



## Molecular systematics of New World lampropeltine snakes (Colubridae): implications for biogeography and evolution of food habits

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We used mitochondrial gene sequences to infer phylogenetic relationships among North American snakes of the colubrid tribe Lampropeltini (*Arizona*, *Bogertophis*, *Cemophora*, New World *Elaphe*, *Lampropeltis*, *Pituophis*, *Rhinocheilus*, *Senticolis*, *Stilosoma*), and assessed the implications of our findings for the biogeography and evolution of food habits among these serpents. The maximum likelihood phylogeny identified *Rhinocheilus* as the sister taxon to all other lampropeltinines, and supported the monophyly of *Lampropeltis* (including *Stilosoma*), New World *Elaphe*, and *Pituophis*, but not that of *Bogertophis*. This phylogeny also suggested a sister group relationship between *Cemophora* and *Lampropeltis*, and between New World *Elaphe* and *Pituophis*, and strongly supported that *Senticolis* belongs within Lampropeltini, thus contradicting previous suggestions that *Senticolis* is not a lampropeltinine. Using a method for approximating ancestral areas of clades, we determined that western North America was most likely the ancestral area of lampropeltinines. Our survey of published studies, combined with unpublished data, indicated that lampropeltinines as a group feed mainly on mammals, less frequently on lizards, birds, and bird eggs, and only rarely on squamate eggs, snakes, anurans, and insects. Some individual species indeed emphasize mammals in their diets, but others most frequently eat lizards, squamate eggs, bird eggs, or snakes, whereas others take two prey types with similar frequency. Our reconstruction of the evolution of food habits among lampropeltinines suggests that a diet emphasizing lizards is ancestral, and therefore diets that mostly consist of mammals, squamate and bird eggs, and snakes are derived within the clade. In at least some species, smaller individuals prey mostly on lizards and larger ones add mammals to their diets.

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ADDITIONAL KEY WORDS:—ancestral area – *Arizona* – *Bogertophis* – *Cemophora* – *Elaphe* – *Lampropeltis* – *Pituophis* – *Rhinocheilus* – *Senticolis* – *Stilosoma*.

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## CONTENTS

Introduction . . . . .	356
Material and methods . . . . .	357
Taxon sampling, DNA isolation, and sequencing . . . . .	357
Phylogenetic analyses . . . . .	360
Estimation of the ancestral area of lampropeltinines . . . . .	362
Food habits of lampropeltinines . . . . .	363
Results . . . . .	364
Sequence variation . . . . .	364
Phylogenetic relationships . . . . .	367
Estimation of the ancestral area of lampropeltinines . . . . .	370
Food habits of lampropeltinines . . . . .	370
Discussion . . . . .	373
Phylogenetic relationships . . . . .	373
Ancestral area and divergence times of lampropeltinines . . . . .	376
Evolution of food habits . . . . .	376
Acknowledgements . . . . .	378
References . . . . .	378

## INTRODUCTION

In addition to contributing to our understanding of the evolution of biodiversity, elucidation of phylogenetic relationships among closely-related taxa is critical to correctly infer patterns of community structure, biogeography, and character evolution (e.g. Arnold, 1993; Eggleton & Vane-Wright, 1994; Riddle, 1995; Harvey *et al.*, 1996; Losos, 1996; Ortolani & Caro, 1996; Zamudio, Jones & Ward, 1997; Da Silva & Patton, 1998; Roderick & Gillespie, 1998). A reliable phylogeny can allow researchers to test the veracity of explicit models of evolutionary diversification (e.g. Patton & Smith, 1992; Patton, Da Silva & Malcolm, 1994; Gascon, Loughheed & Bogart, 1998), to identify instances of correlated character evolution (e.g. Brooks & McLennan, 1991; Rodríguez-Robles & Greene, 1996; Autumn *et al.*, 1997; Vogler & Kelley, 1998), and to assess whether a particular trait has evolved once or repeatedly within a lineage (e.g. Dial & Grismer, 1992; Lanyon, 1992; Greene, 1994; Benabib, Kjer & Sites, 1997; Mueller, Rehner & Schultz, 1998), or whether different communities assemble ecological analogs following the same sequence (e.g. Jackman *et al.*, 1997; Losos *et al.*, 1998).

Colubrid snakes in the tribe Lampropeltini (Dowling, 1975; Dowling *et al.*, 1983) are among the most conspicuous elements of the diverse serpent fauna of North America. Morphological (Keogh, 1996), immunological (Dowling *et al.*, 1983, 1996), and mitochondrial (mt) DNA sequence data (López & Maxson, 1995) suggest that Lampropeltini constitutes a monophyletic group that comprises *Arizona elegans* (glossy snake), *Bogertophis* and New World *Elaphe* (ratsnakes), *Cemophora coccinea* (scarlet snake), *Lampropeltis* (kingsnakes and milksnakes), *Pituophis* (gopher, bull, and pinesnakes), *Stilosoma extenuatum* (short-tailed snake), and perhaps *Rhinocheilus lecontei* (long-nosed snake) and *Senticolis triaspis* (green ratsnake; see Discussion). The approximately 25 species of lampropeltinines are oviparous and nonvenomous constrictors, include small- and large-bodied species, exhibit diurnal, crepuscular, nocturnal, fossorial, terrestrial, and semiariboreal activity patterns, inhabit deserts, rocky canyons, grasslands, arroyos, and woodlands, and possess cryptic as well as mimetic (i.e. *C. coccinea*, *Lampropeltis alterna*, *L. mexicana*, *L. triangulum*, *R. lecontei*) coloration of New World coral

snakes (*Micruroides* and *Micrurus*; Greene, 1997). Lampropeltinines thus provide an excellent opportunity to investigate patterns of diversification within a lineage of vertebrate predators.

Documentation of the diet and foraging behaviour of a snake species is often the first step in the development of an understanding of its ecology. With information on the phylogenetic relationships of a taxon and its close relatives, feeding biology can be placed in an historical framework, and thereby used to elucidate evolutionary divergence within a lineage (e.g. Henderson *et al.*, 1988; Richman & Price, 1992; Gilbert *et al.*, 1994; Rodríguez-Robles, Bell & Greene, 1999b; Rodríguez-Robles, Mulcahy & Greene, 1999). Lampropeltinines have diverse food habits. As a whole, these snakes consume a variety of vertebrate prey, including anurans, 'lizards' (i.e. squamate reptiles other than snakes and amphisbaenians), snakes, birds, mammals, and squamate and bird eggs. On a more inclusive level, some species have stenophagous diets, whereas others are general predators on several types of prey.

The phylogenetic relationships within Lampropeltini remain controversial. The investigations to date have resulted in incongruent hypotheses of evolutionary history for the members of this clade (Fig. 1), which has hampered studies of character evolution among lampropeltinines. Our purpose is to use mtDNA sequences to infer phylogenetic relationships among lampropeltinine snakes, and to discuss the implications of our findings for the biogeography and evolution of food habits within this clade, assuming that our gene genealogy accurately reflects the evolutionary history of these ophidians (see Moore, 1995, 1997; Brower, De Salle & Vogler, 1996).

#### MATERIAL AND METHODS

##### *Taxon sampling, DNA isolation, and sequencing*

We obtained tissue samples from one or two individuals of *Coluber constrictor*, *Masticophis flagellum*, *Salvadora hexalepis*, *Arizona elegans*, *Bogertophis rosaliae*, *B. subocularis*, *Cemophora coccinea*, *Elaphe guttata*, *E. obsoleta*, *Lampropeltis getula*, *L. mexicana*, *L. pyromelana*, *L. zonata*, *Pituophis catenifer*, *P. deppei*, *P. lineaticollis*, *P. melanoleucus*, *P. ruthveni*, and *Rhinocheilus lecontei* (Table 1). We extracted total genomic DNA from ventral scale clips preserved in 95% ethanol or from tissue samples (blood, liver, muscle) stored frozen at  $-74^{\circ}\text{C}$  using the sodium dodecyl sulphate-proteinase K/phenol/RNase method (Sambrook, Fritsch & Maniatis, 1989). Using total cellular DNA as a template, we amplified (with the polymerase chain reaction, PCR [Saiki *et al.*, 1986, 1988]) and used for phylogenetic analyses an 891 base pair (bp) fragment of mtDNA that encompassed a 697 bp portion of the 3' end of the nicotinamide adenine dinucleotide dehydrogenase subunit 4 (*Ndh4*, or 'ND4' gene), and a 194 bp section of three transfer ribonucleic acid (tRNA) genes ( $\text{tRNA}^{\text{His}}$ ,  $\text{tRNA}^{\text{Ser}}$ ,  $\text{tRNA}^{\text{Leu}}$ ) using primers labelled ND4 and Leu (Arévalo, Davis & Sites, 1994). ND4, one of 13 protein-coding genes in the vertebrate mitochondrial genome, is a reliable tracer of evolutionary history (Russo, Takezaki & Nei, 1996; Zardoya & Meyer, 1996; Russo, 1997) and a relatively fast-evolving gene useful for resolving relationships among closely-related taxa (Cracraft & Helm-Bychowski, 1991). The 5' end of primers ND4 and Leu corresponds to

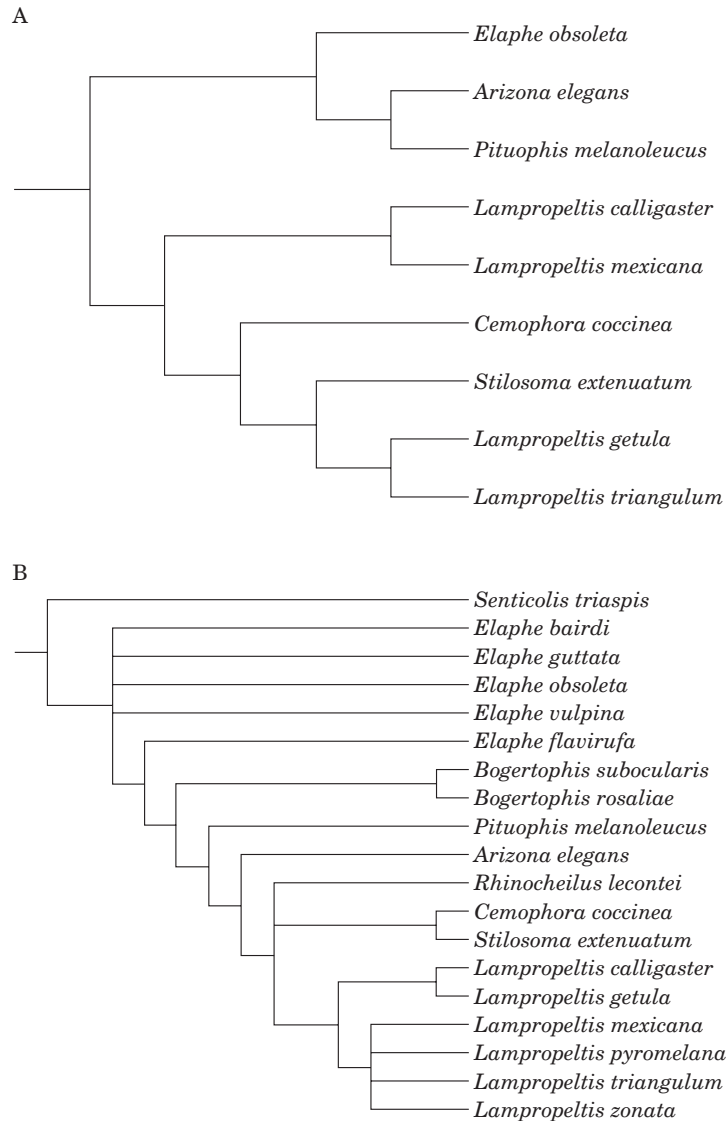


Figure 1. Previous hypotheses of phylogenetic relationships among various lampropeltinine snakes. A, after Dowling & Maxson (1990); B, after Keogh (1996).

