



Systematics of the Common Kingsnake (*Lampropeltis getula*; Serpentes: Colubridae) and the burden of heritage in taxonomy

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Abstract

We present a systematic revision of the *Lampropeltis getula* group, based on a recent range-wide phylogeographic analysis. We define our theoretical and operational concepts of species delimitation, and provide diagnoses based on mitochondrial DNA evidence, ecological niche modeling, morphology, and historical precedence. We find support for the recognition of five distinct species, which bear the name of the nominate subspecies found primarily within the range of each phylogeographic lineage: the Eastern lineage (*Lampropeltis getula*, Eastern Kingsnake), the Mississippi lineage (*L. nigra*, Black Kingsnake), the Central lineage (*L. holbrooki*, Speckled Kingsnake), the Desert lineage (*L. splendida*, Desert Kingsnake), and the Western lineage (*L. californiae*, California Kingsnake). Interestingly, all of these taxa had originally been described as distinct species and recognized as such for up to 101 years (in the case of *L. californiae*) before being demoted to subspecies. We discuss the impact that increasingly detailed genetic information from phylogeographic analyses may have on traditional taxonomy.

Key words: classification, *Lampropeltis getula*, North America, phylogeography, subspecies, taxonomy

Introduction

The delimitation of species is a primary goal of systematic biology (Sites & Marshall 2004; Wiens 2007), and species identification is a major application of molecular phylogenetics (Avice 2000; Wiens & Penkrot 2002; Lemmon *et al.* 2007; Mulcahy 2008). Recently, traditional taxonomy has been in upheaval, as the uncovering of cryptic phylogeographic lineage diversity has resulted in the discovery of many species which are morphologically similar, para- or peri-patric, and represent portions of wide-ranging species complexes that had long been perceived as single species (Wake 1997; Avice 2000; Burbrink *et al.* 2000; Wiens & Penkrot 2002; Sinclair *et al.* 2004). Additionally, historical inertia may promote the continued recognition of hazily defined species or subspecies whose phylogeny may be imprecisely known, resulting in a taxonomic ‘burden of heritage’ for systematists. We speculate that this is a combination of two factors. First is the necessity of continuing to recognize current taxonomic arrangements under the principle of priority of the International Code of Zoological Nomenclature, based on their historical primacy. Second is the tendency for the more obvious, but potentially less evolutionarily significant and phylogenetically less informative attributes such as color pattern variation to dominate the attention of investigators.

This may occasionally result in a tendency both to ascribe differences to visually distinct but genetically homogeneous populations, and to group as conspecific visually similar populations (see, in part, Burbrink *et al.* 2000; Baird *et al.* 2006). While such patterns may reveal intriguing sources of information regarding local adaptations and population interactions, their utility as a source of evolutionary or phylogenetic information is

suspect at best. Therefore, any taxonomic scheme which incorporates explicit phylogenetic hypotheses based on the evolutionary history of genetic loci is arguably superior to arbitrarily defined subspecies or species based on geographically inconsistent variation in color pattern or scalation (see Burbrink *et al.* [2000] and Mulcahy [2008]) or idiosyncratic subdivisions of smoothly grading morphoclines (see Crother *et al.* [2008] on *Sistrurus*).

We address these philosophical, phylogeographic, and taxonomic issues in the species *Lampropeltis getula*, the Common Kingsnake, a medium-sized constrictor that is one of the most widely occurring species in North America (Conant & Collins, 1998). The species also exhibits substantial color pattern variation, which has resulted in the description of at least seventeen different subspecies (Blanchard 1921; Blaney 1977; Conant & Collins 1998; Krysko 2001; Grismer 2003; Stebbins 2003; Krysko & Judd 2006). Recently, a study that sampled individuals from throughout their range revealed that population structure exists in the kingsnake that is only partially concordant with the previously recognized subspecies taxonomy (Pyron & Burbrink 2009c). Based on these results, a systematic revision of the group is warranted. We find evidence for the recognition of five distinct species in the *L. getula* species group. We also discuss the relevance that increasingly detailed, fine-scale phylogeographic DNA data may have on species-level taxonomy.

