Herpetologica, 52(3), 1996, 406–416

EVOLUTION OF THE COLUBRID SNAKE TRIBE LAMPROPELTINI: A MORPHOLOGICAL PERSPECTIVE

J. SCOTT KEOGH[1]

Department of Biological Sciences, Illinois State University, Normal, IL 61761, USA

ABSTRACT: Morphological characters drawn from soft anatomy, squamation, and the literature were used to construct a phylogenetic hypothesis for the New World colubrid snake tribe Lampropeltini. The tribe includes *Arizona*, *Cemophora*, *Lampropeltis*, *Pituophis*, *Rhinocheilus*, and *Stilosoma*. North American species of *Elaphe* are also part of this radiation. A number of Old and New World colubrid species were used as outgroups. Lampropeltini is defined by a single synapomorphy, the presence of an intrapulmonary bronchus which is lacking in all outgroup species and *Senticolis*. The analysis suggests the following relationships: (New World *Elaphe* + (*Bogertophis* + (*Pituophis* + (*Arizona* + (*Lampropeltis* + *Rhinocheilus* + (*Cemophora* + *Stilosoma*))))))). The recently described monotypic genus *Senticolis* is removed from the tribe Lampropeltini and placed in the tribe Colubrini.

Key words: Lampropeltini; Colubrid; Evolution; Cladistics; Phylogeny

THE North American snake fauna is diverse and species rich, and one of its most conspicuous elements is the assemblage of oviparous, non-venomous, colubrid "ratsnake" and "kingsnake" groups usually allocated to the tribe Lampropeltini (Dowling, 1975). Lampropeltini originally included *Cemophora*, *Lampropeltis*, *Rhinocheilus*, and *Stilosoma* (Dowling, 1975). More recently *Arizona*, *Pituophis*, and *Elaphe* have been recognized as part of this radiation by Dowling et al. (1983), who removed them from the tribe Colubrini (Dowling, 1978) based on close immunological similarity. In this paper, I review the pertinent phylogenetic literature and provide new morphological data from the soft anatomy that, coupled with other characters, helps elucidate the evolutionary relationships within this radiation of colubrid snakes.

Previous Studies

Morphological work suggested relationships between species now included in Lampropeltini long ago. Cope (1895) was the first to speculate on these relationships, commenting on the natural grouping of *Cemophora*, *Lampropeltis*, and *Rhinocheilus* based on the complete absence of the vestigial left lung. The close relationship of these genera was also recognized by Dunn (1928) who studied various hemipenis, dentition, squamation, and osteological characters, and associated *Stilosoma* with this group based on hemipenal similarities. In addition, Dunn (1928) noted the similarities of *Arizona*, *Pituophis*, and the North American *Elaphe* in hemipenial morphology, dentition, and squamation characteristics, but he did not associate these species with the genera mentioned above. The close relationship between North American *Elaphe* and *Pituophis* was also recognized by Dowling (1952*a*) based on similarities in hemipenes, body form, and squamation. Underwood (1967) suggested a close relationship between *Arizona*, *Cemophora*, *Lampropeltis*, *Pituophis*, and *Rhinocheilus* based on features of the soft anatomy.

The relationships within some members of this group also have been examined with molecular techniques. The immunological studies of Pearson (1966), George and Dessauer (1970), Minton and Salanitro (1972), and Schwaner and Dessauer (1982) found similarities among *Elaphe*, *Lampropeltis*,

[1] PRESENT ADDRESS: School of Biological Sciences AO8, University of Sydney, NSW 2006 Australia.

and *Pituophis*, suggesting that these genera formed a group distinct from the natricine snakes (*Thamnophis*, *Nerodia*, and allied genera) and the racers (*Coluber*, *Masticophis*, *Opheodrys*, and allied genera). The tight generic affinities of *Cemophora*, New World *Elaphe*, *Lampropeltis*, and *Pituophis*, and their immunological distinctiveness from *Coluber* and *Thamnophis*, were confirmed by Dowling et al. (1983). Dowling and Maxson (1990), using immunological distance methods, suggested that *Arizona*, *Pituophis*, and New World *Elaphe* are closely allied and showed that both *Cemophora* and *Stilosoma* are closely related to *Lampropeltis*. Dowling and Maxson also found the racers to be intermediate in immunological distance between some members of Lampropeltini and the natricines (Fig. 1), and inferred that the racer and natricine groups last shared common ancestors with some members of Lampropeltini in the mid-Miocene and the late Eocene or early Oligocene, respectively.

Electrophoretic evidence for the natural grouping of *Arizona*, *Lampropeltis*, *Pituophis*, and New World *Elaphe* was provided by Lawson and Dessauer (1981) who suggested that these genera "evolved rapidly from a single ancestor following a relatively recent invasion of the continent." Dessauer et al. (1987) concluded, based on data from protein electrophoresis, that *Arizona*, *Cemophora*, New World *Elaphe*, *Lampropeltis*, *Rhinocheilus*, *Pituophis*, and *Stilosoma* form a monophyletic group that underwent a rapid adaptive radiation from a single ancestor and are distinct from *Coluber* and *Thamnophis* and their allies.