nucleotide positions 12900 and 13831, respectively, of the heavy strand of the mitochondrial genome of the pipid frog *Xenopus laevis* (Roe *et al.*, 1985). PCR was carried out in a programmable thermal cycler in 100  $\mu$ l reactions consisting of 2  $\mu$ l of template DNA (50 ng/ $\mu$ l), 2.5  $\mu$ l of primers (40  $\mu$ M), 10  $\mu$ l of 10  $\times$  PCR reaction buffer (Stratagene), 2  $\mu$ l of  $MgCl_2$  (25 mM), 2  $\mu$ l of deoxynucleoside triphosphates (10 mM), 4  $\mu$ l of *Thermus aquaticus* DNA polymerase (5 U/ $\mu$ l), and 77.5  $\mu$ l of  $H_2O$ . DNA was denatured initially at 94°C for 3 min, then 33 cycles of amplification were carried out under the following conditions: 94°C denaturation for 30 sec, 55°C annealing for 30 sec, and 72°C extension for 1 min, followed by a final 5 min

TABLE 1. Taxon, sample number (if necessary), GenBank accession number, voucher number (if available), and locality of the taxa used in this study. Museum and collector abbreviations are: CAS = California Academy of Sciences, San Francisco; LSUMZ = Museum of Zoology, Louisiana State University; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; CJF = Carl J. Franklin; CME = Curtis M. Eckerman; HWG = Harry W. Greene; TP = Theodore J. Papenfuss

Taxon	Sample number	GenBank accession number, voucher number, and locality
<b>Outgroups</b>		
<i>Coluber constrictor</i>	–	AF138746; MVZ 150182; U.S.: California, Santa Cruz Co., Ellicott Pond
<i>Masticophis flagellum</i>	–	AF138747; HWG 2649; U.S.: Arizona, Cochise Co.
<i>Salvadora hexalepis</i>	–	AF138748; TP 24557; U.S.: California, San Bernardino Co., Camp Rock Road, junction of Upper Johnson and Oard valleys
<b>Lampropeltini</b>		
<i>Arizona elegans</i>	1	AF138749; MVZ 137685; U.S.: California, Riverside Co., Highway 195, 21.1 miles west of junction with I–10 at Chiriaco Summit
<i>Arizona elegans</i>	2	AF138750; MVZ 225523; U.S.: California, San Diego Co., Borrego Springs, Country Club Road, 1.5 miles south of Palm Canyon Road
<i>Bogertophis rosaliae</i>	–	AF138751; MVZ 225742; Mexico: Baja California Sur, kilometer marker 70, south of Loreto
<i>Bogertophis subocularis</i>	3	AF138752; CME 116; U.S.: Texas, Culberson Co., 18.1 road miles north of Van Horne on Highway 54
<i>Bogertophis subocularis</i>	4	AF138753; CME 117; U.S.: Texas, Culberson Co., 8.7 road miles north of Van Horne on Highway 54
<i>Cemophora coccinea</i>	–	AF138754; MVZ 150181; U.S.: North Carolina, Brunswick Co., 2 miles north of Southport
<i>Elaphe bairdi</i>	–	AF138755; unknown locality
<i>Elaphe guttata</i>	–	AF138756; MVZ 164928; U.S.: Georgia, Chattahoochee or Muscogee Cos., Fort Benning
<i>Elaphe obsoleta</i>	–	AF138757; MVZ 137700; U.S.: Texas, Blanco Co., vicinity of Pedernales Falls State Park
<i>Elaphe vulpina</i>	–	AF138758; CAS 184362; U.S.: Ohio, Ottawa Co., East Harbor State Park
<i>Lampropeltis getula</i>	–	AF138759; HWG 1485; U.S.: California, San Benito Co., Highway 25, 2.6 miles southeast of junction of Highway 146 and Pinnacles National Monument
<i>Lampropeltis mexicana</i>	–	AF138760; HWG 2650; Mexico: specific locality unknown
<i>Lampropeltis pyromelana</i>	–	AF138761; HWG 2203; U.S.: Arizona, Cochise Co.
<i>Lampropeltis zonata</i>	5	AF138762; MVZ 225913; U.S.: California, Lake Co., Mount Saint Helena, Western Mines Road
<i>Lampropeltis zonata</i>	6	AF136209; MVZ 229888; U.S.: California, San Diego Co., Mount Laguna
<i>Pituophis catenifer</i>	7	AF138763; MVZ 150206; U.S.: California, San Diego Co., University City
<i>Pituophis catenifer</i>	8	AF138764; MVZ 137577; U.S.: Nevada, Mineral Co., Highway 31, 6.6 miles southwest of Hawthorne
<i>Pituophis deppei</i>	9	AF138765; Mexico: Durango
<i>Pituophis deppei</i>	10	AF138766; Mexico: Michoacán
<i>Pituophis lineaticollis</i>	11	AF138767; CJF 1500; Guatemala: Departamento Zacapa, Sierra de las Minas
<i>Pituophis lineaticollis</i>	12	AF138768; MVZ 224308–224310; Guatemala: Departamento Guatemala, near Guatemala City
<i>Pituophis melanoleucus</i>	13	AF138769; USNM 211452; U.S.: Florida, Wakulla Co., St. Mark's Wildlife Refuge, about 1.5 miles southwest of Otter Lake
<i>Pituophis melanoleucus</i>	14	AF138770; MVZ 150219; U.S.: North Carolina, Brunswick Co., 3.5 miles north of Southport

continued

TABLE 1. Taxon, sample number (if necessary), GenBank accession number, voucher number (if available), and locality of the taxa used in this study. Museum and collector abbreviations are: CAS = California Academy of Sciences, San Francisco; LSUMZ = Museum of Zoology, Louisiana State University; MVZ = Museum of Vertebrate Zoology, University of California, Berkeley; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.; CJF = Carl J. Franklin; CME = Curtis M. Eckerman; HWG = Harry W. Greene; TP = Theodore J. Papenfuss—*continued*

Taxon	Sample number	GenBank accession number, voucher number, and locality
<i>Pituophis ruthveni</i>	15	AF138771; U.S.: Louisiana, Bienville Parish, 2 kilometers east of Kepler Creek Lake Bridge
<i>Pituophis ruthveni</i>	16	AF138772; U.S.: Louisiana, Bienville Parish, 2 kilometers south of junction of LA 154 and 507
<i>Rhinocheilus lecontei</i>	17	AF138773; HWG 2585; U.S.: New Mexico, Hidalgo Co., 8.6 miles north of Portal Road on Highway 80
<i>Rhinocheilus lecontei</i>	18	AF138774; HWG 2611; U.S.: Arizona, Cochise Co., 0.5 miles east of Portal
<i>Senticolis triaspis</i>	—	AF138775; U.S.: Arizona, Cochise Co., 1 mile east of Southwestern Research Station
<i>Stilosoma extenuatum</i>	—	AF138776; LSUMZ 40624; U.S.: Florida, Hillsborough Co., Tampa, vicinity of University of South Florida campus

extension at 72°C. Ten microliters of the resulting PCR product were electrophoresed on a 1% agarose gel and stained with ethidium bromide to verify product band size. For each individual, we cloned its PCR product into a phosphatased *EcoRV* pBluescript®II SK +/-phagemid vector (Stratagene) using *Escherichia coli* as the vector, and sequenced both DNA strands in an automated sequencer using the dideoxy chain-termination method (Sanger, Nicklen & Coulson, 1977). The sequences of *Elaphe bairdi*, *E. vulpina*, *Senticolis triaspis*, and *Stilosoma extenuatum* included in this study were provided by R. Lawson (California Academy of Sciences, San Francisco).

#### Phylogenetic analyses

Sequences from the light and heavy DNA strands were input into the Sequence Navigator (version 1.0.1) program and aligned to each other and to the reference sequence of *Sceloporus g. grammicus* (Arévalo *et al.*, 1994). This initial alignment was refined with the MacDNASIS Pro software (version 1.0). Pairwise comparisons of observed proportional sequence divergence ( $p$ -distance) and corrected sequence divergence, and number of transitions and transversions by codon position were obtained using the computer program PAUP\* 4.0b1 (Swofford, 1999).

To estimate the phylogenetic information content of the mtDNA character matrix, we used the  $g$ -test (Huelsenbeck, 1991; Hillis & Huelsenbeck, 1992; but see Källersjö *et al.*, 1992) to assess the skewness of the tree length distribution of 100 000 trees randomly generated with PAUP\*. Probability of phylogenetic structure was assessed using the values provided by Hillis & Huelsenbeck (1992).

We used two methods of phylogenetic reconstruction: maximum parsimony (MP; Camin & Sokal, 1965; Swofford *et al.*, 1996) and maximum likelihood (ML; Felsenstein, 1981; Huelsenbeck & Crandall, 1997), as implemented by PAUP\*, in



combination with two character weighting schemes: equal-weighting, where all nucleotide substitutions were weighted equally regardless of type or codon position, and differential codon position weighting, where we down-weighted third position transitions (see below). Sites with insertion or deletion events were removed from the analyses. Each base position was treated as an unordered character with four alternative states. Ancestral character states were determined via outgroup comparison (Watrous & Wheeler, 1981; Farris, 1982; Maddison, Donoghue & Maddison, 1984; see also Nixon & Carpenter, 1993). We used *Coluber constrictor*, *Masticophis flagellum*, and *Salvadora hexalepis* as the outgroups to all other taxa based on previous systematic studies (Dowling *et al.*, 1983; Dowling & Maxson, 1990; López & Maxson, 1995).

