ECOLOGY, CONSERVATION, AND MORPHOLOGICAL AND MOLECULAR SYSTEMATICS OF THE KINGSNAKE, *Lampropeltis getula* (SERPENTES: COLUBRIDAE)

By

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TABLE OF CONTENTS

page

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
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ECOLOGY, CONSERVATION, AND MORPHOLOGICAL AND MOLECULAR SYSTEMATICS OF THE KINGSNAKE, *Lampropeltis getula* (SERPENTES: COLUBRIDAE)

By

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Kingsnakes, *Lampropeltis getula*, range throughout much of North America. Based on morphology, there are seven currently recognized subspecies in the *L. getula* complex. Two of these taxa, *L. g. getula* and *L. g. floridana*, represent populations in the eastern U.S. *Lampropeltis g. getula* is distributed from southern New Jersey to northern peninsular and panhandle Florida and *L. g. floridana* is distributed from central to southern peninsular Florida.

Historically, kingsnakes were abundant throughout the state of Florida. However, over the last few decades kingsnakes have declined severely or been locally extirpated leaving only a few isolated populations scattered around the state. Furthermore, for more than 80 years the taxonomy of the *L. getula* subspecies in the eastern U.S. has been controversial. In addition to *L. g. getula* and *L. g. floridana*, the taxonomic status of four other potential subspecies remains questionable: *L. g. brooksi* from extreme southern

peninsular Florida, *L. g. goini* from the northwestern Apalachicola Lowlands in panhandle Florida, an unnamed subspecies from the eastern Apalachicola Lowlands, and *L. g. sticticeps* from the Outer Banks of North Carolina.

In this study, I used a multidisciplinary approach to better understand kingsnake ecology and their phylogenetic relationships, and provide management recommendations for their conservation. First, I present a natural history overview of kingsnakes derived mainly from two years of fieldwork in southern Florida. Secondly, I used GIS to document kingsnake declines in Florida, and hypothesize possible causes leading to this event. Finally, I examine morphological and molecular characters of kingsnakes in the *L. getula* complex.

Possible causes for population declines include habitat loss and fragmentation, road mortality, pollution, toxin buildup in tissues, red imported fire ants, and over-collecting by commercial collectors. Populations of *L. g. getula*, *L. g. floridana*, and unnamed populations in the eastern Apalachicola Lowlands appear to represent natural groups, here recognized as subspecies. I found no morphological or genetic evidence supporting the recognition of *L. g. brooksi*, *L. g. goini*, and *L. g. sticticeps.* Habitat protection and improved management practices are crucial to insure survival of kingsnakes in the wild.

CHAPTER 1
INTRODUCTION

Kingsnakes of the *Lampropeltis getula* complex (Linnaeus 1766) range throughout much of temperate and subtropical North America, from Oregon to the Mexican Plateau in the west and from southern New Jersey to southern Florida in the east. In the past, kingsnakes were abundant throughout the state of Florida (Fig. 1-1) from well-known sites including Paynes Prairie (Alachua Co.), Apalachicola National Forest/Tate's Hell State Forest (Liberty and Franklin counties), Lake Okeechobee (Glades, Hendry, and Palm Beach counties) and the extreme southern peninsula (Dade Co.)(Carr, 1940; Kauffeld, 1957; Duellman and Schwartz, 1958; Wilson and Porras, 1983; Krysko, 1995). Despite their previous abundance in Florida, kingsnake populations have severely declined or been locally extirpated for unknown reasons (Wilson and Porras, 1983; Krysko, 1995; Means, 2000), leaving only a few isolated populations scattered around the state. Similar examples of local extirpation of other reptile species have also taken place throughout the southeastern U.S. (Moler, 1992; Tuberville et al., 2000), causing alarm among herpetologists and conservationists.

Based on morphology, Blaney (1977) recognized seven subspecies of *L. getula* throughout its range: *L. g. californiae* (Blainville 1835), *L. g. floridana* Blanchard 1919, *L. g. getula* (Linnaeus 1766), *L. g. holbrooki* Stejneger 1903, *L. g. nigra* (Yarrow 1882), *L. g. nigrita* Zweifel and Norris 1955 and *L. g. splendida* (Baird and Girard 1853).

Furthermore, Blaney (1977) recognized that populations in the eastern U.S. represented a distinct clade consisting of *L. g. getula* and *L. g. floridana*.

Lampropeltis g. getula is distributed from southern New Jersey to northern peninsular and panhandle Florida (Fig. 1-1; Blaney, 1977; Krysko, 1995; Tennant, 1997; Conant and Collins, 1991, 1998). Its dorsal pattern is solid black to chocolate brown with 19-32 narrow (1.5-2.5 dorsal scale rows) crossbands and a lateral chain pattern (Fig. 1-2A; Blaney, 1977; Krysko, 1995; Tennant, 1997). *Lampropeltis g. floridana* is distributed from central to southern peninsular Florida (Fig. 1-1; Blaney, 1977; Krysko, 1995; Tennant, 1997). Its dorsal pattern has > 34 narrow (1.5 dorsal scale rows) crossbands, a degenerate lateral chain pattern and undergoes various degrees of ontogenetic interband (= interspaces between light crossbands) lightening, giving it a yellowish speckled appearance in the adult stage (Fig. 1-2B; Blaney, 1977; Krysko, 1995; Tennant, 1997).