Reality of the Ingroup

Due to the tremendous problem of homoplasy in traditional systematic characters for snakes, definition of monophyletic groups with morphological characters is often extremely difficult. Frequently, there simply is no single character that can define a group as monophyletic, yet it is important to have some basis for recognizing the monophyly of the ingroup. For the Lampropeltini, Underwood (1967) suggested that "a group of North American

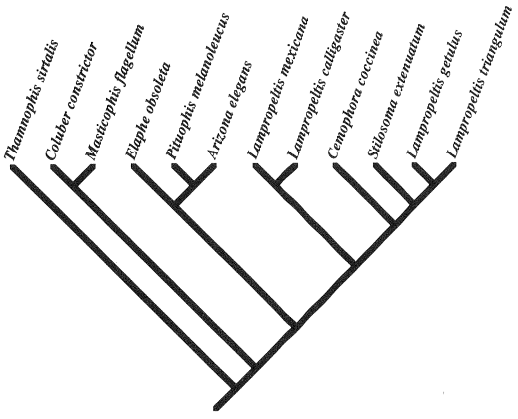

FIG. 1.—Dowling and Maxson's (1990) immunologically based phylogeny of certain members of Lampropeltini as well as representative species from *Coluber*, *Masticophis*, and *Thamnophis*. The topology of the tree is unchanged, but the branches have been rotated to facilitate comparison with the resulting phylogeny from this study shown in Fig. 2.

forms appears to be derived from *Elaphe* stock[;] they are characterised by a long intrapulmonary bronchus: *Pituophis*, *Lampropeltis*, *Cemophora*, *Arizona*, *Rhinocheilus*". I studied the condition of the intrapulmonary bronchus in *Arizona*, *Bogertophis*, *Cemophora*, *Lampropeltis*, *Pituophis*, *Rhinocheilus*, and North American *Elaphe* and discovered that all species posses an intrapulmonary bronchus (of varying lengths) while a sample of Old World *Elaphe*, *Senticolis*, and other outgroup species lack any remnant of an intrapulmonary bronchus. As first noted by Underwood (1967), the presence of an intrapulmonary bronchus is character evidence supporting the close relationship between North American *Elaphe* and other members of Lampropeltini (excluding Old World *Elaphe*). These data, combined with evidence from the previous studies cited above, clearly show that the traditional members of Lampropeltini plus *Pituophis* and *Arizona* and the North American species of *Elaphe* are closely related and probably form a monophyletic group.

Dowling et al. (1983) included *Elaphe* in the Lampropeltini, but the taxonomic treatment of the widespread genus is problematical. *Elaphe* contains approximately 50 species distributed across North Amer-

ica, Europe, Asia, and the East Indies, but the genus is almost certainly polyphyletic. New World species of *Elaphe* are thought to be much more closely related to other members of Lampropeltini than to Old World *Elaphe* on morphological (Dowling, 1952*b*; Dowling and Fries, 1987; Dowling and Price, 1988; Underwood, 1967) and immunological and protein electrophoresis grounds (Dowling et al., 1983; Lawson and Dessauer, 1981; Minton, 1976). For these reasons, only North American species of *Elaphe* were included in the ingroup of this study, but four Old World species of *Elaphe* were included in the outgroup.

There has been some recent progress in the taxonomic understanding of North American *Elaphe*. Two species formally included in *Elaphe* have recently been placed into the new genus *Bogertophis* based on differences in squamation, karyology, and scale microdermatoglyphics (Dowling and Price, 1988). Lawson and Dessauer (1981) found that *B. subocularis* clustered with other New World members of *Elaphe* in their protein electrophoresis study, but Dowling et al. (1983) found that *B. subocularis* was immunologically distinct from New World *Elaphe*.

Dowling and Fries (1987) described the new monotypic genus *Senticolis*, separating *Senticolis triaspis* from *Elaphe* based on aspects of squamation, osteology, body form, color pattern, and hemipenial morphology. This move was supported by earlier work by Lawson and Dessauer (1981) who found that *S. triaspis* was quite distinct electrophoretically from the North American *Elaphe*. *Bogertophis* and *Senticolis* were included in this study to better understand their relationship to North American *Elaphe*.

Materials and Methods

I examined museum specimens of each recognized species of *Arizona*, *Bogertophis*, *Cemophora*, *Lampropeltis*, *Pituophis*, *Rhinocheilus*, *Senticolis*, *Stilosoma*, and North American *Elaphe*. I also studied 12 outgroup species, including four Old World species of *Elaphe* (Table 1). A total of 17 characters was obtained: 12 from squamation, three from soft anatomy, and one from karyology. There were 11 binary characters, five characters with three character states, and one character with four character states. Brief descriptions of each character and the coding of character states are given in Appendix I to facilitate the interpretation of character state transformations. The data matrix used for phylogenetic analyses is shown in Table 1. I dissected 290 museum specimens to obtain data on soft anatomical characters (Appendix II). I examined a large number of soft anatomical and body proportional characters, but intraspecific variation and the inability clearly to define character states left only three soft anatomical characters that could be defined easily: the length of the intrapulmonary bronchus, condition of the left lung, and point of origin of the hemipenis retractor muscles.

Outgroup Choice

Choice of appropriate outgroups for the members of the Lampropeltini is difficult due to scant knowledge of relationships within the Colubridae in general. The molecular studies of Lawson and Dessauer (1981), Dowling et al. (1983), Dessauer et al. (1987), and Dowling and Maxson (1990) have clearly demonstrated that the "best guess" for outgroup choice can be found among members of the *Coluber* radiation and their allies. I have included a number of species from diverse colubrid groups to estimate the outgroup condition: *Coluber constrictor*, *Elaphe radiata*, *Elaphe rufodorsata*, *Elaphe quadrivirgata*, *Elaphe quaturolineata*, *Drymarchon corais*, *Masticophis flagellum*, *Masticophis lateralis*, *Masticophis taeniatus*, *Gonyosoma oxycephala*, *Ptyas mucosus*, and *Thamnophis sirtalis*.

Phylogenetic Analyses

Ancestral character states were determined by the most parsimonious interpretation of outgroup condition for most of the characters and a hypothetical ancestor was constructed (Table 1, and see Appendix I). Phylogenetic hypotheses were generated according to the criterion of maximum parsimony by the computer pro-

TABLE 1.—Data matrix for cladistic analysis. See Appendix I for character descriptions. Character (1) intrapulmonary bronchus length, (2) left lung condition, (3) number of supralabial scales, (4) loreal scales, (5) temporal scales, (6) lorilabial scales, (7) rostral scale, (8) supralabial contact with eye, (9) anal plate, (10) dorsal scales, (11) ventral scale shape, (12) mid-body scale rows, (13) apical pits, (14) body shape, (15) ecotype, (16) chromosome number, (17) origin of hemipenis retractor muscles. The symbol "a" represents character states 0 and 1, and "b" represents character states 0, 1, and 2. Multistate characters were treated as polymorphisms in the phylogenetic analyses.