Because the number of terminal taxa was too large to permit evaluating all trees or employing the branch-and-bound algorithm (Hendy & Penny, 1982), we used heuristic search strategies for each tree-building methodology. We used 100 repeated randomized input orders of taxa for all MP analyses to minimize the effect of entry sequence on the topology of the resulting cladogram(s). MP analyses were conducted without the steepest descent option, and with accelerated character transformation (ACCTRAN) optimization, tree bisection-reconnection (TBR) branch swapping, save all minimal trees (MULPARS), and zero-length branches collapsed to yield polytomies settings in place. We used nonparametric bootstrapping (100 pseudo-replicates, ten addition-sequence replicates, 50% majority rule) to assess the stability of internal branches in cladograms (Felsenstein, 1985; Felsenstein & Kishino, 1993; Sanderson, 1995; Berry & Gascuel, 1996). Nonparametric bootstrap values generally are a conservative measure of the probability that a recovered group represents a true clade (Zharkikh & Li, 1992; Hillis & Bull, 1993; Li, 1997).

For ML analyses we randomly selected as the starting tree one of the trees found during the MP searches. Using empirical nucleotide frequencies and five rate categories, we fixed the probabilities of the six possible nucleotide transformations (A↔C, A↔G, A↔T, C↔G, C↔T, G↔T), the proportion of invariable sites  $\theta$ , and the  $\alpha$  'shape' parameter of the gamma distribution of rate heterogeneity across nucleotide positions (Yang, 1996a) to the empirical values calculated from the starting tree in a search for a better ML tree (a tree with a higher log-likelihood value) under the general time-reversible model of nucleotide substitution (Yang, 1994; Gu, Fu & Li, 1995; Swofford *et al.*, 1996); that is, we used the most parameter-rich model available to search for ML trees. When a tree of higher likelihood was found, we reoptimized and fixed the parameters for a subsequent ML search. We repeated this procedure until the same tree was found in successive iterations.

For sequence data, only five possible characters can occur at a given site (one of four nucleotides or a gap). Thus, a nucleotide position may easily become saturated if more than one mutation ('multiple hits') occurs at that site. To test for the possibility that some types of nucleotide substitutions have become saturated, we plotted  $p$ -distance ( $y$ ) versus corrected (with the Tamura–Nei model; Tamura & Nei, 1993) estimates of proportional sequence divergence ( $x$ ) for first, second, and third codon positions and for transitions and transversions separately. (The Tamura–Nei divergences are analogous to the uncorrected proportional divergences, but they take into account deviations from equal base compositions and differences in substitution rates among nucleotides.) Points that fall along the  $y=x$  line have the same observed and estimated numbers of changes and thus have not been subjected to multiple hits. Points that fall below the  $y=x$  line indicate that multiple hits have

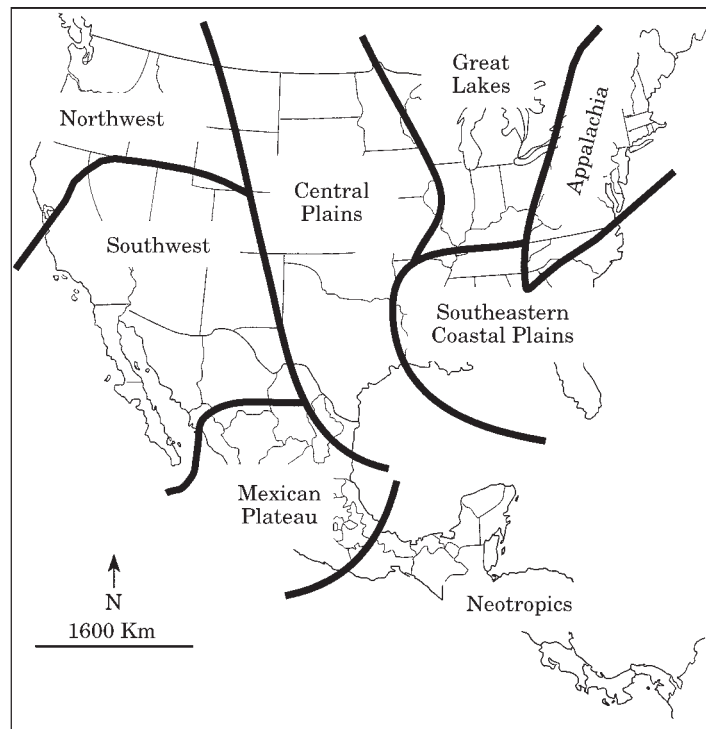


Figure 2. Geographic zones used to estimate the ancestral area of lampropeltinine snakes.

occurred; saturation is reached when observed sequence divergence does not continue to increase, despite the fact that corrected estimates do. Conventional statistical tests of the relationship between estimated and observed sequence divergence are not appropriate because of nonindependence of the data points due to the inclusion of each point in more than one pairwise comparison. Therefore, we used the plots as heuristic devices to help identify classes of changes occurring at different rates which should be weighted differently in phylogenetic analyses (Jockusch, 1996).

#### *Estimation of the ancestral area of lampropeltinines*

All monophyletic groups originated somewhere in the sense that there was a 'centre of origin' or ancestral area corresponding to the distribution of the ancestor of the group. One difficulty in applying this concept (Morrone & Crisci, 1995) is that it implies that areas currently inhabited were inhabitable when the lineages were diverging, yet it is well known that habitats and the species that inhabit them change through time (e.g. Behrensmeyer *et al.*, 1992; Vrba *et al.*, 1995). Nonetheless, the search for ancestral areas becomes legitimate when information from past and present-day distributions is used in combination with a specific phylogenetic hypothesis.

We used current and historical (inferred from fossil records; Powell, 1990; Holman, 1995; Schulz, 1996) distribution to assign lampropeltinines to eight broadly defined geographic areas: Appalachia, Southeastern Coastal Plains, Great Lakes, Central Plains, Northwest, Southwest, Mexican Plateau, and Neotropics (Fig. 2; Table 2).



TABLE 2. Data matrix for the current and historical distribution of 20 species of lampropeltine snakes. AP = Appalachia; SC = Southeastern Coastal Plains; GL = Great Lakes; CP = Central Plains; NW = Northwest; SW = Southwest; MP = Mexican Plateau; NT = Neotropics (see Fig. 2 for demarcation of geographic areas). Absence from an area is coded as 0 and presence is coded as 1

	AP	SC	GL	CP	NW	SW	MP	NT
<i>Arizona elegans</i>	0	0	0	1	0	1	1	0
<i>Bogertophis rosaliae</i>	0	0	0	0	0	1	0	0
<i>Bogertophis subocularis</i>	0	0	0	0	0	1	1	0
<i>Cemophora coccinea</i>	1	1	1	1	0	0	0	0
<i>Elaphe bairdi</i>	0	0	0	1	0	0	1	0
<i>Elaphe guttata</i>	1	1	1	1	0	1	1	0
<i>Elaphe obsoleta</i>	1	1	1	1	0	0	0	0
<i>Elaphe vulpina</i>	1	1	1	1	1	0	0	0
<i>Lampropeltis getula</i>	1	1	1	1	1	1	1	0
<i>Lampropeltis mexicana</i>	0	0	0	0	0	1	1	0
<i>Lampropeltis pyromelana</i>	0	0	0	0	0	1	1	0
<i>Lampropeltis zonata</i>	0	0	0	0	1	1	0	0
<i>Pituophis catenifer</i>	0	1	1	1	1	1	1	0
<i>Pituophis deppei</i>	0	0	0	1	0	0	1	1
<i>Pituophis lineaticollis</i>	0	0	0	0	0	0	1	1
<i>Pituophis melanoleucus</i>	1	1	0	0	0	0	0	0
<i>Pituophis ruthveni</i>	0	1	0	0	0	0	0	0
<i>Rhinocheilus lecontei</i>	0	0	0	1	1	1	1	0
<i>Senticolis triaspis</i>	0	0	0	0	0	1	1	1
<i>Stilosoma extenuatum</i>	0	1	0	0	0	0	0	0

We relied on our ML hypothesis of relationships among lampropeltinines (see Results) to estimate the ancestral area of the group using the method proposed by Bremer (1992). Bremer's method is a cladistic procedure for approximating ancestral areas of clades using the topological information in their area cladograms. Each area is treated as a single character, which is optimized onto the phylogeny using forward and reverse parsimony (Camin & Sokal, 1965). By comparing the numbers of necessary 'gains' (i.e. presence on an area) and 'losses' (i.e. absence from an area) for all taxa under the two optimizations, it is possible to estimate which area(s) were most likely parts of the ancestral area of the clade (see Ronquist, 1994, 1995; Bremer, 1995).

#### *Food habits of lampropeltinines*

We relied on published and unpublished studies that provided quantitative information on the food habits of lampropeltinines to characterize the natural diets of these snakes. We took care to account for redundancy among literature records. We excluded *Lampropeltis mexicana* from these analyses because due to considerable taxonomic confusion in the past, dietary records for this species are found under several different names, and we could not confidently assign them to *L. mexicana*. However, it is unlikely that this omission will significantly alter the results of our analyses. When the available data allowed it, we described the diet of lampropeltinines in enough detail so that general patterns could be noted, but because an exact characterization of the food habits of each snake species was beyond the scope of this study, we did not conduct an exhaustive search of the literature for some

widespread taxa (e.g. *Coluber constrictor*, *Elaphe obsoleta*, *Lampropeltis getula*, *Masticophis flagellum*) for which additional, scattered dietary records may exist. Although we found little information of the natural diet of some species (e.g. *Salvadora hexalepis*, *Pituophis ruthveni*, *Senticolis triaspis*), we included these taxa in our analyses because excluding them was a less desirable alternative.

For our analyses, we assigned all prey to nine general categories (i.e. insects, anurans, lizards, snakes, squamate eggs, birds, bird eggs, mammals, and other prey). Although at least some of the species show temporal, geographic, and/or modest ontogenetic variation in dietary preferences (e.g. *Elaphe obsoleta*, *Pituophis catenifer*, *Arizona elegans*, *Rhinocheilus lecontei*; Fitch, 1963; Rodríguez-Robles, 1998; Rodríguez-Robles, Bell & Greene, 1999a; Rodríguez-Robles & Greene, 1999), we combined all records for a given species from across its range to broadly characterize its diet. For most species, the references consulted included studies that examined a number of wild specimens from different parts of the distribution of the species, which renders our estimates of the importance of various prey types in the diet of different lampropeltinines more accurate (see Rodríguez-Robles, 1998). The natural history of *Stilosoma extenuatum* is very poorly known, but observations on captive specimens indicate that this species feeds mainly on other snakes (Mushinsky, 1984; Rossi & Rossi, 1993), and we included this information in our analyses. Using the computer program MacClade (version 3.06; Maddison & Maddison, 1992), we mapped the food habits of the study species onto the inferred ML tree (see Results) to assess the evolution of this trait in Lampropeltini.