Species accounts

Pyron & Burbrink (2009c) presented a phylogeographic analysis of the *L. getula* group based on 261 individuals sampled from throughout its range, sequenced for the mitochondrial gene cytochrome *b* (1117bp). Analysis of the mtDNA data recovered five geographic lineages, each of which is associated with a distinct North American ecoregion. After diverging from *L. extenuata* during the late Miocene (~6.5 [4.2–8.9]Ma; Fig. 1; Pyron & Burbrink 2009a), the basal geographic break in *L. getula* occurred at the Mississippi River (4.9 [2.6–7.3]Ma; Figs. 1, 2), followed by subsequent divergences across the Rocky Mountains (4.1 [1.9–6.1]Ma), the Cochise Filter Barrier (2.16 [1.1–3.4]Ma), and the Apalachee Complex (1.94 [0.8–3.4]Ma; Pyron & Burbrink 2009c).

Our theoretical species concept is derived from the evolutionary species concept (ESC; Wiley 1978) and the general lineage concept of species (GLCS; de Queiroz 1998, 2007), implemented using the phylogenetic species concept (PSC; Cracraft 1989). We seek to identify uniquely evolving evolutionary lineages as species using operational criteria from Wiens & Penkrot (2002), Rissler & Apodaca (2007), and Bond & Stockman (2008). Based on the haplotype phylogeny of Pyron & Burbrink (2009c), we identify five geographically concordant lineages within the ‘focal species’ *L. getula*. By the criteria of Wiens & Penkrot (2002), the presence of several geographically distinct, reciprocally monophyletic lineages within the ‘focal species’ indicates the presence of multiple species hidden by the previous taxonomy. An apparent lack of distinct geographic structure within each lineage suggests widespread intra-species gene flow, indicating that no further taxonomic subdivision is possible. The five geographic lineages are all para- or allopatric and separated by putative barriers to gene flow, a primary criterion of Bond & Stockman (2008). Finally, adjacent lineages except the Western/Desert pair have significantly different predicted ecological niche preferences (Pyron & Burbrink 2009c). However, the Western/Desert lineages are peripatric with only a small secondary contact zone at a putative genetic barrier, a major criterion of Rissler & Apodaca (2007).

Each of the geographic lineages corresponds roughly with one of five major previously recognized subspecies. Interestingly, and of particular importance regarding taxonomic status, these major subspecies were all originally described as distinct species. In the case of *L. g. californiae* (Blainville 1835; roughly coterminous with the Western lineage), this recognition persisted for 101 years (Klauber 1936). In addition, *L. g. niger* (Yarrow 1882; encompassed by the Mississippi lineage), *L. g. holbrooki* (Stejneger 1902; comprises the Central and Mississippi [part] lineages), and *L. g. splendida* (Baird & Girard 1853; equivalent to the Desert lineage) were all originally described as separate species before being synonymized with *L. getula* (Blanchard 1921). Based on the unique evolutionary, ecological, and geographic identities of these lineages noted above,

we suggest that these species designations be restored, indicating the distinctness of these lineages as independent entities (de Queiroz 1998). This taxonomy recognizes the five phylogeographic lineages as distinct species, each bearing the name of the nominate subspecific race. We retain no subspecies, based on the lack of any well-supported, geographically localized genetic variation that would be indicative of legitimate infraspecific lineages. Detailed histories of synonymy are available in Blanchard (1921), Blaney (1977), and at the JCVI Reptile Database (<http://www.reptile-database.org>).