Taxon	Character																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Ingroup																	
Arizona elegans	3	2	1	0	0	0	1	0	1	1	0	2	1	0	1	0	1
Bogertophis subocularis	1	2	2	0	1	1	0	1	0	0	0	2	0	0	0	1	2
Bogertophis rosaliae	1	2	2	0	1	1	0	1	0	0	0	2	0	0	0	1	?
Cemophora coccinea	3	2	0	0	0	0	1	0	1	1	1	0	0	1	1	0	2
Elaphe bairdi	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Elaphe favirufa	1	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Elaphe guttata	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Elaphe obsoleta	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Elaphe vulpina	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Lampropeltis calligaster	3	2	1	0	0	0	0	0	1	1	1	1	0	1	1	0	2
Lampropeltis getulus	3	2	1	0	0	0	0	0	1	1	1	1	0	1	0	0	2
Lampropeltis mexicana	3	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	2
Lampropeltis pyromelana	3	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	2
Lampropeltis triangulum	3	1	1	a	0	0	0	0	1	1	1	a	0	1	1	0	2
Lampropeltis zonata	3	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	2
Pituophis melanoleucus	2	1	1	0	0	a	1	0	1	0	0	2	0	0	a	0	a
Rhinocheilus lecontei	3	2	1	0	0	0	1	0	1	1	1	1	b	1	1	0	1
Stilosoma extenuatum	3	2	0	1	0	0	1	0	1	1	1	0	2	1	1	0	1
Senticolis triaspis	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	?	0
Outgroups																	
Coluber constrictor	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1
Elaphe quaturolineata	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	?	0
Elaphe quadrivirgata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Elaphe radiata	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	?	0
Elaphe rufodorsata	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	?	?
Drymarchon corais	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Gonyosoma oxycephala	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	?	0
Masticophis flagellum	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Masticophis lateralis	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	?	1
Masticophis taeniatus	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Ptyas mucosus	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Thamnophis sirtalis	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2
Hypothetical ancestor	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0

gram PAUP 3.1.1 (Swofford, 1993). A series of phylogenetic analyses were run, each in two iteratations, under both the "accelerated transformation" (ACCTRAN) and "delayed transformation" (DELTRAN) functions of PAUP. In order to reduce a priori assumptions about character state evolution, each character was given equal weight in the first run and strict consensus trees were produced. In each analysis, the consensus trees were then used to calculate the maximum "rescaled consistency index (RC)", "consistency index (CI)", and "retention index (RI)" for each character, and these values were used as the basis for a posteriori reweighting of characters for the second interations (again under both "ACCTRAN" and "DELTRAN"). Due to the large number of taxa, all analyses were heuristic searches with the following PAUP settings: simple addition sequence, tree-bisection-reconstruction (TBR) branch swapping, and zero length branches collapsed to yield polytomies. Multistate taxa were treated as polymorphic.

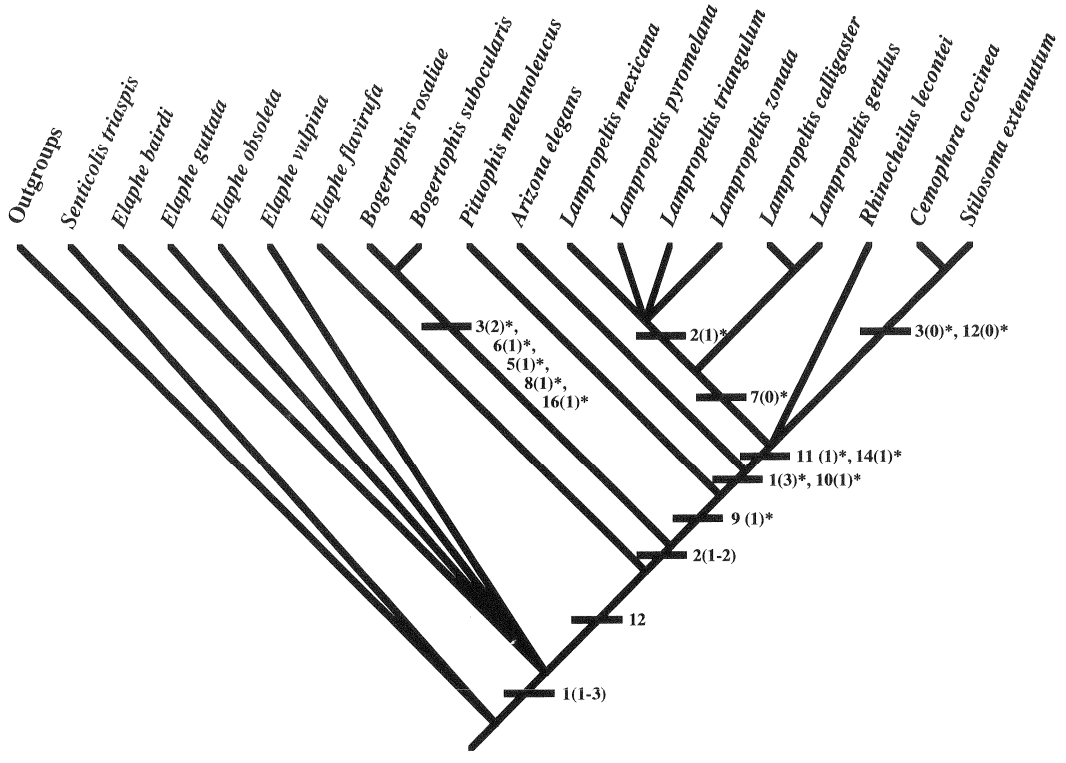

FIG. 2.—Strict consensus of four equally most parsimonious trees derived from the second interation of character weighting (see text for details of analyses). Synapomorphies in support of each branch are indicated with numbers which represent the character number as listed in Table 1. Character states are in parentheses. Asterisks (*) indicate unreversed synapomorphies.