## RESULTS

### *Sequence variation*

The 891 bp mtDNA data matrix contained 232 characters at first and second positions and 233 at third positions, whereas 194 were noncoding. There were 421 variable and 318 potentially phylogenetically informative characters (sites with at least two shared differences among all taxa). Of the informative characters, 57 were at first codon positions, 19 at second positions, 177 at third positions, and 65 at noncoding positions. Within Lampropeltini there were 51, 13, 171, and 55 informative characters at first, second, third, and noncoding positions, respectively. This pattern is at least partly explained by the fact that most changes at third codon positions result in no amino acid substitutions (silent changes), which means that third positions are more free to vary, and as a consequence, change faster. Levels of intergeneric, corrected sequence divergence within Lampropeltini ranged from 8.3%, between *Lampropeltis getula* and *Stilosoma extenuatum*, to 21.4%, between *Rhinocheilus lecontei* (sample 17) and *Senticolis triaspis* (Table 3). Intra-generic sequence divergence ranged from 5.2%, between *Elaphe bairdi* and *E. obsoleta*, to 15.2%, between *Bogertophis rosaliae* and *B. subocularis* (sample 3; Table 3). The  $g_1$  statistic indicated that significant phylogenetic signal was present in the data set ( $g_1 = -0.639$ ,  $P < 0.01$ ; mean  $\pm$  SD tree length =  $2157.5 \pm 37.2$ , range 1939–2276), therefore inferring trees was justified.

Scatter plots of observed versus estimated sequence divergences indicated that first and second position transitions and transversions, and third position transversions

TABLE 3. Tamura–Nei DNA distances among the 32 mtDNA haplotypes included in this study

	1	2	3	4	5	6
1 <i>C. constrictor</i>	—					
2 <i>M. flagellum</i>	0.18857	—				
3 <i>Sa. hexalepis</i>	0.19438	0.17921	—			
4 <i>A. elegans</i> (1)	0.23075	0.23048	0.23303	—		
5 <i>A. elegans</i> (2)	0.23517	0.24492	0.23926	0.01389	—	
6 <i>B. rosaliae</i>	0.20112	0.2301	0.22356	0.1523	0.16062	—
7 <i>B. subocularis</i> (3)	0.19494	0.20687	0.2149	0.14878	0.15391	0.15169
8 <i>B. subocularis</i> (4)	0.19469	0.20666	0.21665	0.14535	0.15049	0.14691
9 <i>C. coccinea</i>	0.20127	0.22536	0.21468	0.15174	0.15745	0.14689
10 <i>E. bairdi</i>	0.18903	0.20798	0.18634	0.15315	0.1612	0.15292
11 <i>E. guttata</i>	0.18925	0.21147	0.19145	0.14803	0.15362	0.1488
12 <i>E. obsoleta</i>	0.1969	0.19931	0.1875	0.14659	0.14864	0.14191
13 <i>E. vulpina</i>	0.21434	0.22529	0.20577	0.16111	0.16957	0.16102
14 <i>L. getula</i>	0.20427	0.21911	0.2004	0.1415	0.14525	0.13486
15 <i>L. mexicana</i>	0.2331	0.24047	0.23543	0.16564	0.1714	0.15555
16 <i>L. pyromelana</i>	0.20434	0.21273	0.19701	0.15938	0.16312	0.14305
17 <i>L. zonata</i> (5)	0.2035	0.21467	0.20098	0.13997	0.1469	0.13761
18 <i>L. zonata</i> (6)	0.19789	0.21459	0.2073	0.14896	0.15437	0.1387
19 <i>P. catenifer</i> (7)	0.18307	0.21558	0.21404	0.16143	0.17553	0.17833
20 <i>P. catenifer</i> (8)	0.19953	0.22328	0.20546	0.15604	0.16445	0.1562
21 <i>P. deppei</i> (9)	0.21017	0.23335	0.20818	0.15095	0.15638	0.16608
22 <i>P. deppei</i> (10)	0.20117	0.21978	0.19836	0.14687	0.15236	0.16067
23 <i>P. lineaticollis</i> (11)	0.1893	0.21033	0.19536	0.15093	0.15285	0.16198
24 <i>P. lineaticollis</i> (12)	0.19648	0.20742	0.19012	0.15093	0.15287	0.16262
25 <i>P. melanoleucus</i> (13)	0.19397	0.20344	0.1942	0.14982	0.15999	0.16157
26 <i>P. melanoleucus</i> (14)	0.20313	0.2184	0.20377	0.15859	0.1715	0.17303
27 <i>P. ruthveni</i> (15)	0.19486	0.20227	0.20374	0.14444	0.15144	0.14597
28 <i>P. ruthveni</i> (16)	0.1936	0.20224	0.2024	0.14437	0.15138	0.14594
29 <i>R. lecontei</i> (17)	0.20138	0.21054	0.20856	0.16534	0.17281	0.18362
30 <i>R. lecontei</i> (18)	0.20742	0.20895	0.20905	0.16136	0.16478	0.1755
31 <i>Se. triaspis</i>	0.23337	0.23331	0.21022	0.19169	0.19916	0.20153
32 <i>St. extenuatum</i>	0.1937	0.20765	0.20525	0.14266	0.15006	0.15121

	7	8	9	10	11	12
7 <i>B. subocularis</i> (3)	—					
8 <i>B. subocularis</i> (4)	0.00567	—				
9 <i>C. coccinea</i>	0.13342	0.13016	—			
10 <i>E. bairdi</i>	0.14277	0.13939	0.11123	—		
11 <i>E. guttata</i>	0.14442	0.14111	0.13855	0.12067	—	
12 <i>E. obsoleta</i>	0.13984	0.13647	0.10668	0.05178	0.10788	—
13 <i>E. vulpina</i>	0.1461	0.14274	0.13143	0.11255	0.11346	0.11607
14 <i>L. getula</i>	0.14159	0.1383	0.11617	0.13539	0.13297	0.13043
15 <i>L. mexicana</i>	0.15744	0.15404	0.11871	0.16683	0.1603	0.14375
16 <i>L. pyromelana</i>	0.11754	0.113	9.10872	0.12399	0.12705	0.12175
17 <i>L. zonata</i> (5)	0.13655	0.13329	0.11301	0.14547	0.1313	0.13605
18 <i>L. zonata</i> (6)	0.13446	0.13122	0.12517	0.14126	0.13366	0.13369
19 <i>P. catenifer</i> (7)	0.15131	0.15107	0.15556	0.10856	0.13151	0.10935
20 <i>P. catenifer</i> (8)	0.15911	0.1556	0.16205	0.13574	0.12878	0.11663
21 <i>P. deppei</i> (9)	0.15233	0.15182	0.15692	0.13016	0.14855	0.12569
22 <i>P. deppei</i> (10)	0.14373	0.14318	0.14992	0.12042	0.14067	0.11755
23 <i>P. lineaticollis</i> (11)	0.15064	0.14716	0.13803	0.10221	0.1311	0.1085
24 <i>P. lineaticollis</i> (12)	0.14464	0.14121	0.13534	0.10812	0.13159	0.11192
25 <i>P. melanoleucus</i> (13)	0.12803	0.1248	0.1294	0.09593	0.1088	0.10475
26 <i>P. melanoleucus</i> (14)	0.14153	0.13851	0.14181	0.10678	0.12343	0.11368
27 <i>P. ruthveni</i> (15)	0.1443	0.14091	0.1371	0.11022	0.11092	0.105
28 <i>P. ruthveni</i> (16)	0.14278	0.1394	0.13595	0.10753	0.10833	0.10241
29 <i>R. lecontei</i> (17)	0.14749	0.14576	0.13801	0.13406	0.13879	0.12689
30 <i>R. lecontei</i> (18)	0.13799	0.13627	0.13038	0.12818	0.12984	0.11834
31 <i>Se. triaspis</i>	0.20311	0.19922	0.19061	0.19447	0.19068	0.18809
32 <i>St. extenuatum</i>	0.13571	0.13243	0.1237	0.12712	0.14174	0.1363

continued

TABLE 3. Tamura–Nei DNA distances among the 32 mtDNA haplotypes included in this study—*continued*

	13	14	15	16	17	18
13 <i>E. vulpina</i>	—					
14 <i>L. getula</i>	0.14466	—				
15 <i>L. mexicana</i>	0.1593	0.11543	—			
16 <i>L. pyromelana</i>	0.13282	0.10578	0.11007	—		
17 <i>L. zonata</i> (5)	0.13538	0.11029	0.09432	0.07972	—	
18 <i>L. zonata</i> (6)	0.12799	0.11453	0.11406	0.08299	0.04348	—
19 <i>P. catenifer</i> (7)	0.12241	0.14831	0.17332	0.13497	0.13133	0.13806
20 <i>P. catenifer</i> (8)	0.13821	0.15456	0.15875	0.13228	0.13849	0.13987
21 <i>P. deppei</i> (9)	0.13852	0.1631	0.17419	0.14887	0.13564	0.14856
22 <i>P. deppei</i> (10)	0.12608	0.15041	0.1589	0.13566	0.13168	0.13871
23 <i>P. lineaticollis</i> (11)	0.13563	0.14498	0.14392	0.13009	0.1347	0.13293
24 <i>P. lineaticollis</i> (12)	0.13563	0.14232	0.14117	0.12434	0.12882	0.13026
25 <i>P. melanoleucus</i> (13)	0.1107	0.13383	0.15076	0.11567	0.11796	0.12073
26 <i>P. melanoleucus</i> (14)	0.12178	0.149	0.16244	0.13044	0.12481	0.13131
27 <i>P. ruthveni</i> (15)	0.12547	0.13954	0.16279	0.12713	0.12871	0.12317
28 <i>P. ruthveni</i> (16)	0.12275	0.13947	0.1627	0.12705	0.12725	0.12314
29 <i>R. lecontei</i> (17)	0.15437	0.13912	0.16996	0.14243	0.15804	0.14994
30 <i>R. lecontei</i> (18)	0.14876	0.13738	0.15968	0.12749	0.14811	0.14024
31 <i>Se. triaspis</i>	0.18669	0.20378	0.19452	0.19936	0.18294	0.20358
32 <i>St. extenuatum</i>	0.14601	0.0826	0.1256	0.1127	0.11538	0.11603
	19	20	21	22	23	24
19 <i>P. catenifer</i> (7)	—					
20 <i>P. catenifer</i> (8)	0.06101	—				
21 <i>P. deppei</i> (9)	0.09587	0.09323	—			
22 <i>P. deppei</i> (10)	0.08403	0.0868	0.02423	—		
23 <i>P. lineaticollis</i> (11)	0.08037	0.08866	0.09527	0.08593	—	
24 <i>P. lineaticollis</i> (12)	0.08055	0.08891	0.09256	0.0833	0.00913	—
25 <i>P. melanoleucus</i> (13)	0.07615	0.07745	0.0869	0.08185	0.07006	0.07016
26 <i>P. melanoleucus</i> (14)	0.07993	0.08876	0.09842	0.09462	0.0813	0.08143
27 <i>P. ruthveni</i> (15)	0.0607	0.0762	0.08557	0.07638	0.0714	0.07142
28 <i>P. ruthveni</i> (16)	0.05821	0.07366	0.08298	0.07383	0.06888	0.0689
29 <i>R. lecontei</i> (17)	0.14499	0.15887	0.16237	0.15097	0.14534	0.14596
30 <i>R. lecontei</i> (18)	0.13978	0.14681	0.14859	0.1359	0.13304	0.13363
31 <i>Se. triaspis</i>	0.1834	0.17803	0.18798	0.17876	0.16889	0.16448
32 <i>St. extenuatum</i>	0.14838	0.1569	0.14951	0.13502	0.14144	0.13826
	25	26	27	28	29	30
25 <i>P. melanoleucus</i> (13)	—					
26 <i>P. melanoleucus</i> (14)	0.01252	—				
27 <i>P. ruthveni</i> (15)	0.06754	0.07867	—			
28 <i>P. ruthveni</i> (16)	0.06501	0.07611	0.00226	—		
29 <i>R. lecontei</i> (17)	0.14756	0.15362	0.14684	0.1441	—	
30 <i>R. lecontei</i> (18)	0.13727	0.15125	0.13767	0.13496	0.01606	—
31 <i>Se. triaspis</i>	0.17678	0.18611	0.18049	0.1805	0.21375	0.20653
32 <i>St. extenuatum</i>	0.13028	0.1455	0.14275	0.14267	0.13668	0.13222
	31	32				
31 <i>Se. triaspis</i>	—					
32 <i>St. extenuatum</i>	0.18173	—				