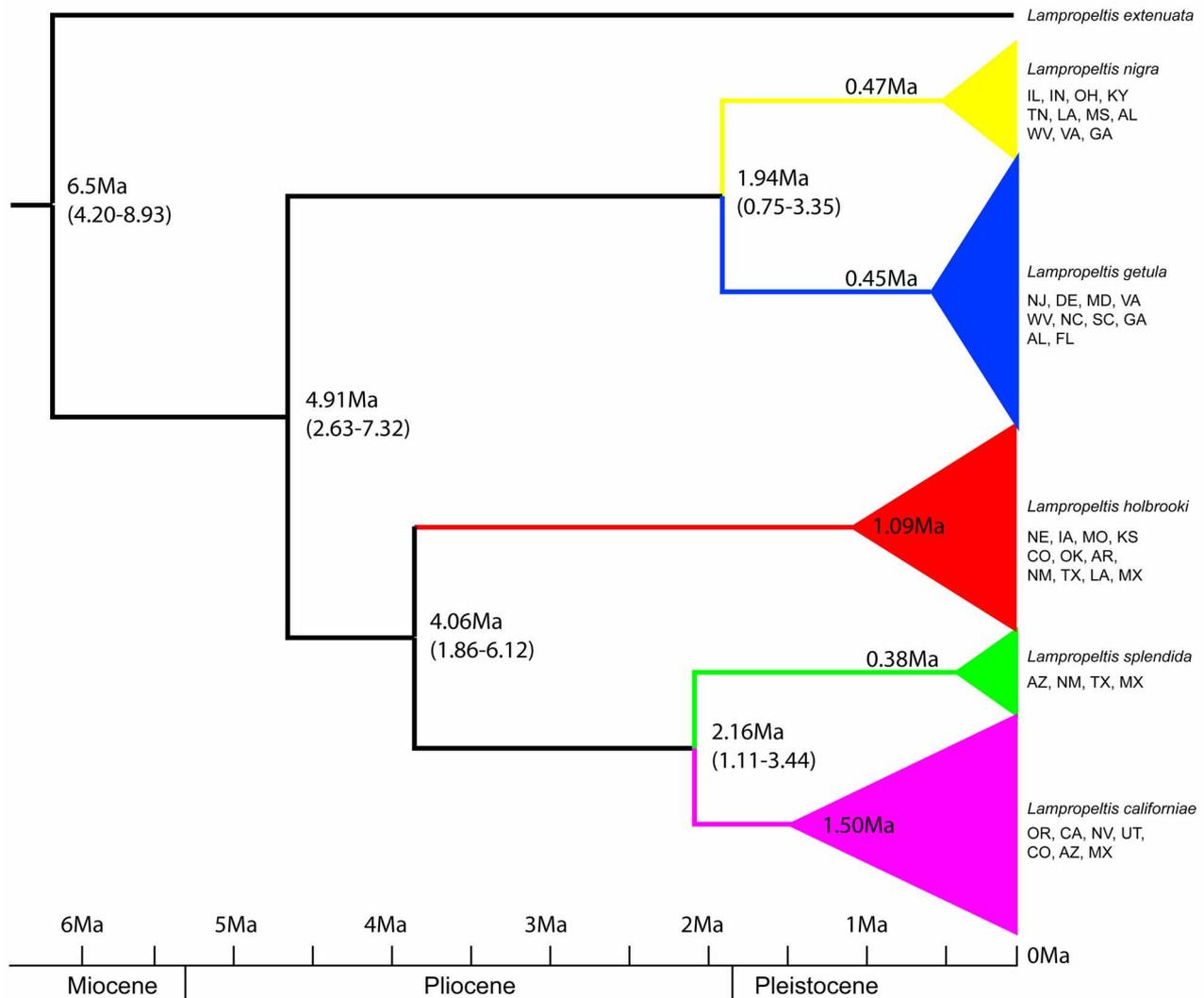


FIGURE 1. Chronogram showing genetic structure, geographic location, and divergence times of the five species in the *Lampropeltis getula* complex, from Pyron & Burbrink (2009c). The dates and depth of the terminal triangles represent the time of the most recent common ancestor of that lineage, while the height of the triangles is proportional to the number of samples in the clade. Dates at nodes represent the mean and 95% credible interval for that node, while numbers above branches represent Bayesian posterior probability support. Divergence times and support values are from Pyron & Burbrink (2009c).

***Lampropeltis getula* (Linnaeus 1766)**

(Figs. 1–3)

Eastern Kingsnake

Holotype: Unknown.

Type Locality: ‘Carolina’ (Linnaeus 1766), restricted to Charleston, SC by Klauber (1948)

Etymology: Specific epithet refers to the Getulian people of northern Morocco, whose tribal insignia bears a resemblance to the ‘chain’ pattern of the kingsnakes of the Eastern Seaboard of the United States.