RESULTS AND DISCUSSION

The first iterations of phylogenetic analyses (assuming equal weights) produced eight equally most parsimonious trees (41 steps: CI = 0.513) under both the assumptions of "ACCTRAN" and "DELTRAN". The strict consenus of these trees is identicle in topology to Fig. 2 except that *Senticolis triaspis* was included in the *Elaphe* polytomy. Each of the second iteration analyses with successive reweighting of characters and under both "ACCTRAN" and "DELTRAN" produced identicle results, four equally most parsimonious trees which are summarized in the strict consensus shown in Fig. 2 (strict consensus of RC, CI, and RI analyses with 25, 31, and 31 steps respectively: CI = 0.622). Each branch in the tree is supported by at least one synapomorphy.

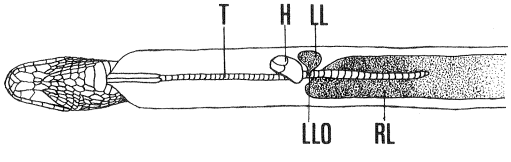

FIG. 3.—Relevant features of a snake respiratory system. The left lung (LL), when present, is attached to the trachea (T) by a small bronchus. When the left lung is absent, the orifice into the left lung (LLO) may remain, covered by a sheath, or the entire left lung system may be absent. The intrapulmonary bronchus (IPB) is defined as the continuation of the trachea caudad of the left lung orifice [or the apex of the heart (H) if the left lung orifice is absent] into the right lung (RL), and was measured as a proportion of SVL.

North American snakes have been hypothesized to represent dispersals of several groups from the Old World to the New World (Cadle, 1984, 1987). For the members of Lampropeltini, a "proto-*Elaphe*" like snake has been hypothesized

to have invaded North America via the Bering land bridge, undergone a diverse adaptive radiation, and given rise to *Arizona, Cemophora,* New World *Elaphe, Lampropeltis, Pituophis, Rhinocheilus,* and *Stilosoma* (Dessauer et al., 1987; Dowling and Maxson, 1990; Dowling et al., 1983; Lawson and Dessauer, 1981; Underwood, 1967; Williams and Wilson, 1967). The tree shown in Fig. 2 supports this phylogenetic hypothesis.

The Lampropeltini radiation is defined by a single synapomorphy, the presence of an intrapulmonary bronchus (IPB) (Fig. 3). The length of the IPB in the Lampropeltini varies from <10% snout–vent length (SVL) to almost 50% SVL and so was divided into four character states, but it is always present in some form. The North American species of *Elaphe* have a short IPB, *Pituophis* has an IPB of intermediate length, and *Arizona, Cemophora, Lampropeltis, Rhinocheilus,* and *Stilosoma* all have quite long IPB (Fig. 4). Length of the IPB displays little ontogenetic change and thus does not show major allometric shifts in proportional length (my unpublished data). This structure is absent in all of the outgroup species used in this study and all other colubrid species with which I have familiarity.

Senticolis triaspis is the only member of the ingroup that lacks an intrapulmonary bronchus, and it is indistinguishable from the outgroup species in the analysis. Dowling and Fries (1987) placed *Senticolis* in their "ratsnake group" within the Lampropeltini but stated that the closest relatives of *Senticolis* were as yet unknown. The relationships of *S. triaspis* to other members of the ingroup are still obscure, and neither I nor Dowling and Fries were able easily to associate this species with any other species in the New World or Old World. Based on this evidence, the placement of *S. triaspis* in the large and undefined tribe Colubrini, rather than Lampropeltini, is more appropriate.

The New World species of *Elaphe* are conservative in most aspects of their morphology. They possess a left lung, like the outgroups, and an intrapulmonary bronchus that is intermediate in length between the outgroup species and the other members of the ingroup. Underwood (1967) failed to find a left lung in *E. guttata* and *E. vulpina,* but left lungs were found in all individuals of these species in my study. *Elaphe flavirufa* is differentiated from the other New World species in my analysis only by the higher number of mid-body scale rows, which is reversed at higher nodes in the tree, and the more anterior origin of the hemipenis retractor muscles.

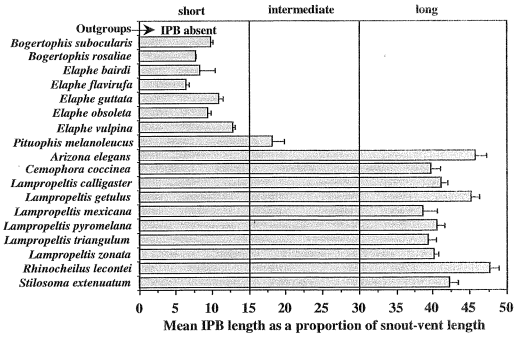

FIG. 4.—Mean length of the intrapulmonary bronchus measured as a proportion of SVL with standard error bars in the tribe Lampropeltini. The 11 outgroup species plus *Senticolis* lack an intrapulmonary bronchus. Four character states were determined: absent (0), short (1), intermediate (2), and long (3).

The taxonomic treatment of *Elaphe* is problematical. Based on my study and previous molecular studies (Dessauer et al., 1987; Dowling and Maxson, 1990; Dowling et al., 1983; Lawson and Dessauer, 1981) it is clear that New World species of *Elaphe* are most closely related to other members of Lampropeltini, but it is still not clear which of the Eurasian species of *Elaphe* are most closely related to New World species (Dowling and Fries, 1987; Dowling and Price, 1988). Thus, a generic level distinction of New World and Old World *Elaphe* may be warranted so that New World *Elaphe* and any Old World *Elaphe* that may be closely related can be included in Lampropeltini, but this action would be premature without a complete revision of the genus.