are linear (Fig. 3). Third position transitions deviated greatly from a linear pattern, suggesting that these mutations are saturated. To estimate the transition-to-transversion bias for third position transitions, we fitted a least-squares regression line,

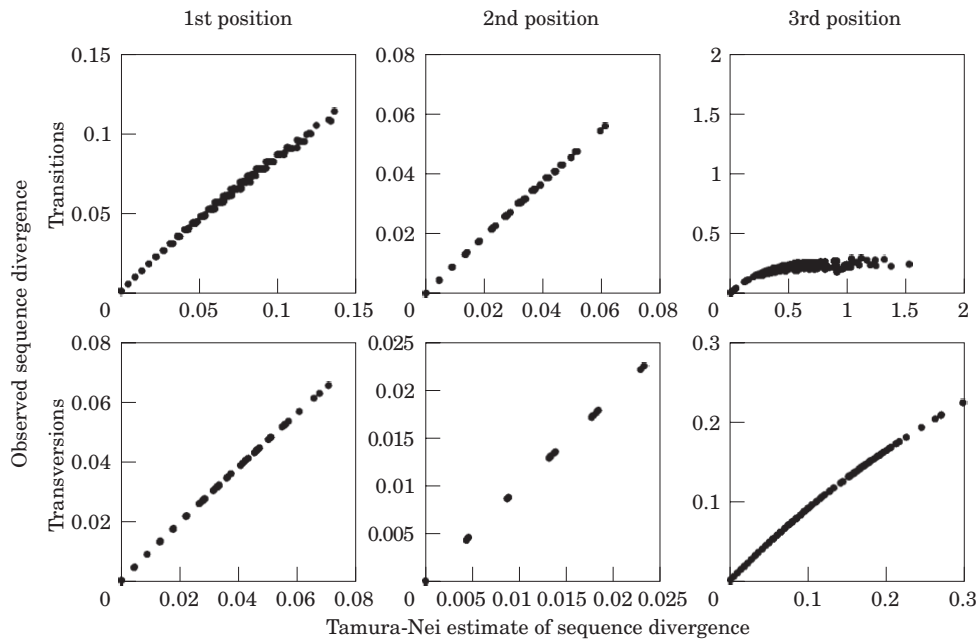


Figure 3. Scatter plots of pairwise sequence differences (uncorrected) in transitions and transversions at first, second, and third codon positions versus Tamura–Nei estimates of pairwise divergence for the same class of substitutions.

forced through the origin, to the part of the curve that was roughly linear. The slope of the regression line, 0.506, is an estimate of this bias (Lara, Patton & Da Silva, 1996; Moore & DeFilippis, 1997). Therefore, we down-weighted third codon transitional changes by a factor of 5 using a 1:1:0.2 codon position weighting (first, second, and third codon position, respectively) to correct for the biased substitution rates at this position.

#### *Phylogenetic relationships*

The MP analysis using equally-weighted characters resulted in five most parsimonious trees 1442 steps in length (L), a consistency index (CI) of 0.41 and a retention index (RI) of 0.54. The bootstrap consensus tree for this weighting scheme had little structure (Fig. 4A); only the monophyly of *Pituophis* and a close relationship between *Lampropeltis getula* and *Stilosoma extenuatum* and between *Elaphe bairdi* and *E. obsoleta* were strongly supported. Adjusting for the third position transitional bias evident in our data set resulted in two most parsimonious trees (L=2314, CI=0.43, RI=0.57). The bootstrap consensus tree for this weighting scheme also supported the monophyly of *Pituophis* and, weakly, that of *Lampropeltis* (including *Stilosoma*), and confirmed the close relationship between *L. getula* and *S. extenuatum* and between *E. bairdi* and *E. obsoleta* (Fig. 4B); otherwise this phylogeny was as

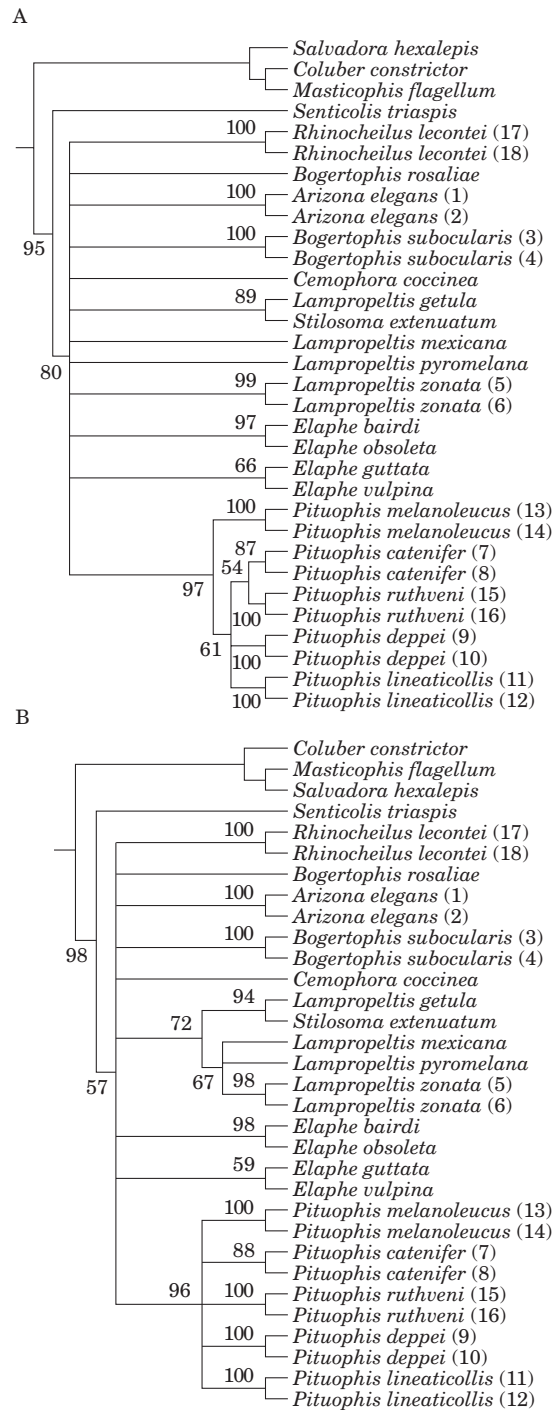


Figure 4. Maximum parsimony bootstrap consensus trees for 20 lampropeltine mtDNA haplotypes obtained using *Coluber constrictor*, *Masticophis flagellum*, and *Salvadora hexalepis* as outgroups. Numbers on tree indicate percentage of nonparametric bootstrap support for nodes retained by more than 50% of bootstrap replicates. A, with all characters weighted equally; B, with third position transitions down-weighted by a factor of 5:1.

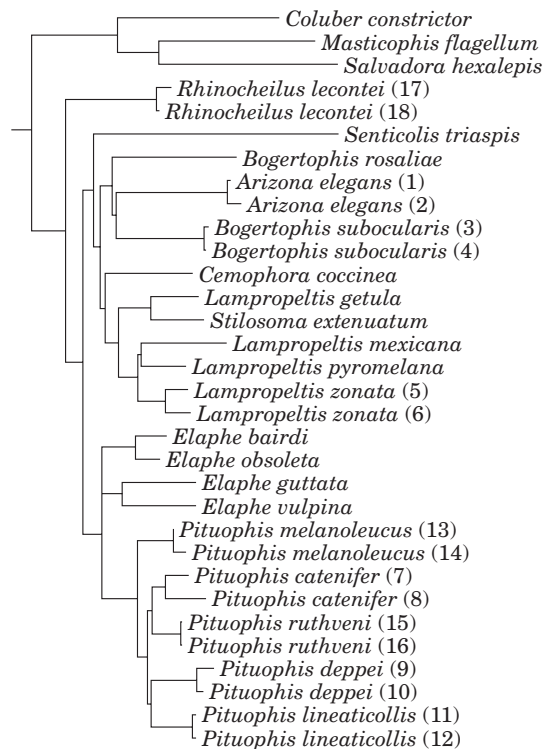


Figure 5. Maximum likelihood tree for 20 lampropeltinine mtDNA haplotypes obtained using *Coluber constrictor*, *Masticophis flagellum*, and *Salvadora hexalepis* as outgroups. Branches are drawn proportional to branch lengths (expected amount of character change) estimated by the maximum likelihood algorithm.

poorly resolved as the MP bootstrap consensus tree inferred from the equally-weighted data. The log-likelihood score for the single ML tree obtained (Fig. 5) is  $\text{LnL} = -7404.66629$ . The completely resolved ML tree identified *Rhinocheilus lecontei* as the sister group to all other lampropeltinines, supported the monophyly of New World *Elaphe* and *Pituophis*, and indicated that *Arizona* and *Stilosoma* nest phylogenetically within *Bogertophis* and *Lampropeltis*, respectively.