Synonymy: This species comprises the previously recognized subspecies *L. g. getula*, *L. g. floridana* and *L. g. meansi*, as well as the historically recognized subspecies *L. g. goini* and *L. g. sticticeps*. The nominate subspecies was first designated by Cope (1875).

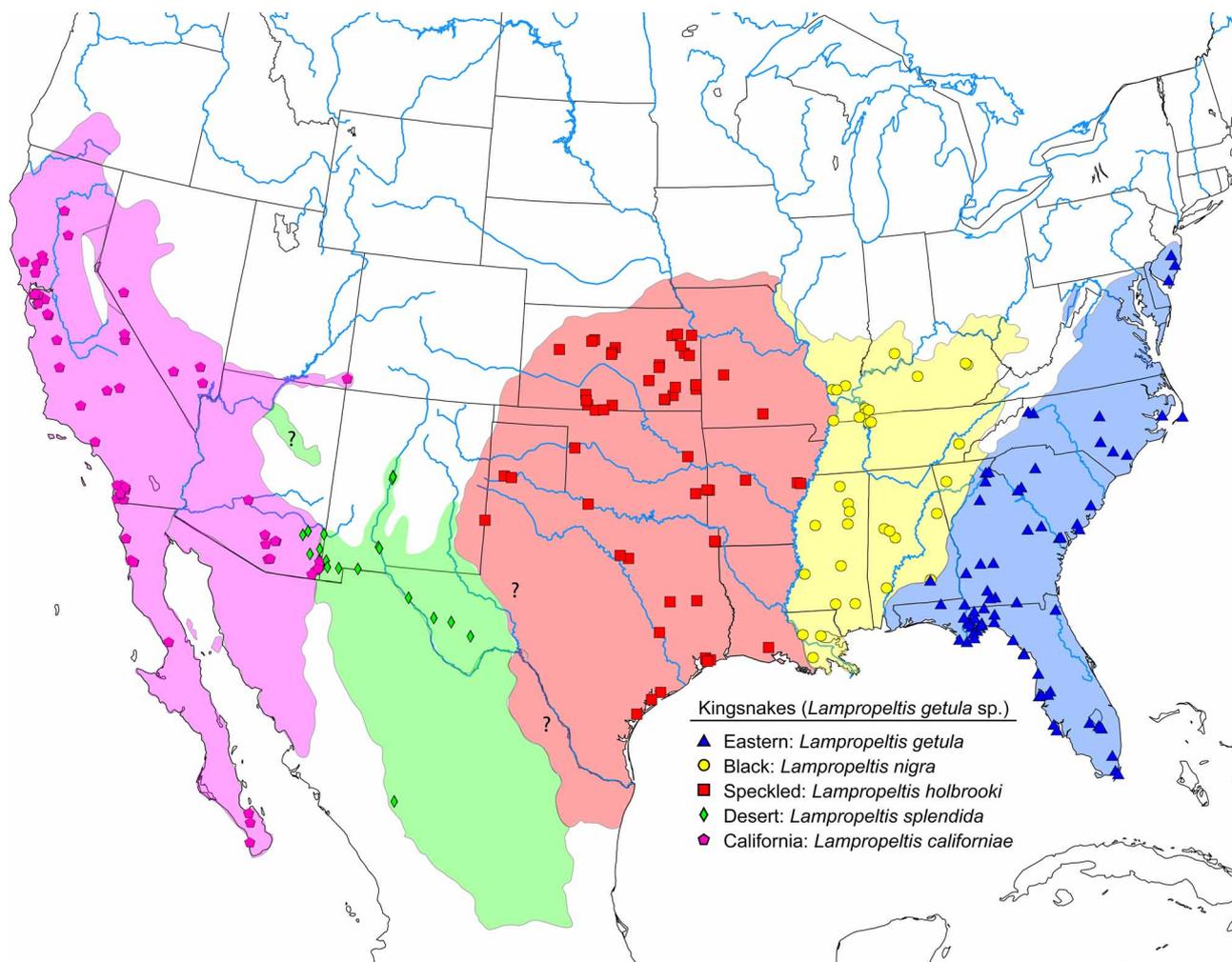


FIGURE 2. Range map of the five lineages recovered by Pyron & Burbrink (2009c), corresponding to five distinct species in North America. Note the zones of sympatry between *L. californiae* and *L. splendida*, and *L. nigra* and *L. getula*.