For more than 80 years the taxonomy of *L. getula* subspecies in the eastern U.S. has been controversial. In addition to *L. g. getula* and *L. g. floridana*, the taxonomic status of three other named subspecies from the eastern U.S. remains questionable: *L. g. brooksi* Barbour 1919 from the extreme southern Florida peninsula (Fig. 1-1), *L. g. goini* Neill and Allen 1949 from the Florida panhandle on the western side of the Apalachicola River in the northwestern Apalachicola Lowlands (Figs. 1-1, 1-3), and *L. g. sticticeps* Barbour and Engles 1942 from the Outer Banks of North Carolina. In addition, Means (1977) believed that an unnamed subspecies existed on the eastern side of the Apalachicola River in the eastern Apalachicola Lowlands (Fig. 1-3). The dorsal pattern of *L. g. brooksi* is like that of *L. g. floridana*, but it undergoes extreme ontogenetic interband

lightening that almost completely obscures the presence of the narrow crossbands (Fig. 1-4A; Barbour, 1919). The dorsal pattern of *L. g. goini* has 15-17 wide (4-8 dorsal scale rows) crossbands, and undergoes slight interband lightening, yet the interband areas remain nearly black (Fig. 1-4B; *see* Figs. 1-3, Neill and Allen, 1949). The dorsal pattern of individuals in the eastern Apalachicola Lowlands (Fig. 1-3) is polymorphic and may be wide-banded (up to 8 dorsal scale rows) or non-banded (striped or patternless)(Fig. 1-5; Means, 1977; Krysko, 1995). The dorsal pattern of *L. g. sticticeps* is like that of *L. g. getula*, but it undergoes slight interband lightening. All newborn, banded eastern U.S. *L. getula* individuals have bold light-colored crossbands with black interbands (Fig. 1-6A-C), yet newborn non-banded eastern Apalachicola Lowlands individuals have only remnant black interbands (Fig. 1-6D, E). The lightened interband pattern of adult *L. g. floridana* (Fig. 1-2B), *L. g. brooksi* (Fig. 1-4A), *L. g. goini* (Fig. 1-4B), Apalachicola drainage individuals (Fig. 1-5) and *L. g. sticticeps* is derived from ontogenetic lightening of the normally black interbands (Fig. 1-6).

In this study, I provide 1) a natural history overview of *L. getula* in Florida and attempt to document its decline and suggest possible causes leading to this event, 2) an analysis of sexual and geographic variation in Florida using morphology, and 3) analysis of morphological and molecular characters throughout the *L. getula* complex. I relate morphological and molecular data to historical geological events and attempt to clarify taxonomic relationships of *L. getula* populations in the eastern U.S. My interpretation of valid taxa along with their geographic ranges is presented using the Apomorphic Species Concept (Phylogenetic Species Concept *sensu* Mishler and Theriot, 2000). Under the Apomorphic Species Concept (ASC), species are considered to be well-supported

minimal monophyletic groups, and subspecies may be considered as subclades within species, having lesser support because of interbreeding and a more recent evolution (see Mishler and Theriot, 2000). This definition of subspecies is similar to that of Mayr (1969) and Smith et al. (1997), in which subspecies are geographically-delimited populations that possess relatively homogeneous characters produced by evolution, yet are genetically non-discrete because of gene flow with surrounding morphologically-divergent populations.