Bogertophis is, nonetheless, a probable derivative of New World *Elaphe. Bogertophis* differs from *Elaphe* and other members of the ingroup in a number of

morphological features: presence of a lorilabial scale row, a high number of supralabial and temporal scales, and dorsal scale rows. Species of *Bogertophis* also possess unique chromosome numbers (*B. rosaliae*, 2N = 38; *B. subocularis*, 2N = 40). Also, *Bogertophis* lacks a left lung but does possess a left lung orifice which distinguishes it and the other members of Lampropeltini from the outgroup species and *Elaphe* which always possesses a left lung. However, *Bogertophis* is similar to North American *Elaphe* in the short length of the intrapulmonary bronchus and most other aspects of its biology. This evidence, combined with that of other workers, supports the new generic allocation made by Dowling and Price (1988).

The comparisons of the hemipenis, body form, scutellation, and scale microdermatoglyphic patterns made by Dowling and Price (1988) suggested that *Bogertophis* and *Pituophis* are more closely related to each other than either is to *Elaphe*. However, the immunological distance study of Dowling et al. (1983) showed that *E. obsoleta* and *P. melanoleucus* differ by an immunological distance of only three while *E. obsoleta* and *B. subocularis* differ by 23, a distance equal to the difference between *E. obsoleta* and *L. getulus*. The visceral survey of my study shows that *Pituophis* has a longer intrapulmonary bronchus than *Elaphe* and *Bogertophis*, which suggests that *Pituophis* may be directly derived from the New World *Elaphe-Bogertophis* group.

The clade formed by *Pituophis, Arizona, Lampropeltis, Rhinocheilus, Cemophora, and Stilosoma* is unambiguously supported by the presence of an undivided anal plate.

Pituophis and *Arizona* have long been thought to be closely related because of their high degree of morphological similarity (Cope, 1875). They were differentiated only by two aspects of scalation: *Arizona* has paired prefrontal scales and smooth dorsal scales whereas *Pituophis* usually has four prefrontals and keeled dorsal scales (Klauber, 1946). Hemipenial differences are slight (Klauber, 1946), and Walls (1934), who studied eye structure in snakes, stated: "The diurnal genus *Pituophis* stands very close to *Arizona* and is probably the genus from which the latter was derived. *Arizona* can thus be thought of as a *Pituophis* which has become generically distinct partly as a result of changes accompanying its tendency toward nocturnality." My study shows that *Arizona* and *Pituophis* are quite similar and closely related but morphologically more divergent than previously thought. *Arizona* and *Pituophis* differ in other morphological features besides those already mentioned. *Pituophis* is highly polymorphic in the condition of the left lung; it may have a left lung, lack a left lung but still posses a left lung orifice, or sometimes may have no remnant of a left lung. I examined the condition of the left lung in museum specimens from throughout most of the geographic range of *Pituophis* and thus most of the subspecies. The condition of the left lung showed no apparent taxonomic or geographic correlation, with variation evident even within populations. *Arizona* lacks a left lung and may or may not have a left lung orifice. *Arizona* has only one apical pit on its scales; *Pituophis* and the rest of the Lampropeltini (except *Rhinocheilus*) have two. *Arizona* has an elliptical pupil; *Pituophis* and the rest of Lampropeltini have a round pupil. While these data suggest that *Arizona* is intermediate between *Pituophis* and the more recent members of the radiation, Dowling and Maxson (1990) hypothesized that *Elaphe, Pituophis,* and *Arizona* are closely related and are distinct from the "kingsnake" group, and they suggested that these genera last shared a common ancestor in the late Miocene, about 20 MYA based on immunological distance. However, the authors did not present immunological distance data on the relationship between *Arizona* and *Pituophis*.

The "kingsnake" clade formed by *Lampropeltis, Rhinocheilus, Cemophora,* and *Stilosoma* is distinguished from the other members of the radiation by two synapomorphies, ventral scales with a rounded as opposed to an angulate shape and a round body shape as opposed to a "loaf" shape. Blanchard (1921) described two

natural groups within *Lampropeltis:* the *getulus* group which includes *L. calligaster* and *L. getulus,* and the *triangulum* group which includes *L. mexicana, L. pyromelana, L. triangulum,* and *L. zonata.* The only new evidence from my data set to lend support to Blanchard's hypothesis is the condition of the left lung in these species. Earlier statements that members of *Lampropeltis* lack a left lung (Cope, 1895; Underwood, 1967) are in error. The specimens of *L. calligaster* and *L. getulus* that I examined do lack a left lung, but the members of the *triangulum* group may or may not have a left lung.

My data support earlier suggestions that the genera *Cemophora, Stilosoma,* and *Rhinocheilus* are derivatives of, or closely related to, *Lampropeltis* (Dessauer et al. 1987; Dowling and Maxson, 1990; Dowling et al. 1983). Dowling and Maxson (1990), based on a single specimen, found that *Rhinocheilus* had an immunological distance of 29 from *L. getulus,* and they suggested that *Rhinocheilus* may be a member of a different clade. The results of my study do not support this suggestion, and the position of *Rhinocheilus* should be reassessed.

The two highly specialized snakes *Cemophora* and *Stilosoma* are united in this analyses by the reduction in supralabial scales and dorsal scale rows. These character states simply may be consistent with their fossorial nature and small size, therefore homoplasy cannot be ruled out. *Stilosoma extenuatum* is morphologically divergent and is distinguished by several autapomorphies. *Stilosoma* completely lacks apical scale pits and a loreal scale, and it has a single nasal scale and an extremely slender body. Also, *Stilosoma,* alone within the Lampropeltini, completely lacks any remnant of a left lung. Based on immunological distance data, Dowling and Maxson (1990) concluded that *Stilosoma* and *Cemophora* evolved from within *Lampropeltis,* with *Stilosoma* and *Cemophora* differing from *L. getulus* by immunological distances of six and nine, respectively, while *L. getulus* differed from *L. calligaster* by an immunological distance of 11.