Diagnosis: The Eastern Kingsnake (*L. getula*) is a medium- to large-bodied constrictor, the largest in the genus *Lampropeltis* with a maximum total length of 208.3cm, though the average adult size range is 90–122cm (Conant & Collins 1998). Scales are smooth, anal plate single, and individuals typically exhibit 19–25 scale rows at midbody. Ventral scales number 200 to 223 in both sexes, while subcaudals number 45–58 in males and 37–55 in females (Blaney 1977). The Eastern Kingsnake ranges from New Jersey to the Florida keys in the east, and west to the western panhandle of Florida and southeastern Alabama (Fig. 2). The species *L. getula* can be distinguished from all other related snakes primarily on the basis of color pattern, which can be divided into two primary variants. From northern Florida to New Jersey, individuals typically exhibit a dark brown or black ground color, which is punctuated by 17–36 narrow crossbands of white, yellow, or reddish yellow (Blaney 1977), giving the appearance of a ‘chain’ pattern (Fig. 3). In peninsular Florida, the bands increase in both number (22–54) and width, and the ground color lightens considerably to a light brown color with yellow stippling (Blaney 1977; Fig. 3). Isolated populations of other aberrant color pattern variants

can be found in the panhandle of Florida (Krysko & Judd 2006). The shift between the Eastern Kingsnake and the Mississippi lineage is fairly abrupt, and previous authors have noted the narrow transition zone and apparent lack of morphological intermediacy in southern Alabama and central Georgia (Fig. 2, 3; Blanchard 1921; Blaney 1977; Mount 1980).

***Lampropeltis nigra* (Yarrow 1882)**

(Figs. 1–3)

Black Kingsnake

Holotype: USNM12149, collected by Robert Ridgway.

Type Locality: Wheatland, Knox Co. Indiana.

Etymology: Specific epithet refers to the predominantly black dorsal coloration of many specimens.

Synonymy: This species comprises the previously recognized subspecies *L. g. nigra* and *L. g. holbrooki* (part).

Diagnosis: The Black Kingsnake (*L. nigra*) is a large- to medium-bodied constrictor with an average adult size of 90–122cm, with larger individuals attaining maximum lengths of 147–183cm (Conant & Collins 1998). Scales are smooth, anal plate single, and individuals typically exhibit 19–25 scale rows at midbody. Ventral scale counts range from 197–222 in both sexes (fewer in the north), while subcaudals range from 45–59 in males and 37–51 in females (Blaney 1977). The Black Kingsnake can be distinguished from other species in the genus based on a combination of geography and color pattern. The Black Kingsnake ranges from southern Illinois to the Gulf coast along the Mississippi River, and east to the Appalachian mountain and the Alabama River drainage in south Alabama (Fig. 2). Black Kingsnakes all exhibit a black ground color, typically with a black-and-white checkered venter, and rarely faint traces of dorsal crossbands (Blanchard 1921; Blaney 1977; Conant & Collins 1998). Each dorsal scale is punctuated by a yellow or white speckle near the center of the scale; this is strongest in the southern portion of their range and fades considerably in the north, where many adults may be almost completely black (Conant & Collins 1998; Fig. 3). The Black Kingsnake can be distinguished from the morphologically similar Central lineage on the basis of geography, as the Black Kingsnake is only found east of the Mississippi River (Fig. 2).

***Lampropeltis holbrooki* (Stejneger 1903)**

(Figs. 1–3)

Speckled Kingsnake

Holotype: Unknown

Type Locality: ‘Valley of the Mississippi’ (Holbrook 1842), restricted to Hot Springs, Arkansas (Schmidt 1953).

Etymology: Specific epithet is a patronym honoring John Edwards Holbrook, a prominent American herpetologist of the 19th century, known as the ‘father of North American Herpetology’.