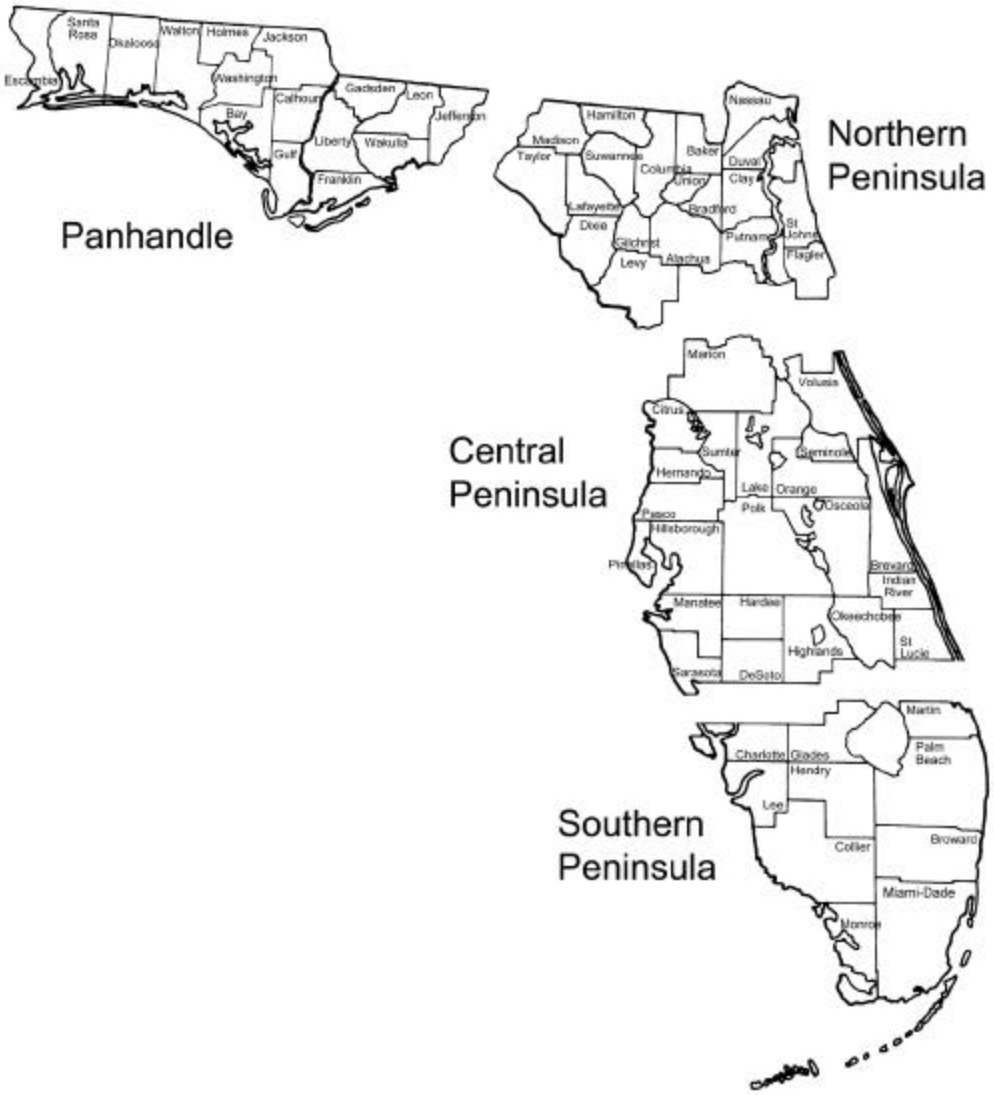

Fig. 1-1. Florida panhandle and northern, central, and southern peninsula (modified after Enge, 1994).

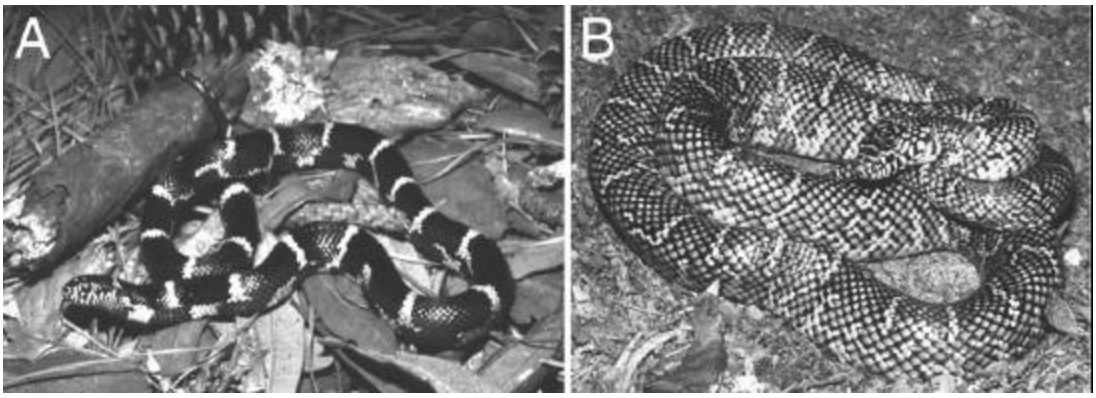

Fig. 1-2. Pattern variation of A = *Lampropeltis g. getula* from southern New Jersey to northern peninsular and panhandle Florida and B = *L. g. floridana* from central to southern peninsular Florida.

