATCCATTATATATTTAATCTGGAGGGTATGGGCATCATCCGAATAACACAAAC
CCTACCAACAATTTAAAAACAGAATCATTCTATCCACTACTTTTAGCTACTCCCTATAGGG
GGCAACACAGCCAAACCTAAGCGCTCAAAACAAACAGATTAAAAAGCCCTATACGC
CATACTCATCATTGACCCATAGGGAACCTACTTGAATACGTCTTACACACGATG
TTATTACCCACATATAGCTCAATGATCCAAATCCACGAGGGCTCAGGGAATGT
TGTTTCTAATTTTTCGAGGACCATAGCTAACTCCCTTCTGGTAAATATAATTACCAGCCCA
CTCTACAAAGGATAATAGTATTC [819]
'MXBajaNorte(JRO266)'
CTAGCCGCAATCCATTATATATTTAATCTGGAGGGTATGGGCATCATCCGAATAACACAAAC
CCTACCAACAATTTAAAAACAGAATCATTCTATCCACTACTTTTAGCTACTCCCTATAGGG
GGCAACACAGCCAAACCTAAGCGCTCAAAACAAACAGATTAAAAAGCCCTATACGC
CATACTCATCATTGACCCATAGGGAACCTACTTGAATACGTCTTACACACGATG
TTATTACCCACATATAGCTCAATGATCCAAATCCACGAGGGCTCAGGGAATGT
TGTTTCTAATTTTTCGAGGACCATAGCTAACTCCCTTCTGGTAAATATAATTACCAGCCCA
CTCTACAAAGGATAATAGTATTC [819]
'CASanDiego(5/6/99)'
CTAGCCGCAATCCATTATATATTTAATCTGGAGGGTATGGGCATCATCCGAATAACACAAAC
CCTACCAACAATTTAAAAACAGAATCATTCTATCCACTACTTTTAGCTACTCCCTATAGGG
GGCAACACAGCCAAACCTAAGCGCTCAAAACAAACAGATTAAAAAGCCCTATACGC
CATACTCATCATTGACCCATAGGGAACCTACTTGAATACGTCTTACACACGATG
TTATTACCCACATATAGCTCAATGATCCAAATCCACGAGGGCTCAGGGAATGT
TGTTTCTAATTTTTCGAGGACCATAGCTAACTCCCTTCTGGTAAATATAATTACCAGCCCA
CTCTACAAAGGATAATAGTATTC [819]
'CASanDiego(5/6/99)'
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CCTACCAACAATTTAAAAACAGAATCATTCTATCCACTACTTTTAGCTACTCCCTATAGGG
GGCAACACAGCCAAACCTAAGCGCTCAAAACAAACAGATTAAAAAGCCCTATACGC
CATACTCATCATTGACCCATAGGGAACCTACTTGAATACGTCTTACACACGATG
TTATTACCCACATATAGCTCAATGATCCAAATCCACGAGGGCTCAGGGAATGT
TGTTTCTAATTTTTCGAGGACCATAGCTAACTCCCTTCTGGTAAATATAATTACCAGCCCA
CTCTACAAAGGATAATAGTATTC [819]
ATACTCATCCATGCACCTGGGTTGGTCATTGCCGCAACCAGATGATCCAAACACA
ATGAAGCTTTTCAGAGCTATAGCCTAATAATCGCCACCAGGATTTCATTCATACGC
ACTATTTCTGCCTAGCAACACCACTATGAGAAGACAAACACTGCGATATATTAATCT
CACCAGGATTTTCCAACACCATTTTGCTTATATCAACAAACTCTGATGACATCATTACAAA
CCTAAATAATTTGCAATTCACCACCCCAAGCATTAAATATCGCCACGGAAACTTCT
AAACCACTATTAACTGCGTGTCCAAACAACAAATACATCAGTTGGAATTACATTATATCT
TAATACCTGCTCATACTACATACATGATTTTATCACAACAAAAAGACACCCATCGCA
TACTCATTCATCATTCCACTACATATATTATATCAACACAAATAGGCAACCCCAA
TTAAACAAATATACACGGCCACCACACCTCACGGAGACACCCAAACCAAAACCCAGC
CTTTAAAACATTTCAAGCTGTGACCATGACAATAGGAGATACTCCTCGCACACC:
GAGGGGGACATAAGACCTGCTAACTCTTTTTCCTGG:AAATAACCA:CCAGCCCCCTCT
TACCAAGAGATAATAGTATTCC [817]
'tauMXMich.(Hin.288)'
CTAGCCGCAATCTCTTAAAAACTGGGGGGGTACGGTATCATTCGAATGATACAAACC
CTGCCAACAATAAAAACAGACATTTTCTTACTCCGTGGGCTCAATGAGGG
GCAACACTAGCTAATTTAATCCGTGTTAACACACAGCACTTAAAAAGCCCTATCGCA
TACTCATTCATCATTCCACTACATATATTATATCAACACAAATAGGCAACCCCAA
TTAAACAAATATACACGGCCACCACACCTCACGGAGACACCCAAACCAAAACCCAGC
CTTTAAAACATTTCAAGCTGTGACCATGACAATAGGAGATACTCCTCGCACACC:
GAGGGGGACATAAGACCTGCTAACTCTTTTTCCTGG:AAATAACCA:CCAGCCCCCTCT
ACCAAAGGATAATAGTATTCC [817]
'tauMXToliman'
CTAGCCGCAATCTCTTAAAAACTGGGGGGGTACGGTATCATTCGAATGATACAAACC
CTGCCAACAATAAAAACAGACATTTTCTTACTCCGTGGGCTCAATGAGGG
GCAACACTAGCTAATTTAATCCGTGTTAACACACAGCACTTAAAAAGCCCTATCGCA
TACTCATTCATCATTCCACTACATATATTATATCAACACAAATAGGCAACCCCAA
TTAAACAAATATACACGGCCACCACACCTCACGGAGACACCCAAACCAAAACCCAGC
CTTTAAAACATTTCAAGCTGTGACCATGACAATAGGAGATACTCCTCGCACACC:
GAGGGGGACATAAGACCTGCTAACTCTTTTTCCTGG:AAATAACCA:CCAGCCCCCTCT
ACCAAAGGATAATAGTATTCC [817]
'tauMXSonora(JRO649)'
CTAGCCGCAATCTCTTAAAAACTGGGGGGGTACGGTATCATTCGAATGATACAAACC
CTGCCAACAATAAAAACAGACATTTTCTTACTCCGTGGGCTCAATGAGGG
GCAACACTAGCTAATTTAATCCGTGTTAACACACAGCACTTAAAAAGCCCTATCGCA
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CTTTAAAACATTTCAAGCTGTGACCATGACAATAGGAGATACTCCTCGCACACC:
GAGGGGGACATAAGACCTGCTAACTCTTTTTCCTGG:AAATAACCA:CCAGCCCCCTCT