Synonymy: This species is essentially co-terminous with populations of the previously recognized subspecies *L. g. holbrooki* occurring west of the Mississippi River.

Diagnosis: The Speckled Kingsnake (*L. holbrooki*) is a medium- to large-bodied constrictor with a maximum adult size of 183cm and a mean adult range of 90–122cm (Conant & Collins 1998). Scales are smooth, anal plate single, and midbody scale rows number 19–25 (Blaney 1977). Ventral scales number 197–222 in both sexes, with subcaudals ranging from 46–59 in males and 37–51 in females (Blanchard 1921; Blaney 1977). The Speckled Kingsnake occurs west of the Mississippi River, from Iowa and Nebraska in the north to the Gulf Coast, and west to west-central Texas (Fig. 2). The majority of the range of *L. holbrooki* is characterized by the ‘speckled’ pattern, which consists of a black ground color, with a white or yellow speckle

in the center of each scale, and very occasionally a faint trace of dorsal crossbanding (Fig. 3). Large geographical areas harboring at least superficial morphological intermediacy between the Speckled Kingsnake and the Desert lineage in west central Texas are apparently inhabited only by the Speckled Kingsnake, suggesting that such color pattern variation may be due to phenotypic responses to ecological gradation, rather than hybridization or introgression (Pyron & Burbrink 2009c). The precise western extent of the range of *L. holbrooki* is unclear, but ecological niche modeling predicts that the range extends approximately to the Pecos and Rio Grande River drainages (see Fig. 4 in Pyron & Burbrink 2009c; Fig. 2).

***Lampropeltis splendida* (Baird & Girard 1853)**

(Figs. 1–3)

Desert Kingsnake

Holotype: USNM1726, collected by Col. J.D. Graham.

Type Locality: Sonora, Mexico (no further locality given).

Etymology: Specific epithet refers to the ‘splendid’ visage of the dorsal coloration.

Synonymy: This species is essentially co-terminous with the formerly recognized subspecies *L. g. splendida*.

Diagnosis: The Desert Kingsnake (*L. splendida*) is a medium- to large-bodied constrictor with an average adult size range of 90–114cm and a maximum size of 152cm (Conant & Collins 1998). Scales are smooth, anal plate single, with midbody scale rows typically numbering 23–25 (Blaney 1977). Ventral scales number 199–227 in males and 203–237 in females, while subcaudals range from 45–62 in males and 40–52 in females (Blaney 1977). The Desert Kingsnake can be distinguished from related species primarily on the basis of color pattern. The pattern of the Desert Kingsnake is characterized by a black or dark brown ground color with heavy yellow lateral and dorsolateral stippling. The remnant crossbands formed by this stippling yield a row of black or brown dorsal blotches or saddles, numbering 42–97. The head is typically black or dark brown, and the onset of the yellow dorsal patterning sometimes gives the appearance of a collar (Fig. 3; Blanchard 1921; Blaney 1977; Conant & Collins 1998). The Desert Kingsnake inhabits the Chihuahuan desert east of the Cochise Filter Barrier, from western Texas to extreme southeastern Arizona, north from central New Mexico in the Rio Grande River valley south to the south central portion of the Mexican Plateau (Fig. 2). Additionally, the ecological niche modeling results from Pyron & Burbrink (2009c) predict an area of habitat in north-central Arizona as suitable for *L. splendida* which is not predicted as suitable for the geographically adjacent California lineage (Fig. 2; Pyron & Burbrink 2009c). While kingsnakes are known from this region of Arizona (Stebbins 2003), it is not known to which species this population belongs. The Desert Kingsnakes may hybridize with the Western lineage in a narrow area in extreme southeastern Arizona and extreme southwestern New Mexico, where haplotypes co-occur and some apparent hybrids have been found (Fig. 2; R.A. Pyron, *pers. obs.*), though morphological intermediacy is apparently not widespread (Conant & Collins 1998).

***Lampropeltis californiae* (Blainville 1835)**

(Figs. 1–3)

California Kingsnake

Holotype: Unknown, collected by M. Botta.

Type Locality: ‘California’ (Blainville 1835). Restricted to Fresno, California by Schmidt (1953).