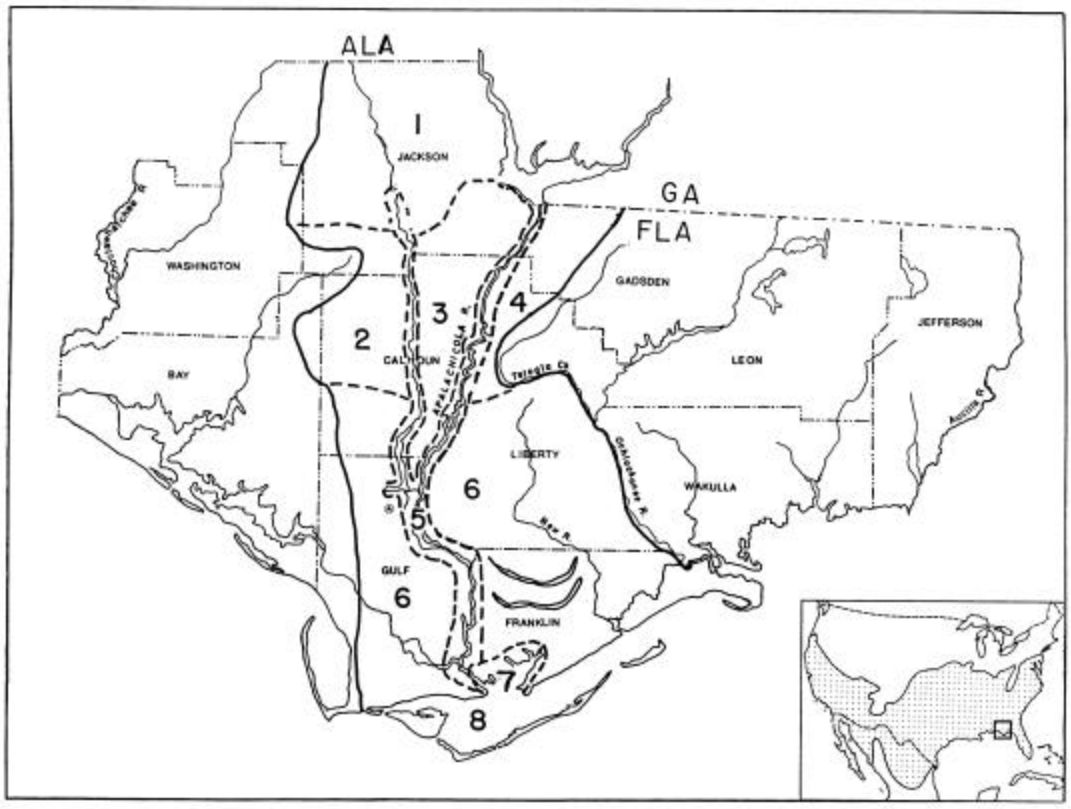

Fig. 1-3. Apalachicola drainage in the Florida panhandle with recognized natural areas (after Means, 1977). 1 = Marianna Lowlands; 2 = Western Red Hills; 3 = Grand Ridge; 4 = Apalachicola Bluffs and Ravines; 5 = River Bottomlands; 6 = Apalachicola Lowlands; 7 = Coastal Marshes; 8 = Offshore Spits, Bars, and Barrier Islands. The two crescent-shaped structures in mainland Franklin Co. are ancient barrier islands. Shading on the inset map = geographic distribution of *Lampropeltis getula*.

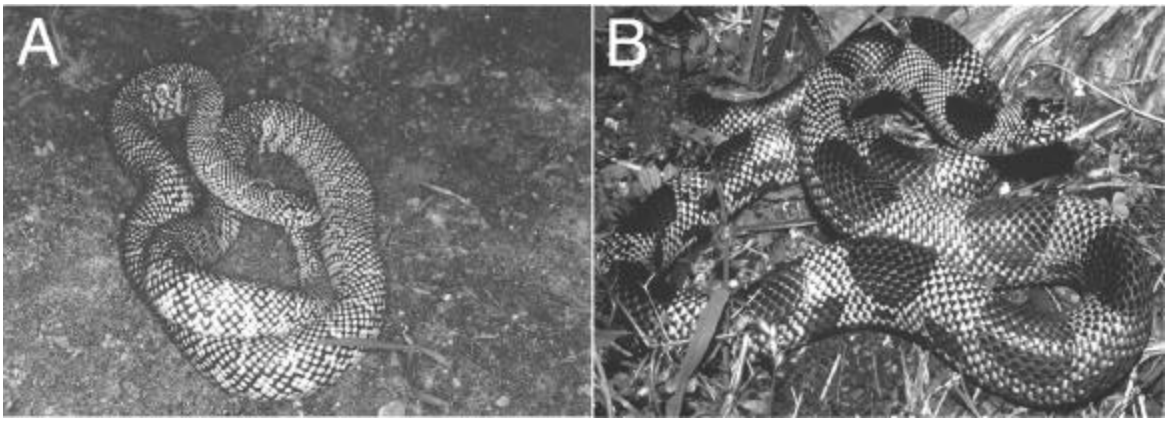

Fig. 1-4. Pattern variation of A = *Lampropeltis getula brooksi* and B = *L. g. goini.* Note that adult *L. g. brooksi* (A) and *L. g. floridana* (Fig. 1-2B) are distinctly banded as newborns (Fig. 1-6A) and although their ontogenetic interband lightening may obscure the presence of crossbands they are not truly non-banded like those in Figs. 1-5B, C; 1-6D, E.