Several studies have demonstrated the overall superiority of the ML method over MP and distance methods to infer phylogenetic relationships using DNA sequence data (e.g. Hillis, Huelsenbeck & Swofford, 1994; Kuhner & Felsenstein, 1994; Huelsenbeck, 1995; Yang, 1996b; Cunningham, Zu & Hillis, 1998). MP involves stringent assumptions concerning the process of sequence evolution (Lewis, 1998), such as constancy of substitution rates between nucleotides, constancy of rates across nucleotide sites, and equal branch lengths (Yang, 1996b). All these assumptions are likely to be violated by real data sets. On the other hand, ML is an especially desirable method of phylogenetic inference in the presence of variable substitution rates among lineages, highly biased transition rates, and substantial evolutionary changes (Yang, 1997); that is, ML is a consistent estimator of phylogeny over a larger set of conditions than MP and distance methods. For these reasons, we chose as our best hypothesis of relationships within Lampropeltini the ML tree (Fig. 5), and based our phylogenetic conclusions and discussion of patterns of biogeography and character evolution among lampropeltinines on this tree.



TABLE 4. Estimation of the ancestral area of lampropeltinine snakes obtained using the method of Bremer (1992). G = number of necessary gains under forward Camin–Sokal parsimony; L = number of necessary losses under reverse Camin–Sokal parsimony; AA = ancestral area (G/L quotients rescaled to a maximum value of 1 by dividing by the largest G/L value). Numbers in parentheses indicate the values obtained when *Pituophis ruthveni* was excluded from the analysis. Refer to Fig. 2 for demarcation of geographic areas

	G	L	G/L	AA
Appalachia	5	7	0.71	0.63 (0.61)
Southeastern Coastal Plains	6	6	1.0	0.89 (0.85)
Great Lakes	5	9 (8)	0.56 (0.625)	0.50 (0.53)
Central Plains	7	8 (7)	0.875 (1.0)	0.78 (0.85)
Northwest	5	10 (9)	0.50 (0.56)	0.44 (0.48)
Southwest	7	7 (6)	1.0 (1.17)	0.89 (1.0)
Mexican Plateau	9 (8)	8 (7)	1.125 (1.14)	1.0 (0.97)
Neotropics	2	5	0.40	0.36 (0.34)

#### *Estimation of the ancestral area of lampropeltinines*

We determined the number of gains and losses under forward and reverse Camin–Sokal parsimony for the eight areas used in this study on which lampropeltinines occur or are known to have occurred. We used the gain/loss (G/L) quotient to compare the relative probabilities that individual regions were part of the ancestral area of Lampropeltini (Table 4). A high value of the G/L quotient indicates a higher probability that the region was part of the ancestral area, and vice versa. To make comparisons easier, we rescaled the G/L quotients to a maximum value of 1 (i.e. AA values, for ancestral area) by dividing them by the largest G/L value (Bremer, 1992). The sequence of areas indicated by the AA values listed in Table 4 is (1) Mexican Plateau, (2) Southeastern Coastal Plains and Southwest (equally probable), (3) Central Plains, (4) Appalachia, (5) Great Lakes, (6) Northwest, and (7) Neotropics, in that order. Therefore, Bremer’s method identified the Mexican Plateau as the most likely ancestral area of lampropeltinines, provided that the ancestral area of the group was smaller than its present distribution and that actual and known historical distribution of these snakes reflects the areas they have occupied since their origin. Because the recognition of *Pituophis ruthveni* as a distinct species from *P. catenifer* remains controversial (Rodríguez-Robles & De Jesús-Escobar, in press), we repeated this analysis excluding the former species. The sequence of areas then obtained was (1) Southwest, (2) Mexican Plateau, (3) Central Plains and Southeastern Coastal Plains (equally probable), (4) Appalachia, (5) Great Lakes, (6) Northwest, and (7) Neotropics (Table 4).

#### *Food habits of lampropeltinines*

The percentages of various prey categories in the natural diets of lampropeltinine snakes are given in Table 5. Lampropeltinines as a group feed mainly on mammals, less frequently on lizards, birds, and bird eggs, and only rarely on squamate eggs, snakes, anurans, and insects. On an individual basis, although some species indeed emphasize mammals in their diets (*Bogertophis subocularis*, *Elaphe guttata*, *E. obsoleta*, *Pituophis catenifer*, *P. melanoleucus*), others feed most frequently on lizards (*Lampropeltis*

TABLE 5. Frequencies and percentages (below frequencies) of prey types eaten by *Coluber constrictor*, *Masticophis flagellum*, *Sabradora hexalepis*, and 18 species of lampropeltine snakes. INS = insects; ANU = anurans; LIZ = 'lizards' (i.e. squamate reptiles other than snakes and amphisbaenians); SNA = snakes; SQEG = squamate eggs; BIR = birds; BIEG = bird eggs; MAM = mammals; OTH = other prey; TP = total prey

Species	Prey											Source <sup>a</sup>
	INS	ANU	LIZ	SNA	SQEG	BIR	BIEG	MAM	OTH	TP	TP	
<b>Outgroups</b>												
<i>Coluber constrictor</i>	792	39	92	130	—	11	5	197	12	1278	3, 6, 11, 13, 18, 19, 24, 26, 32, 46, 51, 61	
	62.0	3.1	7.2	10.2	—	0.9	0.4	15.4	0.9	120	4, 7, 18, 24, 25, 26, 29, 32, 34, 35, 38, 44, 67	
<i>Masticophis flagellum</i>	13	1	68	4	3	5	4	19	3	120	4, 14, 23	
	10.8	0.8	56.7	3.3	2.5	4.2	3.3	15.8	2.5	6	—	
<i>Sabradora hexalepis</i>	—	—	4	—	2	—	—	—	—	—	—	
	—	—	66.7	—	33.3	—	—	—	—	—	—	
<b>Lampropeltini</b>												
<i>Arizona elegans</i>	—	—	53	1	—	4	—	47	2	107	63	
	—	—	49.5	0.9	—	3.7	—	43.9	1.9	23	28, 34, 53, 65	
<i>Bogertophis subocularis</i>	—	—	—	—	1	4	—	18	—	1	65	
	—	—	—	—	4.3	17.4	—	78.3	—	—	—	
<i>Bogertophis rosaliae</i>	—	—	—	—	—	—	—	1	—	—	—	
	—	—	—	—	—	—	—	100	—	26	20, 31, 46, 58, 60, 61	
<i>Cenophora coccinea</i>	—	—	—	—	20	—	—	—	6	—	—	
	—	—	—	—	76.9	—	—	—	23.1	1	54	
<i>Elathe bairdi</i>	—	—	—	—	—	—	—	—	—	—	—	
	—	—	—	—	—	—	100	—	—	50	6, 24, 32, 40, 42, 46, 61	
<i>Elathe guttata</i>	—	2	3	2	—	8	3	32	—	—	—	
	—	4.0	6.0	4.0	—	16.0	6.0	64.0	—	489	3, 5, 6, 18, 26, 32, 40, 41, 42, 45, 46, 47, 48, 49, 51, 52, 56, 61	
<i>Elathe obsoleta</i>	8	10	9	1	6	127	82	243	3	—	—	
	1.6	2.0	1.8	0.2	1.2	26.0	16.8	49.7	0.6	28	2, 3, 10, 12, 15, 50, 55	
<i>Elathe vulpina</i>	—	—	—	—	—	2	17	6	3	—	—	
	—	—	—	—	—	7.1	60.7	21.4	10.7	222	6, 8, 12, 21, 26, 29, 35, 36, 40, 46, 61, 66	
<i>Lampropeltis getula</i>	1	1	34	52	39	1	25	56	13	7	—	
	0.5	0.5	15.3	23.4	17.6	0.5	11.3	25.2	5.9	—	—	
<i>Lampropeltis pyromelana</i>	—	—	4	—	—	1	—	2	—	—	—	
	—	—	57.1	—	—	14.3	—	28.6	—	34	1, 9, 11, 17, 22, 35, 57	
<i>Lampropeltis zonata</i>	—	—	28	—	1	1	3	1	—	—	—	
	—	—	82.4	—	2.9	2.9	8.8	2.9	—	—	—	

continued

TABLE 5. Frequencies and percentages (below frequencies) of prey types eaten by *Coluber constrictor*, *Masticophis flagellum*, *Salvadora hexalepis*, and 18 species of lampropeltine snakes. INS = insects; ANU = anurans; LIZ = 'lizards' (i.e. squamate reptiles other than snakes and amphisbaenians); SNA = snakes; SQEG = squamate eggs; BIR = birds; BIEG = bird eggs; MAM = mammals; OTH = other prey; TP = total prey—continued

Species	Prey											Source <sup>a</sup>
	INS	ANU	LIZ	SNA	SQEG	BIR	BIEG	MAM	OTH	TP		
<i>Pituophis catenifer</i>	1	—	33	4	2	77	87	699	2	905	62	
<i>Pituophis deppii</i>	0.1	—	3.6	0.4	0.2	8.5	9.6	77.2	0.2	1	65	
<i>Pituophis lineaticollis</i>	—	—	—	—	—	—	—	100	—	9	65	
<i>Pituophis melanoleucus</i>	—	—	—	—	—	—	—	100	—	19	16, 26, 30, 46, 59	
<i>Pituophis rulhveni</i>	—	—	—	—	—	—	—	—	—	3	54	
<i>Rhinocheilus lecontei</i>	1	—	89	—	9	—	—	35	1	135	64	
<i>Senticolis triaspis</i>	0.7	—	65.9	—	6.7	—	—	25.9	0.7	3	33, 37, 39	
Totals (for lampropeltines only)	11	13	254	62	80	225	222	1163	33	2063		
	0.5	0.6	12.3	3.0	3.9	10.9	10.8	56.4	1.6			