Etymology: Specific epithet refers to the type locality.

Synonymy: This species is essentially co-terminous with the previously recognized subspecies *L. g. californiae*, and *L. g. nigrita*.

Eastern Kingsnake
Lampropeltis getula
 L) Chain pattern
 R) 'Floridana' pattern



Black Kingsnake
Lampropeltis nigra
 L) Black pattern
 R) Speckled pattern



Speckled Kingsnake
Lampropeltis holbrooki
 L) Speckled pattern
 R) 'Desert Intergrade'



Desert Kingsnake
Lampropeltis splendida
 L) Desert pattern
 R) Darker adult



California Kingsnake
Lampropeltis californiae
 L) Banded pattern
 R) Striped pattern



FIGURE 3. Primary color pattern variants of five species of the *Lampropeltis getula* group. Many additional variants occur regionally; these are simply the primary color pattern classes of the five species. See Blaney (1977), Conant & Collins (1998), Stebbins (2003), and Krysko & Judd (2006) for more detailed descriptions of color pattern variation. Photographs of *L. getula* (R), *L. nigra* (R), *L. holbrooki* (L), and *L. californiae* are compliments S.L. & J.T. Collins, CNAH. The photograph of *L. holbrooki* (R) is compliments D.B. Shepard, CUNY-CSI.

Diagnosis: The California Kingsnake (*L. californiae*) is a medium- to large-bodied constrictor, with a mean adult size range of 76–122cm, and a maximum size of ~200cm (Stebbins 2003). In both sexes, ventral scale counts range from 213–255, with 46–63 subcaudal scales in males and 44–57 in females (Blaney 1977). Scales are smooth and anal plate single, with 23–25 dorsal scale rows at midbody. The California Kingsnake exhibits one of the broadest ranges of any kingsnake species, occupying most habitats west of the continental divide at the Cochise filter barrier (Fig. 2). The species ranges from Oregon in the north, through the Great Basin in Nevada and Utah, east to extreme southwestern Colorado, south through the majority of California, Arizona and the Mexican states of Sonora, Baja California Norte, and Baja Sur (Fig. 2). The California Kingsnake can be distinguished from other species on the basis of color pattern, possibly the most distinct of the group. Throughout the majority of their range, California Kingsnakes exhibit a black or dark brown ground color, with 21–44 broad crossbands of white or light yellow, which typically widen laterally. Along the Pacific coast from Los Angeles to San Diego counties, individuals can be found possessing a black or dark brown ground color and a single thin, white dorsal stripe beginning at the neck and continuing to the tail (Fig. 3). Finally, populations in the Mexican states of Sonora and Sinaloa may exhibit considerable ontogenetic darkening, with adults, and occasionally subadults and even juveniles turning jet black, with almost no trace of pattern (Blaney 1977; Stebbins 2003). To which species the Sonora populations belong is unclear; while we group them with *L. californiae* on the basis of geography, some authors have suggested that they resemble and hybridize with both *L. g. 'splendida'* and *L. g. 'californiae'* (Blanchard 1921; Blaney 1977).

Discussion

Given a prevailing philosophical climate which stresses the necessity for a taxonomic system that reflects the evolutionary history of a group (see Frost *et al.* 1992; Wiens & Penkrot 2002; de Queiroz 1998, 2007), modern phylogenetic methods have resulted in an upheaval in many groups as existing taxonomies are tested for the first time using molecular phylogenetic data to infer evolutionary histories. Continuing to recognize poorly defined infraspecific taxa while failing to recognize the presence of distinct lineages may cause a potentially severe underestimate of biodiversity due only to a taxonomic burden of heritage. Accurately documenting this diversity is a crucial goal of systematics, and one which is particularly important, not only for studies of species richness (e.g., Pyron & Burbrink 2009b), but for studying and conserving biodiversity on a broad scale (Wiens 2007). While the choice of genetic marker (such as mtDNA) may affect phylogenetic inference (Avice 2000; Edwards & Beerli 2000; Brito & Edwards 2008; Zink & Barrowclough 2008; Burbrink & Castoe 2009), the use of molecular phylogenetic data analyzed using rigorous statistical methodologies is preferable in any case to ad-hoc morphological diagnoses for species, or appeals to an existing status quo based solely on historical precedence. Particularly in future studies, the inclusion of multiple independent nuclear loci will further strengthen such hypotheses (e.g., Brito & Edwards 2008).