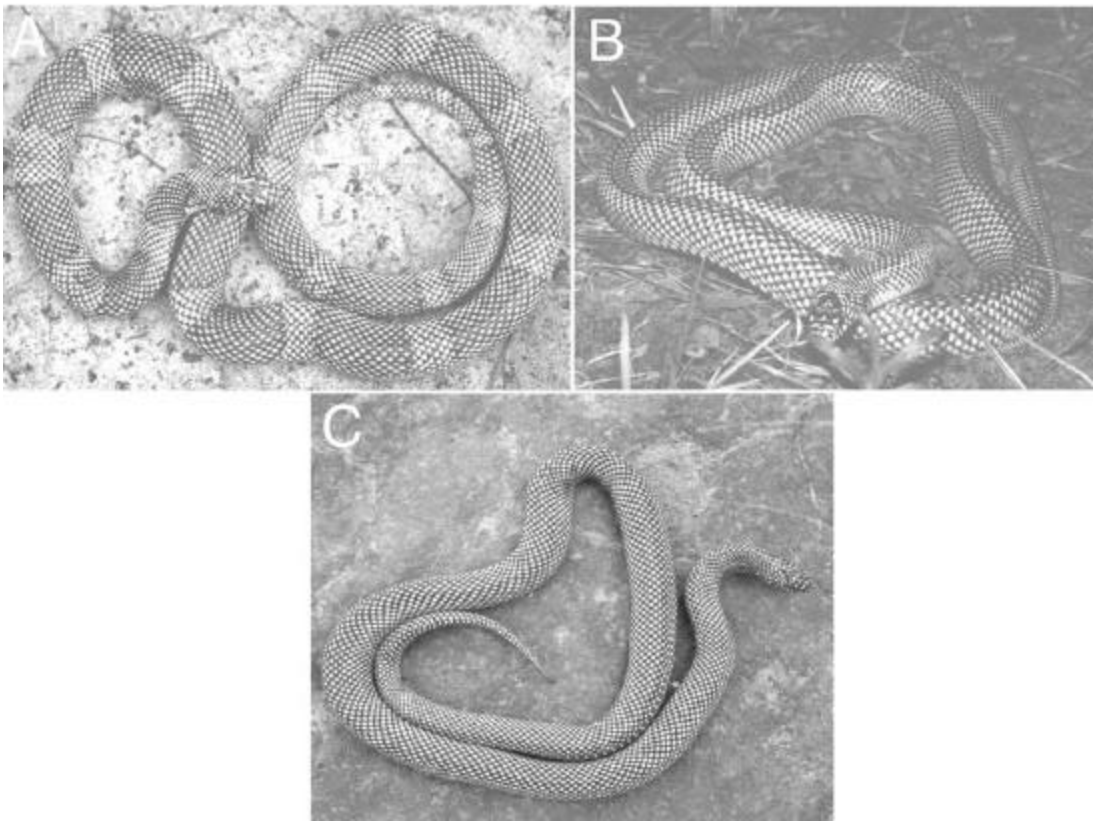

Fig. 1-5. Eastern Apalachicola Lowlands *Lampropeltis getula*, A = wide-banded, B = non-banded striped, C = non-banded patternless. Note that wide-banded specimen in A is the same as in Fig. 1-6C and has undergone considerably more ontogenetic interband lightening than adult *L. g. goini* from the surrounding region.

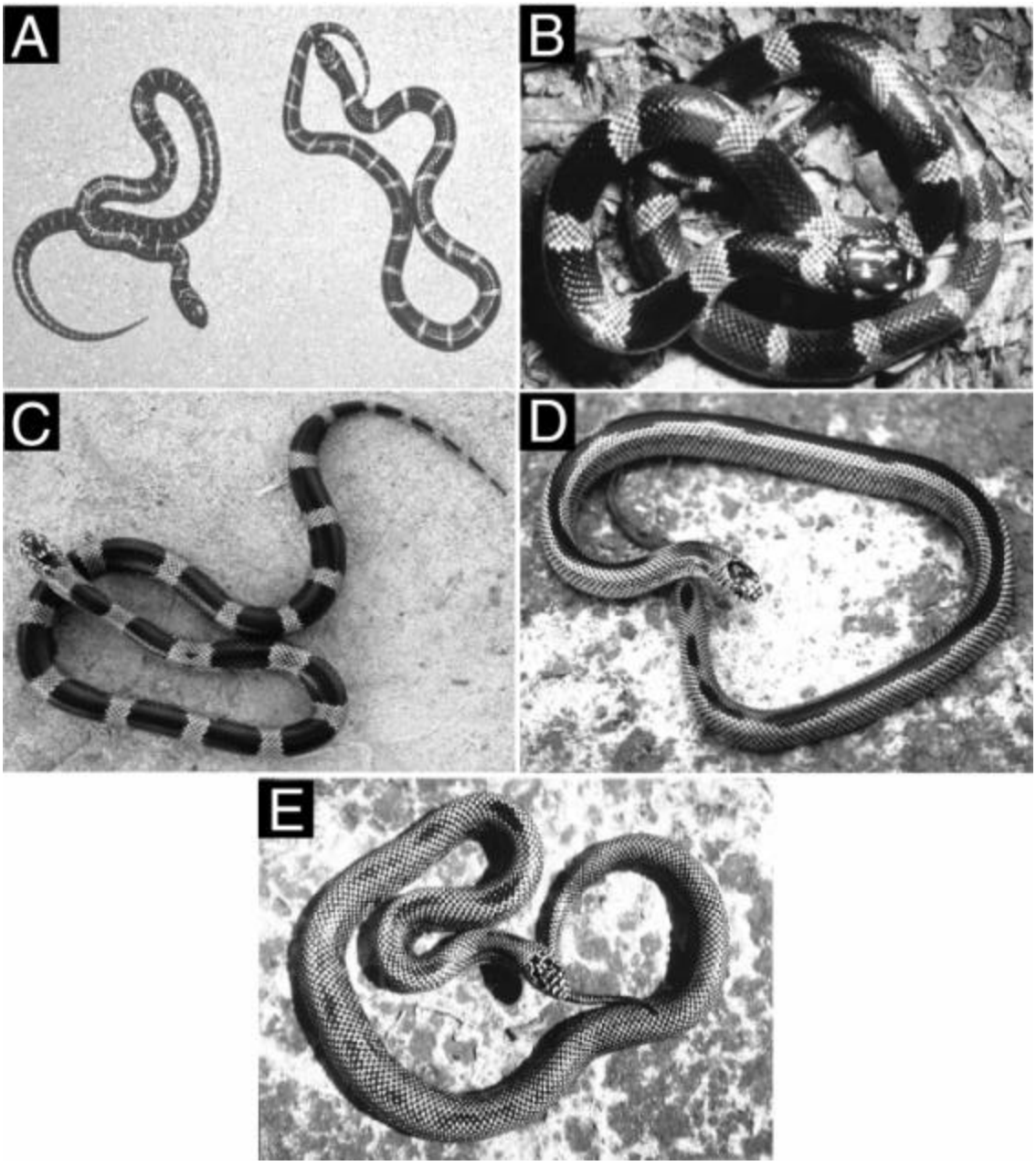

Fig. 1-6. Newborn eastern U.S. *Lampropeltis getula* with bold light-colored crossbands and black interbands. A = *L. g. floridana* (left) and *L. g. getula* (right); B = *L. g. goini*; C = wide-banded eastern Apalachicola Lowlands; D = striped eastern Apalachicola Lowlands; E = patternless eastern Apalachicola Lowlands. Note that 1) wide-banded specimen C is the same as in Fig. 1-5A and will undergo considerably more ontogenetic interband lightening than *L. g. goini* from the region surrounding the eastern Apalachicola Lowlands and 2) striped and patternless eastern Apalachicola Lowlands snakes have only remnant black interbands.