<sup>a</sup> 1 = Van Denburgh, 1897; 2 = Cope, 1900; 3 = Surface, 1906; 4 = Ruthven, 1907; 5 = Hurter, 1911; 6 = Wright & Bishop, 1915; 7 = Van Denburgh & Slevin, 1921; 8 = Van Denburgh, 1922; 9 = Grinnell & Storer, 1924; 10 = Logier, 1925; 11 = Fitch, 1936; 12 = Conant, 1938; 13 = Richmond & Goin, 1938; 14 = Bogert, 1939; 15 = Logier, 1939; 16 = Carr, 1940; 17 = Petrides, 1941; 18 = Marr, 1944; 19 = Hoffman, 1945; 20 = Dickson, 1948; 21 = Fitch, 1949; 22 = Wentz, 1953; 23 = Stebbins, 1954; 24 = Fouquette & Lindsay, 1955; 25 = Gehlbach, 1956; 26 = Hamilton & Pollack, 1956; 27 = Woodin, 1956; 28 = Dowling, 1957; 29 = Gates, 1957; 30 = Wright & Wright, 1957; 31 = Brode & Allison, 1958; 32 = Carpenter, 1958; 33 = Duellman, 1958; 34 = Minton, 1958; 35 = Cunningham, 1959; 36 = Myers, 1959; 37 = Dowling, 1960; 38 = Miller & Stebbins, 1964; 39 = Mankins & Meyer, 1965; 40 = Huheey & Stupka, 1967; 41 = Jackson, 1970; 42 = White & Woolfenden, 1973; 43 = Iverson, 1975; 44 = Tyler, 1977; 45 = Blem, 1979; 46 = Brown, 1979; 47 = Fendley, 1980; 48 = Stickle & Schmid, 1980; 49 = Haggerty, 1981; 50 = Vogt, 1981; 51 = Fitch, 1982; 52 = Mirarchi & Hitchcock, 1982; 53 = Reynolds & Scott, 1982; 54 = Tennant, 1984; 55 = Wheeler, 1984; 56 = Hensley & Smith, 1986; 57 = McGurty, 1988; 58 = Burger *et al.*, 1992; 59 = Franz, 1992; 60 = Mitchell, 1994; 61 = Palmer & Braswell, 1995; 62 = Rodríguez-Robles, 1998; 63 = Rodríguez-Robles, Bell & Greene, 1999a; 64 = Rodríguez-Robles & Greene, 1999a; 65 = J. A. Rodríguez-Robles & H. W. Greene, unpublished data; 66 = H. W. Greene, unpublished data; 67 = R. S. Reiserer, personal communication.

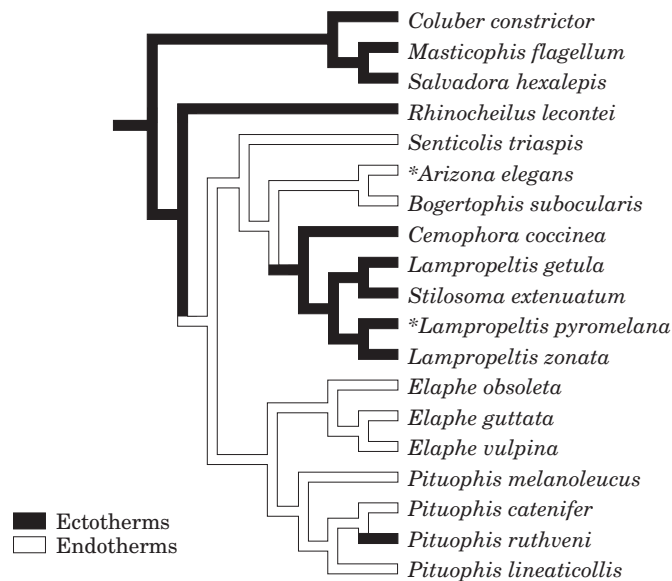


Figure 6. Evolution of food habits among lampropeltinine snakes. Assignment of states to branches is based on character optimization on the maximum likelihood tree depicted in Fig. 5. Asterisks indicate species that eat ectothermic and endothermic prey with similar frequency.

*zonata*, *Rhinocheilus lecontei*), squamate eggs (*Cemophora coccinea*), bird eggs (*E. vulpina*), and snakes (*Stilosoma extenuatum*), whereas others (*Arizona elegans*, *L. getula*, *L. pyromelana*) take two prey types with similar frequency.

We used our ML tree to assess patterns of evolution of food habits among lampropeltinines. Our character optimization analyses suggest that a diet that emphasizes endothermic prey (i.e. mammals, birds, bird eggs) is a derived trait in Lampropeltini (Fig. 6), having evolved in the most recent common ancestor (MRCAs) of the *Senticolis*–*Arizona*–*Bogertophis*–*Cemophora*–*Lampropeltis*–*Stilosoma*–*Elaphe*–*Pituophis* clade, with a subsequent loss in the MRCA of the *Cemophora*–*Lampropeltis*–*Stilosoma* clade. The scant food records available for *Pituophis ruthveni* (three unidentified amphibians) also suggest that this taxon reversed to a diet mainly consisting of ectothermic prey. However, because we suspect that this finding may be an artifact of our poor knowledge of the natural history of *P. ruthveni*, we regard this conclusion as tentative until additional information on the diet of this species becomes available. The ML tree also indicates that lizards probably were the ancestral modal prey of the clade, and that diets that emphasize mammals, squamate and bird eggs, and snakes evolved more recently (Fig. 7). Because we only have one food record each for *Bogertophis rosaliae* (one mammal), *Elaphe bairdi* (one bird egg), and *Pituophis deppei* (one mammal), we cannot characterize the diets of these species to compare them to those of their close relatives.

## DISCUSSION

### *Phylogenetic relationships*

The ML tree indicated that *Rhinocheilus lecontei* is the sister taxon to other lampropeltinines. In contrast, previous studies based on immunological (Dowling &

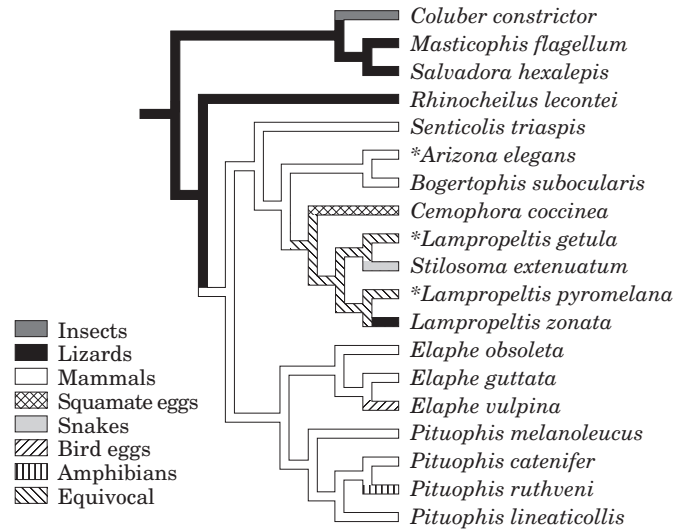


Figure 7. Evolution of prey type preferences among lampropeltinine snakes. Assignment of states to branches is based on character optimization on the maximum likelihood tree depicted in Fig. 5. Asterisks indicate species that consume two prey types with similar frequency (see Table 5). 'Equivocal' indicates that the assignment of more than one character state to that branch is equally parsimonious.

Maxson, 1990) and morphological (Keogh, 1996) data suggested, respectively, that *Rhinocheilus* may not belong within Lampropeltini, or that *Rhinocheilus* is a derivative of, or closely related to *Lampropeltis*. Nevertheless, Dowling & Maxson's suggestion was based on a single immunological distance comparison, and evolutionary relationships inferred without using reciprocal immunological data remain questionable (Guyer, 1992; but see Hass & Maxson, 1993), and Keogh's cladogram was based on only 17 characters for 31 taxa, which suggests that the results of these studies may not represent an accurate estimate of the relationships within Lampropeltini. We believe that *Rhinocheilus* belongs within Lampropeltini, but in consideration of its basal position, we cannot categorically deny the possibility that it might belong to a different clade. Further studies that include other close relatives of Lampropeltini (e.g. *Chilomeniscus*, *Trimorphodon*; Cadle, 1988; Dowling & Maxson, 1990), as well as several lampropeltinines, are needed to confirm the taxonomic position of *Rhinocheilus*.

The four species of New World *Elaphe* formed a weakly supported clade, with *E. guttata* and *E. vulpina* clustering in one group, and *E. bairdi* and *E. obsoleta* in another, more strongly supported clade (Fig. 5). In contrast, earlier works suggested that New World *Elaphe* are paraphyletic with respect to *Pituophis* (Dowling *et al.*, 1983), with respect to *Arizona*, *Bogertophis*, *Cemophora*, and *Lampropeltis* (Dowling *et al.*, 1996), or with respect to *Arizona*, *Bogertophis*, *Cemophora*, *Lampropeltis*, *Pituophis*, *Stilosoma*, and *Rhinocheilus* (Keogh, 1996; Fig. 1). Because there are various factors potentially responsible for these discrepancies (e.g. differences in taxon sampling and choice of outgroup, errors in determination of character polarity, insufficient number of characters used to infer evolutionary relationships), it is clear that additional studies that include representatives of *E. bairdi*, *E. guttata*, *E. obsoleta*, and *E. vulpina* from various localities, as well as of *E. flavirufa*, are needed to confirm the monophyly of extant New World *Elaphe*.

The four species of *Lampropeltis* also formed a monophyletic clade, again differing from previous studies that suggested that *Lampropeltis* is paraphyletic with respect to *Senticolis* and *Cemophora* (Dowling *et al.*, 1983; Dowling & Maxson, 1990). Phylogenetic analyses of mtDNA sequences of the eight recognized species of *Lampropeltis* (*L. alterna*, *L. calligaster*, *L. getula*, *L. mexicana*, *L. pyromelana*, *L. ruthveni*, *L. triangulum*, *L. zonata*), including most of the approximately 45 described subspecies, supported the monophyly of the genus (J.W. Fetzner, pers. comm.) and thus confirmed our results.

Our ML tree corroborates previous suggestions (Williams & Wilson, 1967; Dowling *et al.*, 1983; Dowling & Maxson, 1990) of a close relationship between *Cemophora coccinea*, *Stilosoma extenuatum*, and *Lampropeltis*. However, in contrast to studies based on immunological data (Dowling *et al.*, 1983; Dowling & Maxson, 1990), we did not find that *C. coccinea* nests within *Lampropeltis*, but instead that *Cemophora* is the sister taxon to *Lampropeltis*. This finding agrees with Meylan's (1982) suggestion, based on fossil evidence, that *C. coccinea* diverged from an ancestor of *Lampropeltis*. On the other hand, our results confirm that *Stilosoma* belongs within *Lampropeltis* (Dowling & Maxson, 1990), and therefore suggest that to maintain a phylogenetic classification (de Queiroz & Gauthier, 1992) *Stilosoma* should be referred to the synonymy of *Lampropeltis*.