The concordance between the original species descriptions in terms of geography and color pattern ranges is strong for some of the species (*L. californiae*), but weaker for others (i.e., *L. holbrooki* and *L. nigra*), where there is significant overlap in phenotype between deeply diverged lineages. There exist wide zones of morphological intermediacy between both the Desert and Speckled Kingsnakes and the Speckled and Black Kingsnakes, despite their apparent lack of female-mediated hybridization, significantly different ecological niche preferences, and relatively narrow zones of predicted niche overlap (Pyron & Burbrink 2009c). We hypothesize that color pattern evolution in these snakes may be driven by phenotypic responses to changes in ecological or environmental variables, or clinal variation thereof (i.e., from eastern mesic forests to western deserts), rather than by gene flow or hybridization, as has typically been assumed by other authors in the past (e.g., Blaney 1977; Conant & Collins 1998).

Here, we have shown that the original description of at least five distinct species in the *L. getula* complex yields a far more useful and accurate picture of the evolutionary history and current genetic structure of the

group than the seventeen subspecies described over the last 75 years. Indeed, the most morphologically and geographically distinct form, *L. californiae* (Blainville 1835), was recognized as a distinct species for over a century before being demoted to a subspecies (Klauber 1936). While hybridization may occur between some of the adjacent lineages, recent research suggests that this may be common among recently diverged species (e.g., Niemiller *et al.* 2008; Nosil 2008), and the apparent lack of any broad regions of sympatry between the species suggests that they are not experiencing widespread introgression (Fig. 2; Pyron & Burbrink 2009c). Recognition within the *L. getula* complex of five distinct species, *L. getula*, *L. nigra*, *L. holbrooki*, *L. splendida*, and *L. californiae*, provides a phylogenetically robust taxonomic description of the Common kingsnake group, while retaining the historical connection to the original descriptions of those taxa extending back over 250 years.

Acknowledgments

This research was supported by the American Museum of Natural History, the American Philosophical Society, and the Professional Staff Congress, the College of Staten Island, and the Graduate School and University Center, all of the City University of New York. We would like to thank the numerous people and institutions who assisted with the acquisition, collection, or loan of samples, including the Museum of Vertebrate Zoology (J.A. McGuire), the University of Texas, Arlington (J.A. Campbell, E.N. Smith, C.J. Franklin and R. Jadin), the Texas Cooperative Wildlife Collection, Texas A&M University (T.J. Hibbitts), the University of Alabama (L.J. Rissler), the San Diego Natural History Museum (B.D. Hollingsworth), the Peabody Museum, Yale University (G. Watkins-Colwell), California State University, Northridge and University of Nevada, Reno (B. Espinoza), the Florida Museum of Natural History (K.L. Krysko), the Texas Natural History Collection, the University of Texas, Austin (D.C. Cannatella, T.J. LaDuc, D. Hall), Southeastern Louisiana University (B.I. Crother), the University of Louisiana, Lafayette (B. Moon), the Sternberg Museum, Fort Hays State University (T.W. Taggart, C.J. Schmidt, J.T. Collins), the Illinois Natural History Survey (C. Phillips), K. Swaim (Swaim Biological), the USGS San Diego Field Station, F.M. Fontanella, P. Warny, T.J. Guiher, N. Howe, S.G. Pyron, M.E. Pyron, D.B. Shepard, L.J. Vitt, K.J. Irwin, L.K. Irwin, C.G. Jimenez, S.R. McNearney, R.W. Hansen, D.G. Mulcahy, C. Roelke, A. Harper, P.G. Frank, C. Whitney, G.N. Weatherman, S. Ruane, M.R. Rochford, R.W. Bryson, J. Harrison, S. Boback, C.D. Camp, and D. Siegel. We would also like to thank D. Gower, J.J. Wiens, and an anonymous reviewer for reviewing earlier versions of this manuscript.

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