CHAPTER 2
THE DECLINE AND EXTIRPATION OF KINGSNAKES (*Lampropeltis getula*) IN FLORIDA

Materials and Methods

Natural history data and Florida locality records of kingsnakes were obtained from the literature, herpetologists, and systematic collections throughout the U.S. Reference points were plotted for each collection record dated between 1858 and 1999 with latitude-longitude coordinates using ArcView GIS (ver. 3.2, ESRI, Inc). All individual and county records were plotted on maps of Florida to show the historical distribution of kingsnakes in Florida. Additionally, those records from 1990 to1999 were plotted separately to show the distribution of records over the last decade.

Results

Natural History Overview

The diet of kingsnakes consists of both venomous and non-venomous snakes, including their own species, as well as lizards, amphibians, turtle eggs, rabbits and rodents (Conant and Collins, 1991; Tennant, 1997). Newborn kingsnakes range in size from 13 to 20 cm snout-vent length (SVL), adults range from 90 to 122 cm SVL with a maximum size of 208.3 cm total length (Conant and Collins, 1991; Tennant, 1997). Sexual maturity has been found at 80 cm SVL in the southern Florida peninsula (Krysko, unpubl. data). Males usually attain a greater size than females. The breeding season occurs from February through June. During this time, males are encountered more often

than females, apparently because they are actively searching for mates. Combat rituals have been observed between two males (Krysko et al., 1998). Females are also observed more frequently from February through June, possibly because they are waiting for males to pick up their pheromones, feeding more frequently to increase yolk masses, or basking before oviposition. Oviposition occurs within two weeks after ecdysis. Three to 29 eggs are deposited from April through July, and hatching occurs after an incubation period of ca. 60 days (Tennant, 1997).

Kingsnakes are usually found in the vicinity of water-containing microhabitats that allow them to burrow (Wright and Bishop, 1915; Carr, 1940; Enge, 1997). In the southern Florida peninsula, they occur in or near tropical hardwood hammocks, cypress (*Taxodium ascendens* and *T. distichum*) strands, sawgrass (*Cladium jamaicense*) prairies, Australian pine (*Casuarina equisetifolia*), and melaleuca (*Melaleuca quinquenervia*) forests, along drainage canals in sugarcane fields, and where excavated oolitic limestone is piled up alongside man-made canals (Wilson and Porras, 1983; O'Hare and Dalrymple, 1997; Tennant, 1997; Krysko, unpubl. data). In the central and northern peninsula, they occur in or near hardwood hammocks, pine flatwoods (*Pinus elliottii*), cypress strands, freshwater prairies, salt marshes, and estuaries with black (*Avicennia germinans*), red (*Rhizophora mangle*), and white (*Laguncularia racemosa*) mangroves. In the panhandle, they occur in or near mesic pine (*Pinus* spp.) flatwoods, clay hills, cypress strands, pitcher plant and sphagnum bogs, and salt marshes. They are typically not found in xeric sandhill habitats (Enge, 1997).

Kingsnakes are primarily diurnal and spend much of their time underground (Krysko, unpubl. data; Means, unpubl. data), yet when above ground their large size

makes them very conspicuous. In southern peninsular Florida, they are primarily active in February through June and October through December (Krysko, unpubl. data). The first activity period is correlated with the breeding season and an increase in rainfall and day length. The second activity period is correlated with cooling weather and a decrease in day length. They are found above ground mostly between 24ºC and 29ºC ambient air temperatures, with the highest frequency at 27ºC (Krysko, unpubl. data). At lower and higher temperatures, encounter rates decrease as kingsnakes may retreat into refugia. Adults are primarily diurnal, whereas juveniles are more secretive and exhibit crepuscular or nocturnal behaviors (Krysko, unpubl. data). An apparent ontogenetic shift in diel activity occurs, with secretive juveniles gradually become more diurnal. At approximately 90 cm SVL they may become less wary of diurnal predators.

Ecological Status

I obtained 821 Florida locality records where *L. getula* has been collected with known date of collection (Appendix A). Of these, 291 records came from two intensive kingsnake surveys (Table 2-1, Fig. 2-1). The first study compiled 110 records from the panhandle (Fig. 1-1) in 1969 through 1990 and consisted of 110 records (D. Bruce Means, unpubl. data). The second study compiled 181 records from the southern peninsula in 1993 through 1995 (Krysko, unpubl. data). Of the southern peninsula records, 109 consisted of captures, non-captures, dead on road specimens (DORs), shed skins and skeletons that were not collected as vouchers and, therefore, are not listed in Appendix A.

Individual records are summarized by county and decade in Table 2-2 and Figures 2-1 and 2-2. The number of kingsnake records have gradually increased over time as the

number of collectors increased, especially around the 1930s (Fig. 2-1). The number of records reported here was inflated in the 1970s through the 1990s because of intensive efforts aimed at documenting large numbers of individuals (Table 2-1, Fig. 2-1).

Historical records indicate a nearly statewide distribution for kingsnakes in Florida. Records for fifty-four (80.5%) of 67 counties exist for the period from 1858 to 1999 (Fig. 2-3). However, only 23 (34.3%) counties are represented during the last decade (Fig. 2-4). Similar to kingsnake records by decade (Fig. 2-1), county records also gradually increased over time as the number of herpetologists and collectors increased (Fig. 2-2). The largest number of county records occurred during the 1970s in conjunction with the first intensive kingsnake study (Table 2-1, Fig. 2-2). Even though the number of herpetologists and collectors has increased since the 1970s, the number of records documented has declined sharply.