ACCAAAGGATAATAGTATTCC [817]
GGGGGGTAAATAAGACCTGCTAATCTTTTTTCCTGG:AAATAACCA:CCAGCCCCCTC
TACCAAAGGATAGTAGTATTTCC [817]
'MXOaxaca(MVZ143524)'
CTAGCCGCAATCTATTTAAAAATTTGGGGGTTGATGTATCATTCGGAATAACACAAACC
CTGCAAAGAAATATAAAAGCAGTCTATTTCTACATTTATTGATCTCGGCTATGGAGGA
GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
TCTCATCCTATTAGCCACACTGTTTGTTGTCATCGCGCAACTATAATCCAAACACAA
TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
CTTATCTCTCACTCATCTATCACTCATCTATCACTCATTAAACTTTATCACATCTTTTCC
'MXOaxaca(ENS9929)'
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GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
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TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
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'MXGuerrero(LSUMZ39531)'
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GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
TCTCATCCTATTAGCCACACTGTTTGTTGTCATCGCGCAACTATAATCCAAACACAA
TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
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'MXGuerrero(LSUMZ39531)'
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TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
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'MXGuerrero(LSUMZ39531)'
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CTGCAAAGAAATATAAAAGCAGTCTATTTCTACATTTATTGATCTCGGCTATGGAGGA
GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
TCTCATCCTATTAGCCACACTGTTTGTTGTCATCGCGCAACTATAATCCAAACACAA
TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
CTTATCTCTCACTCATCTATCACTCATCTATCACTCATTAAACTTTATCACATCTTTTCC
'MXGuerrero(LSUMZ39531)'
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CTGCAAAGAAATATAAAAGCAGTCTATTTCTACATTTATTGATCTCGGCTATGGAGGA
GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
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TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
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'MXGuerrero(LSUMZ39531)'
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TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
CTTATCTCTCACTCATCTATCACTCATCTATCACTCATTAAACTTTATCACATCTTTTCC
'MXGuerrero(LSUMZ39531)'
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CTGCAAAGAAATATAAAAGCAGTCTATTTCTACATTTATTGATCTCGGCTATGGAGGA
GCAACACTAGCTAAACTTACCTGCTACAACAAACAGATCTAAAGGGCCCTTTATCGCA
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TGAAGCTTTTCAGGAGCAATTAGCTCTTAACTACAGGGAACACTTACATACACTC
CTTATCTCTCACTCATCTATCACTCATCTATCACTCATTAAACTTTATCACATCTTTTCC
VITA

Thomas James Devitt was born in St. Paul, Minnesota, on March 2, 1977, the son of Robert George Devitt and Diane Lansing Devitt. In 1984, he and his family moved to Austin, Texas. After completing high school at St. Michael’s Academy in Austin, Texas, in May of 1995, he matriculated to the University of California at Davis. After a brief tenure at the University of California, he transferred to the University of Texas at Austin in January 1996. There, he received the degree of Bachelor of Science majoring in biology, with an emphasis on ecology, evolution and conservation in December 1999. In August 2000, he began graduate work at Louisiana State University. He received the degree of Master of Science majoring in zoology in May 2003. Upon completion of his master’s degree, he continued his graduate work in the doctoral program in integrative biology at the University of California at Berkeley, beginning in January 2003.