Members of Lampropeltini are an important part of the New World herpetofauna and have received considerable research attention in all aspects of their biology. They are morphologically and ecologically variant, they occupy a diversity of habitats, display a considerable range of adult body sizes, colors and patterns, diets, and behaviors, and show both restricted and wide ranging distributions. Despite this, many questions remain, especially in terms of their evolutionary relationships such as (1) what are the relationships both within the New World *Elaphe* clade and for the entire genus, (2) what are the intrageneric relationships of *Lampropeltis,* (3) what is the exact relationship of *Lampropeltis, Cemophora, Rhinocheilus,* and *Stilosoma,* and (4) which are the true sister groups to Lampropeltini? Answers to these questions will make the ecological, behavioral, and physiological data sets that are available for these species interpretable within an evolutionary framework and also will help to elucidate further a phylogenetic understanding of these well known colubrid snakes.

Acknowledgments.—I thank my graduate supervisor, L. Brown, for help and encouragement. W. Duellman and J. Simons at the Museum of Natural History at The University of Kansas, A. Greer and R. Sadlier at the Australian Museum, D. Rossman at the Museum of Natural Sciences at Louisiana State University, and H. Voris and A. Resitar at the Field Museum of Natural History kindly allowed me to examine the specimens in their care. V. Wallach taught me measurement techniques for snake visceral morphology, and M. Hutchinson pointed me in appropriate directions in the search for outgroups. The friendship of T. Frankino, F. DeSerto, M. Walsh, and O. Keogh are greatly appreciated. Earlier drafts of the manuscript were improved by many helpful comments from S. Blomberg, L. Brown, A. Capparella, A. Greer, K. Katsikaros, E. Mockford, C. Qualls, G. Shea, R. Shine, V. Wallach, and two anonymous reviewers. This research was supported by grants from the Chicago Herpetological Society. Phi Sigma, the Society of Sigma Xi, and the Biological Sciences Department at Illinois State University.

Literature Cited

Baker, R., J. J. Bull, and G. A. Mengden. 1971. Chromosomes of *Elaphe subocularis* (Reptilia: Serpentes), with description of an in vivo technique for preparation of snake chromosomes. Experentia 27:1228–1229.

Baker, R. J., G. A. Mengden, and J. J. Bull. 1972.

Karyotypic studies of thirty-eight species of North American snakes. Copeia 1972:257–265.

BECAK, W., AND M. L. BECAK. 1969. Cytotaxonomy and chromosomal evolution in serpentes. Cytogenetics 8:247–262.

BLANCHARD, F. N. 1921. A revision of the king snakes: Genus *Lampropeltis*. Bull. U.S. Natl. Mus. 114:1–260.

BURY, B. R., F. GRESS, AND G. C. GORMAN. 1970. Karyotypic survey of some colubrid snakes from western North America. Herpetologica 26:461–466.

CADLE, J. E. 1984. Molecular systematics of Neotropical xenodontine snakes. III. Overview of xenodontine phylogeny and the history of New World snakes. Copeia 1984:641–652.

———. 1987. Geographic distribution: Problems in phylogeny and zoogeography. Pp. 77–105. *In* R. Seigel, J. T. Collins, and S. S. Novak (Eds.), Snakes Ecology and Evolutionary Biology. McGraw-Hill, New York, New York.

COPE, E. D. 1875. Check-list of North American Batrachia and Reptilia. U.S. Nat. Mus. Bull. 1:1–104.

———. 1894. On the lungs of the Ophidia. Proc. Am. Philos. Soc. 33:217–224.

———. 1895. The classification of the Ophidia. Trans. Am. Philos. Soc. (Ser. 2) 18:186–219.

DESSAUER, H. C., J. E. CADLE, AND R. LAWSON. 1987. Patterns of snake evolution suggested by their proteins. Fieldiana Zool. 34:1–34.

DOWLING H. G. 1952*a*. A Taxonomic Study of the American Representatives of the Genus *Elaphe* Fitzinger, with Particular Attention to the Forms Occurring in Mexico and Central America. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan. [University Microfilms 3743:1–234.]

———. 1952*b*. A taxonomic study of the ratsnakes, genus *Elaphe* Fitzinger. IV. A checklist of the American forms. Occ. Pap. Univ. Michigan Mus. Zool. 541:1–12.

———. 1975. A provisional classification of snakes. Yearbook of Herpetology 1:167–170.

———. 1978. Serpentes. Pp. 110–114. *In* H. G. Dowling and W. E. Duellman (Eds.), Systematic Herpetology. HISS Publications, New York, New York.

DOWLING, H. G., AND I. FRIES. 1987. A taxonomic study of the ratsnakes. VIII. A proposed new genus for *Elaphe triaspis* (Cope). Herpetologica 43:200–207.

DOWLING, H. G., R. HIGHTON, G. C. MAHA, AND L. R. MAXSON. 1983. Biochemical evaluation of colubrid snake phylogeny. J. Zool. 201:309–329.

DOWLING, H. G., AND L. R. MAXSON. 1990. Genetic and taxonomic relations of the short-tailed snakes, genus *Stilosoma*. J. Zool., Lond. 221:77–85.

DOWLING, H. G., AND R. M. PRICE. 1988. A proposed new genus for *Elaphe subocularis* and *Elaphe rosaliae*. Snake 20:52–63.

DOWLING, H. G., AND J. M. SAVAGE. 1960. A guide to the snake hemipenis: A survey of basic structure and systematic characteristics. Zoologica 45:17–28.