The taxonomic status of *Bogertophis rosaliae*, *B. subocularis* and *Senticolis triaspis* is controversial. Based mostly on its unique hemipenial morphology, Dowling and Fries (1987) removed *triaspis* from *Elaphe*, placed it in the new monotypic *Senticolis*, and stated that its closest relatives were unknown. Morphological traits shared by *rosaliae* and *subocularis* also led Dowling & Price (1988) to transfer these two taxa from *Elaphe* to the newly erected *Bogertophis* (see also Price, 1990). Van Devender & Bradley (1994) questioned the latter arrangement and kept *rosaliae* and *subocularis* in *Elaphe*, whereas Schulz (1996:7) elected to keep *rosaliae*, *subocularis*, and *triaspis* in *Elaphe* arguing that "the genus *Elaphe* requires an overall revision [which] should include every species in the Old and New World to clarify the entire relationship and cannot be restricted to single representatives." After determining that *S. triaspis* lacked the single putative morphological synapomorphy of the Lampropeltini (an intrapulmonary bronchus), Keogh (1996) proposed the removal of this taxon from Lampropeltini. Our results clearly support that *S. triaspis* is a lampropeltinine and that it is the sister taxon to the *Bogertophis*–*Arizona*–*Cemophora*–*Lampropeltis*–*Stilosoma* clade, and that *B. rosaliae*, *B. subocularis*, and *S. triaspis* do not belong within New World *Elaphe*, but they do not confirm that *B. rosaliae* and *B. subocularis* are each other's closest relatives, as proposed by Schmidt (1925) and Dowling (1957). We interpret our findings as suggestive of a closer relationship between *Arizona* and *Bogertophis* than previously suspected, but the limited taxon sampling herein used requires caution and prompts us to suggest that a more comprehensive study using specimens from across the ranges of *Senticolis*, *Bogertophis*, and *Arizona* be completed before deciding which taxonomic arrangement better reflects the evolutionary relationships of these snakes.

The sister group relationships of *Pituophis* and the number of species recognized within this genus in the United States (U.S.A.) have also been controversial issues for several decades (e.g. Smith & Kennedy, 1951; Conant, 1956; Reichling, 1995). Morphological evidence (Dowling & Price, 1988; Keogh, 1996) suggests that *Bogertophis* is the sister taxon to *Pituophis*, whereas molecular data indicate that either New World *Elaphe* (Dowling *et al.*, 1983; López & Maxson, 1995), *Arizona elegans*



(Dowling & Maxson, 1990), *Lampropeltis* or *Rhinocheilus lecontei* (Dowling *et al.*, 1996) are *Pituophis*' closest relatives. Our findings unambiguously indicate that New World *Elaphe* is the sister taxon to *Pituophis*, and support suggestions that *Pituophis* snakes in the U.S.A. belong to three species: *P. melanoleucus* (*sensu stricto*) in the eastern U.S.A., *P. catenifer* in the central and western parts of the country (and northern Mexico), and *P. ruthveni* in Louisiana and eastern Texas (Reichling, 1995; Rodríguez-Robles & De Jesús-Escobar, in press).

#### *Ancestral area and divergence times of lampropeltinines*

When we included *Pituophis ruthveni* in our estimation of the ancestral area of Lampropeltini, Bremer's method suggested that the clade originated in the Mexican Plateau. Nonetheless, when we excluded this species from the analysis, Bremer's procedure indicated that either the Southwest or the Mexican Plateau were the ancestral areas of Lampropeltini. We interpret these results as collectively suggesting that the clade probably evolved in western North America (either the Southwest or the Mexican Plateau), from which they dispersed eastward, northward, and to a lesser extent, southward through southern Mexico, Central America, and northern South America.

The use of the 'molecular clock' to estimate divergence times is a contentious subject in evolutionary biology (e.g. Collins, 1996; Hillis, Mable & Moritz, 1996; Smith, Littlewood & Wray, 1996; Li, 1997; Sanderson, 1998). Despite the difficulties in applying this concept, we believe that molecular estimates of divergence can be used to help formulate initial, falsifiable evolutionary hypotheses for the taxa under study. The smallest uncorrected percentage sequence divergence between the ingroup (*Pituophis catenifer*, sample 7) and the outgroup (*Coluber constrictor*) was 15.9%. Estimates of mtDNA sequence divergence for reptile species for which branching events have been confidently dated range from 0.47 to 1.32% per million year (Zamudio & Greene, 1997). Using these figures, we estimated that a lineage including the ancestors of modern lampropeltinines split from *Coluber constrictor* 33.8–12.0 million years ago (Mya; late Eocene to late Miocene), whereas divergences between the major lampropeltinine clades identified in the ML tree (Fig. 5) occurred 33–6.7 Mya. To our knowledge, the oldest fossils confidently assigned to Lampropeltini (the extinct *Elaphe nebraskensis*) are known from the early Miocene of North America (Holman, 1977), which corresponds to the minimum age of the genus suggested by molecular data. Provided that our upper divergence estimate constitutes a fair approximation of actual divergence times, the ancestors of modern lampropeltinines evolved during a time of long-term change toward drier climatic conditions and conversion from forests to savannas and other more open environments (Behrensmeyer *et al.*, 1992). By Clarendonian times (11.5–8 Mya), increased aridity in the southwestern part of North America may have begun to limit faunal interchange with the central regions of the continent, perhaps facilitating the independent evolution of the faunas from the two areas.

#### *Evolution of food habits*

An important distinction to be made when studying the diet of a predator is between ectothermic (e.g. anurans, lizards, snakes, squamate eggs) and endothermic



prey. These two groups differ in mean body size, activity levels, and other traits likely to influence their vulnerability to predators (Pough, 1980). Optimization of modal prey type(s) onto our ML tree suggests that food habits that emphasize ectothermic prey are ancestral for lampropeltinines (Fig. 6), and therefore a diet that mostly consists of endothermic prey evolved later within the clade. In many snake species, larger individuals eat larger prey, which raises the possibility that an increase in lampropeltinine mean adult body size may have played an important role in the evolution of a diet that emphasizes endotherms, but the fact that most lampropeltinines attain similar mean adult body sizes does not support this hypothesis. Nonetheless, in snakes and other gape-limited predators that swallow their prey whole, specimens with larger heads relative to their body size can eat larger prey (Pough & Groves, 1983; Shine, 1991; Forsman & Lindell, 1993; Houston & Shine, 1993; Rodríguez-Robles *et al.*, 1999a), so perhaps an increase in relative head size characterizes *Senticolis triaspis* and the *Bogertophis*–*Arizona* and *Elaphe*–*Pituophis* clades (Fig. 5).

Our comparative analyses of lampropeltinine food habits uncovered other interesting patterns regarding dietary diversity among these snakes. *Elaphe vulpina* has a uniquely derived diet that consists mostly of bird eggs. Ratsnakes (*Elaphe*) are usually skillful climbers [in fact, *E. guttata* is regarded as a semiarboreal serpent (Schulz, 1996)], but *E. vulpina* is probably the least adept climber of the genus (Ditmars, 1936; Schulz, 1996), which implies that this snake usually raids the nests of ground-nesting birds. The *Cemophora*–*Lampropeltis*–*Stilosoma* clade (Fig. 5) exhibits the greatest diversity of food habits within Lampropeltini (Table 5; Fig. 7). Squamate eggs compose most of the diet of *C. coccinea*; *L. getula* feeds mainly on mammals and squamate eggs, but also frequently takes lizards and snakes; *L. zonata* eats mostly lizards; the scant available data for *L. pyromelana* indicate that it eats lizards, mammals, and birds; and observations on captive specimens strongly suggest that *Stilosoma extenuatum* feeds mainly on snakes. Interestingly, a species of *Lampropeltis* not included in this study, *L. calligaster*, takes mostly mammals (Fitch, 1982). Elucidating the causes (historical and/or proximal), as well as the behavioral, morphological, and physiological correlates of such diversity of food habits in the *Cemophora*–*Lampropeltis*–*Stilosoma* clade will likely contribute to our understanding of evolutionary and ecological diversification of closely-related taxa.

Although useful for broadly characterizing the diet of the clade, combining dietary records from across the geographic range and from all age classes of lampropeltinine snakes can obscure interesting aspects of the feeding ecology of these predators. For example, for those lampropeltinines for which appropriate data are available, geographic variation in food habits occurs. Mexican specimens of *Rhinocheilus lecontei* are larger and consume mammals with higher frequency than smaller individuals from more northern latitudes (Rodríguez-Robles & Greene, 1999). The reverse seems to be true for *Arizona elegans*. In this species, Mexican specimens containing prey were smaller and took significantly more lizards than individuals from more northern parts of the species range (J. A. Rodríguez-Robles, C. J. Bell & H. W. Greene, unpublished data). The diet of *Pituophis catenifer* varies geographically, with the frequency of birds and bird eggs eaten being different across populations (von Bloeker, 1942; Fitch, 1949, 1982; Eichholz & Koenig, 1992; Diller & Wallace, 1996).

Some lampropeltinines exhibit size-related variation in their diets. Juveniles of *Rhinocheilus lecontei* prey almost exclusively on lizards, whereas larger snakes add

mammals to their diets (Rodríguez-Robles & Greene, 1999). Specimens of *Arizona elegans* that eat birds are larger than those that take mammals, which in turn are larger than the ones that feed on lizards (Rodríguez-Robles *et al.*, 1999a). Anecdotal information indicates that smaller *Elaphe guttata* and *E. obsoleta* prey on lizards with some frequency, whereas adults eat mainly mammals (Palmer & Braswell, 1995). At least one population (from northeastern Kansas, U.S.A.) of a species of *Lampropeltis* not included in this study, *L. triangulum*, also seems to conform to this pattern, with smaller individuals feeding mostly on scincid lizards and larger ones taking mainly rodents and insectivores (H. S. Fitch, pers. comm.). This ontogenetic shift in food habits does not seem to occur on *Pituophis*. Available data indicate that *P. catenifer* (J. A. Rodríguez-Robles, unpublished data) and *P. lineaticollis* (J. A. Rodríguez-Robles & H. W. Greene, unpublished data) of all sizes eat mostly mammals. Thus, perhaps the suppression of a juvenile diet accompanied the evolution of *Pituophis*. Additional data on the feeding biology of *P. deppei* and *P. ruthveni* are needed to assess the veracity of this hypothesis.

This study has contributed to our understanding of the phylogenetic relationships, biogeography, and aspects of the evolutionary ecology of a conspicuous group of predominantly North American snakes. Nevertheless, some of our conclusions are tentative and await confirmation by future studies due to the absence of a complete phylogeny for lampropeltinines and the paucity of detailed information on the feeding biology of some of these species. When this knowledge becomes available, Lampropeltini will likely continue to prove a fruitful subject for investigating patterns of evolutionary and ecological divergence in gape-limited, vertebrate predators.

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