Discussion

Kingsnake ecology is poorly known and has only been studied thoroughly in southern peninsular Florida populations (Krysko, unpubl. data). Because of apparent population declines or extirpation, studies of kingsnakes have been inefficient or impossible elsewhere in Florida, and other populations in the state can only be assumed to exhibit similar biological patterns.

Because museum records reflect collecting biases, they are unreliable by themselves in determining the present status and distribution of a species (Dodd and Franz, 1993). However, they are valuable for determining a species historical distribution. In this study, in addition to museum records I used all data available to me including literature and herpetologists' field notes. However, records for Florida by

county (Fig. 2-2) do illustrate a collecting bias. From 1858 through the 1960s kingsnakes were probably present statewide, but few individuals were recorded because only a small number of collectors was active in Florida. The peak in kingsnake records occurred in the 1970s, when 118 individuals were recorded from 30 counties (Figs. 2-1, 2-2). Assuming that the number of field biologists and collectors has increased since the 1970s, there has been a considerable decrease in the number of counties represented, which probably does not indicate a collecting bias but rather a reduced number of encounters with kingsnakes. Excluding the intensive kingsnake studies during the last decade (Table 2-1), there have been only 93 kingsnake records documented from 21 counties from 1990 to 1999 (Figs. 2-2, 2-4). A reduction in the number of collected individuals may reflect in part the present-day conservation attitudes and reluctance to collect animals from the wild. But most young biologists have never seen a wild kingsnake in Florida, and many experienced biologists report few or no encounters with kingsnakes over the last two decades (P. A. Meylan, pers. comm.).

Paynes Prairie (Alachua County)

Kauffeld (1957) claimed that he had never seen such an abundance of kingsnakes anywhere like that on Paynes Prairie. Prior to the 1970s, 20 kingsnakes could commonly be found on a spring morning along U.S. Highway 441 traversing the prairie (Kauffeld, 1957; F. W. King and D. Franz, pers. comm.). However, from 13 January 1958 through 27 February 1960, U.S. Highway 441 was changed from two to four lanes (G. Busscher, pers. comm.), which drastically changed the habitat. Concurrently, dredging created a deep-water habitat along the roadsides (Smith, 1996). For the next few years the road shoulders were mostly sand with little vegetation, and frequent trips were made by

biologists in the mornings to observe numerous kingsnakes foraging on *Ophisaurus* sp. (F. W. King, pers. comm.). During the 1960s, hundreds of kingsnakes were killed by vehicles, the prairie was mostly drained, dense hardwoods invaded the margins, and kingsnakes became extremely scarce (F. W. King and D. Franz, pers. comm.). During three separate intensive studies on the prairie from 1973-1977, no kingsnakes were found (Franz and Scudder, 1977; Smith, 1996). The last verified kingsnake found on the prairie was nearly two decades ago, in 1984, and kingsnakes appear to have been extirpated in this region. Although the prairie habitat has been highly modified, D. Jouvenaz (pers. comm.) believed that decreasing kingsnake populations resulted from increasing densities of red imported fire ants (*Solenopsis invicta*).

Apalachicola National Forest/Tate's Hell State Forest (Liberty and Franklin Counties)

During the 1970s, it was not uncommon to encounter five or more kingsnakes in one day crossing roads during the breeding season in the Apalachicola National Forest (ANF) and Tate's Hell Swamp (D. B. Means, unpubl. data). Yet, near the end of the 1970s, Livingston (1977) reported that the southern half of the Apalachicola region had been under extensive development including agricultural activities, timber harvesting, dredging, and damming. By the early 1980s, kingsnakes had begun to decline drastically in this region (Table 2-1). After surveying thousands of kilometers of these same roads during the 1990s as Means had done in the 1970s, Krysko (unpubl. data) found only one dead on road (DOR) individual in 1996. Even though few kingsnakes have been found crossing roads during the last decade, some individuals have recently been captured using drift fences (K. M. Enge, pers. comm.). Management practices are currently restoring

native longleaf pine (*Pinus palustris*) in the ANF. However, Tate's Hell State Forest has yet to establish an effective restoration program of the native habitat, and the management plan still allows extensive clear cutting, timber harvesting (Fig. 2-5) and replacing of native longleaf pine forests with slash pine (*Pinus elliotii*) tree farms.

Lake Okeechobee (Glades, Hendry and Palm Beach Counties) and Extreme Southern Peninsula (Dade County)

Godley (1982) reported capturing 58 kingsnakes at Rainey Slough on the western side of Lake Okeechobee from November 1975 through August 1978. Wilson and Porras (1983) noted that the sugarcane fields around Lake Okeechobee attracted large rodent populations and associated drainage canals provided refuge for kingsnakes. Presently, the Lake Okeechobee region, where 101 individuals were recorded from 1993 to 1995 (Table 2-1), appears to be the only area in Florida where large numbers of kingsnakes are still found.

Wilson and Porras (1983) also suggested that kingsnake populations in southern Dade Co. and along the Tamiami Trail had experienced drastic declines as a result of increasing urban and agricultural development. Many kingsnakes had also been killed as vermin in the 1960s along the Tamiami Trai and Loop Road (F. W. King, pers. comm.). However, 80 individuals were recorded in the Everglades region from 1993-1995 (Table 2-1). Yet, during these two years local collectors were observed taking every individual found in this area, illustrating the intense collecting pressure put on these populations. This prompted Krysko (1995) to blame habitat loss, habitat fragmentation, and over-collecting by commercial collectors for the pet trade as alternative explanations for declining populations in this area. In the six years following Krysko's (1995) survey,

only two kingsnakes (both in 1995) were found at the study sites despite extensive searches during the breeding season.