DUNN, E. R. 1928. A tentative key and arrangement of the American genera of Colubridae. Bull. Antivenin Inst. Am. 2:18–24.

GEORGE, D. W., AND H. C. DESSAUER. 1970. Immunological correspondence of transferrins and the relationships of colubrid snakes. Comp. Biochem. Physiol. 33:617–627.

GILBOA, I. 1975. Karyotypes of amphibians and reptiles: A bibliographic review. Yearbook of Herptology 1:91–156.

KEOGH, J. S. Origin of the hemipenis retractor muscles: Evidence for utility in snake systematics. Snake: In press.

KLAUBER, L. M. 1946. The glossy snake, *Arizona*, with descriptions of new subspecies. Trans. San Diego Soc. Nat. Hist. 10:311–398.

LAWSON, R., AND H. C. DESSAUER. 1981. Electrophoretic evaluation of the colubrid genus *Elaphe* (Fitzinger). Isozyme Bull. 14:83.

MINTON, S. A. 1976. Serological relationships among some congeneric North American and Eurasian colubrid snakes. Copeia 1976:672–678.

MINTON, S. A., AND S. K. SALANITRO. 1972. Serological relationships among some colubrid snakes. Copeia 1972:246–252.

PEARSON, D. D. 1966. Serological and immunoelectrophoretic comparisons among species of snakes. Bull. Serol. Mus. 36:8.

SCHWANER, T. D., AND H. C. DESSAUER. 1982. Comparative immunodiffusion survey of snake transferrins focused on the relationships of the natricines. Copeia 1982:541–549.

SLOWINSKI, J. B. 1993. "Unordered" versus "ordered" characters. Syst. Biol. 42:155–165.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1. Computer program distrubuted by the Illinois Natural History Survey, Champaign, Illinois.

TRINCO, L. A., AND H. M. SMITH. 1971. The karyology of ophidians: A review. Trans. Kansas Acad. Sci. 74:138–146.

UNDERWOOD, G. 1967. A Contribution to the Classification of Snakes. British Museum (Natural History), London, U.K.

WALLACH, V. 1985. A cladistic analysis of the terrestrial Australian Elapidae. Pp. 223–252. *In* G. Grigg, R. Shine, and H. Ehmann (Eds.), Biology of Australasian Frogs and Reptiles. Surrey Beatty and Sons, Sydney, Australia.

———. 1991. Comparative Visceral Topography of African Colubrid Snakes of the Subfamilies Aparallactinae and Atractaspininae. M.S. Thesis, Louisiana State Univiversity, Baton Rouge, Louisiana.

WALLS, G. L. 1934. The reptilian retina. Am. J. Ophthal. 17:892–915.

WILLIAMS, K. L., AND L. D. WILSON. 1967. A review of the colubrid snake genus *Cemophora* Cope. Tulane Stud. Zool. 13:103–125.

Accepted: 29 July 1995
Associate Editor: Stephen Tilley

APPENDIX I

Character Descriptions

(1) *Intrapulmonary bronchus length.*—The intrapulmonary bronchus was defined as the continuation

of the trachea posterior to the orifice which leads into the left lung (Fig. 3). The intrapulmonary bronchus length was measured as a proportion of SVL following Wallach (1985, 1991). A total of 290 snakes was dissected to obtain intrapulmonary bronchus lengths and to record left lung condition (Appendix II). I was able to score intrapulmonary bronchus length on 250 specimens. Though the data are continuous in nature, four discrete character states were easily determined (Fig. 4): absence of the intrapulmonary bronchus was found in all the outgroups and *Senticolis* and is considered the ancestral condition (0), with short (1), intermediate (2), and long (3) the derived character states. Character states were arranged in a linear transformation series or "minimally connected" (Slowinski, 1993).

(2) *Left lung condition.*—Most snakes have a large right lung system which extends far down the body and a highly reduced left lung system (Cope, 1894). The left lung may or may not be present. When the left lung is present, it is connected to the trachea by a short bronchus just caudad to the heart (Fig. 3). If the left lung is absent, the small orifice that was the entrance to the lung may still be present though covered by a piece of tissue. Some snakes possess no remnant of a left lung. A total of 264 snakes was scored for left lung condition, and three character states were determined: left lung present (0), polymorphism in left lung condition (1), and left lung absent (2). The character states were ordered in a linear transformation series or "minimally connected" (Slowinski, 1993). A left lung was found in all the outgroup species and is considered ancestral. Several species displayed polymorphism in left lung condition, and one showed intra-population variation (*Pituophis melanoleucus*). I have scored this condition as a separate character state (rather than allocating both "presence" and "absence" character states to each of these species in the analyses) because I interpret the polymorphism as an intermediate condition.

(3) *Number of supralabial scales.*—The most typical number of supralabial scales is six or fewer (0), 7–9 (1), or 10 or more (2). Character state (1) was determined to be ancestral with character states (0) and (2) derived states. The character states were assigned this way so that they could be ordered in a linear transformation series or "minimally connected" (Slowinski, 1993).

(4) *Loreal scales.*—The ancestral condition of the loreal scales is present (0) and the derived condition is absent (1).

(5) *Temporal scales.*—The ancestral condition for the most typical number of anterior temporal scales is 1–2 (0) and the derived condition is three or more (1).

(6) *Lorilabial scales.*—The ancestral condition of the lorilabial scales is absent (0) and the derived condition is present (1).

(7) *Rostral scale.*—The ancestral condition of rostral scale shape is round and unmodified (0) and the derived condition is a large and/or pointy rostral scale (1).

(8) *Supralabial contact with eye.*—The supralabial scales are in contact with the eye (0) or are separated from the eye by lorilabial scales (1).

(9) *Anal plate.*—The anal plate is divided (0) or single (1).

(10) *Dorsal scales.*—The dorsal scales are either keeled (0) or smooth (1).

(11) *Ventral scale shape.*—The ventral scales are angulate in shape (also called "notched" or "keeled") at the lateral edges (0) or are rounded (1).

(12) *Midbody scale rows.*—The most typical number of midbody scales rows is 17–20 (0), 21–28 (1), or 29 or more (2). Character state (1) was determined to be ancestral with character states (0) and (2) derived states. Character states were ordered in a linear transformation series.

(13) *Apical pits.*—The number of apical pits per scale is 2(0), 1(1), or 0(2).

(14) *Body shape.*—The body in cross section is "loaf" shaped with a flat ventral surface (0) or is round (1).

(15) *Ecotype.*—The snakes are either primarily terrestrial (0) or fossorial (1) in nature.

(16) *Chromosome number.*—The chromosome number is 2N = 36 (0) or 2N > 36(1). Data were obtained from Becak and Becak (1969), Bury et al. (1970), Baker et al. (1971, 1972), Gilboa (1975), and Trinco and Smith (1972).

(17) *Origin of hemipenis retractor muscles.*—The large paired hemipenis retractor muscles originate from bands of fascia which attach to caudal vertebrae (Dowling and Savage, 1960). The point of orgin was recorded as the caudal vertebrae number posterior to the vent on which the muscles attach. Character state details are presented elsewhere (Keogh, 1995). Three characters states where determined: (0) 38 or more caudal vertebrae, (1) 33–37 caudal vertebrae, or (2) 32 or fewer caudal vertebrae. Character states were treated as unordered.

Appendix II

Museum Specimens Examined

In Group.—*Arizona elegans* (KU 2335, 3560, 20785, 20793, 22843, 62900, 68897, 69160, 80938, 90836, 126865, 176664; FMNH 563, 6201, 26036, 26130, 47088, 47087). *Bogertophis rosaliae* (KU 185646). *Bogertophis subocularis* (KU 82076, 174801–174802, 175565, 175566, 176729–176732, 182076, 182761). *Cemophora coccinea* (KU 60973–60974, 69906, 137761, 143767, 197235; FMNH 427, 3388, 8574–8575, 21556, 21987, 22665, 40767, 48443, 48444, 53677, 53678, 65160, 135178). *Elaphe bairdi* (KU 28092; LSUMZ 34528–34529, 36567). *Elaphe flavirufa* (FMNH 153563, 153565; LSUMZ 271, 5388, 33159, 33565, 33709). *Elaphe guttata* (KU 18529, 45355, 55377, 55378, 61003, 61004, 61007–61008, 68912, 68913, 81976, 81978, 92702, 145868, 145869, 154029, 154481, 159778, 159779, 170627; FMNH 34843, 194503, 194504, 194507). *Elaphe obsoleta* (KU 2462, 8441, 19107, 22671, 68914, 69657, 82066, 82074, 92703, 97832, 105906, 144775, 145876, 187742, 197241, 197242, 214400, 214410–214412). *Elaphe vulpina* (KU 8078, 68916, 82077, 82079, 176735, 193597; FMNH 3060, 19171, 19271, 21621, 38068,

38090, 38241, 41851). *Lampropeltis calligaster* (KU 6608, 13873, 24559, 144793, 154428, 176761, 185823–185825, 209642, 214450, 214451; FMNH 46403, 53073, 62085, 62086). *Lampropeltis getulus* (KU 5541, 6637–6639, 48926, 48927, 68922, 126868, 182245, 182290). *Lampropeltis mexicana* (KU 174807, 174944, 175568, 180258; LSUMZ 33880, 36634, 37490). *Lampropeltis pyromelana* (KU 182303, 206852; FMNH 810, 2575, 2703a–b, 38069). *Lampropeltis triangulum* (KU 8379, 21834, 30053, 33225, 55403, 61029, 61030, 82205, 84671, 145886, 174622). *Lampropeltis zonata* (KU 6641, 50423, 50424; FMNH 1426, 26121; LSUMZ 38688). *Pituophis melanoleucus* (KU 23103, 27727, 70880, 83117, 83119, 83122, 83141, 83145, 87752, 95960, 102968, 137653, 157984, 174631, 179553, 204081; FMNH 626, 69434, 69435, 95334–95335). *Rhinocheilus lecontei* (KU 8499–8501, 13815, 61109, 61110, 61112–61113, 61115, 73620–73622, 73624, 73625, 78916, 91427, 97836; FMNH 26785, 28496, 48807, 55009). *Senticolis triaspis* (KU 70856, 70858, 73503, 78938, 80749–80751). *Stilosoma extenuatum* (FMNH 3389, 38016–38017, 38018, 48434, 48438, 48440).

Outgroups.—*Coluber constrictor* (KU 17723, 17927, 81151, 92701, 129657, 130305, 214372, 214374, 216156, 218615). *Elaphe quadrivirgata* (AM 101001, 101005, 101167; FMNH 73964, 200615, 200616). *Elaphe quaturolineata* (AM 133; FMNH 130811). *Elaphe radiata* (AM 119626, 120387; FMNH 15303, 15304, 15307, 15308). *Elaphe rufodorsata* (AM 117831; FMNH 11435, 11438, 11445, 24915). *Drymarchon corais* (AM 92941; FMNH 165511). *Gonyosoma oxycephala* (AM 97028; FMNH 71603, 121435, 131718, 148965). *Masticophis flagellum* (FMNH 95234–95236, 95238). *Masticophis lateralis* (AM 112237; FMNH 2911, 21547, 25863, 33797). *Masticophis taeniatus* (AM 107740). *Ptyas mucosus* (AM 131512; FMNH 199725, 199726, 199728, 199730, 199731). *Thamnophis sirtalis* (KU 83927, 83928, 83930, 83933, 170643, 171156, 192185, 203839, 207180, 207181).