Table. 2-1. Kingsnakes, *Lampropeltis getula*, recorded from two unpublished studies in Florida: D. B. Means (1969-1990) in the panhandle and K. L. Krysko (1993-1995) in the southern peninsula.

Means

County	1960s	1970s	1980s	1990s	Total
Calhoun	0	2	2	0	4
Franklin	1	7	4	0	12
Gulf	0	9	1	0	10
Jefferson	0	3	1	0	4
Leon	0	5	4	0	9
Liberty	0	53	5	1	59
Wakulla	0	9	3	0	12
Total	1	88	20	1	110

Krysko

County	1993-1995
Dade	80
Glades	45
Hendry	23
Palm Beach	33
Total	181

Table. 2-2. Kingsnake, *Lampropeltis getula*, records by Florida county from 1858 to 1999.

	1858-1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	Total
Alachua	1	0	4	3	11	8	19	10	10	2	0	68
Baker	0	0	0	0	0	1	0	1	0	0	0	2
Bay	0	0	0	0	0	0	0	1	0	0	1	2
Bradford	0	0	0	0	0	0	0	0	0	0	0	0
Brevard	0	0	0	0	0	1	0	0	5	3	0	9
Broward	0	0	0	0	0	0	4	2	1	0	0	7
Calhoun	0	0	0	0	0	0	0	0	2	5	5	12
Charlotte	1	0	0	0	1	1	0	0	0	0	0	3
Citrus	0	0	0	0	0	0	0	0	2	1	1	4
Clay	0	0	0	0	0	0	0	0	0	0	0	0
Collier	0	0	0	0	0	3	8	3	5	3	3	25
Columbia	0	0	0	0	0	0	0	0	1	1	1	3
Dade	0	1	0	2	6	0	4	0	2	7	83	105
DeSoto	1	0	0	0	0	0	0	0	0	0	0	1
Dixie	0	0	0	0	0	0	0	0	4	2	1	7
Duval	2	0	0	0	0	0	1	0	1	1	8	13
Escambia	0	0	0	0	0	0	0	0	0	0	0	0
Flagler	0	0	0	0	0	0	0	0	0	0	0	0
Franklin	0	0	0	0	0	0	0	3	18	8	2	31
Gadsden	0	0	0	0	0	0	0	0	1	3	0	4
Gilchrist	0	0	0	0	0	0	0	0	0	0	0	0
Glades	0	0	0	0	0	1	3	0	0	0	50	54
Gulf	0	0	0	0	0	2	1	0	32	6	7	48
Hamilton	0	0	0	0	0	0	0	0	1	0	0	1
Hardee	0	0	0	0	0	0	0	0	1	0	0	1
Hendry	0	0	0	0	0	0	1	1	1	0	24	27
Hernando	0	0	0	0	0	0	0	0	1	0	4	5
Highlands	0	0	0	1	0	1	0	0	0	0	0	2
Hillsborough	0	0	0	0	1	0	2	2	0	1	17	23
Holmes	0	0	0	0	0	0	1	0	0	1	1	3
Indian River	1	0	0	0	0	0	0	0	0	0	0	1
Jackson	0	0	0	0	0	0	1	0	0	1	6	8

Table 2-2.—Continued.

	1858-1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	Total
Jefferson	0	0	0	0	0	0	0	1	6	3	0	10
Lafayette	0	0	0	0	0	0	0	1	0	0	0	1
Lake	0	1	0	1	3	1	0	0	0	0	0	6
Lee	0	0	0	0	0	0	0	0	0	0	0	0
Leon	0	0	0	0	1	0	0	8	7	8	4	28
Levy	1	0	0	0	0	3	5	1	6	2	0	18
Liberty	0	0	0	0	0	0	0	0	62	13	7	82
Madison	0	0	0	0	0	0	0	2	0	0	0	2
Manatee	0	0	0	0	0	0	0	0	0	0	0	0
Marion	0	1	3	3	3	1	2	0	1	0	0	14
Martin	0	0	0	0	0	0	0	0	0	0	0	0
Monroe	0	0	0	0	2	0	1	4	0	0	0	7
Nassau	1	0	0	0	0	0	0	0	0	0	0	1
Okaloosa	0	0	0	0	1	0	0	1	0	7	1	10
Okeechobee	0	0	0	0	1	0	0	0	0	0	5	6
Orange	0	1	1	0	1	3	0	0	1	0	0	7
Osceola	0	7	6	0	0	0	0	0	0	0	0	13
Palm Beach	0	0	0	0	0	1	10	0	1	0	33	45
Pasco	0	0	0	0	0	0	0	0	0	1	0	1
Pinellas	0	0	2	0	0	3	0	2	0	6	8	21
Polk	0	0	0	1	1	5	3	0	0	2	0	12
Putnam	0	0	0	0	0	0	1	0	0	0	0	1
Santa Rosa	0	0	0	0	0	0	2	0	2	3	0	7
Sarasota	0	0	0	0	0	0	0	0	0	0	0	0
Seminole	0	0	0	0	1	0	1	0	0	0	0	2
St Johns	0	0	0	2	0	0	0	0	0	0	0	2
St Lucie	0	0	0	0	0	0	0	0	0	0	0	0
Sumter	0	0	0	0	0	0	0	0	1	0	0	1
Suwannee	0	0	0	0	0	0	0	0	0	0	0	0
Taylor	0	0	0	0	1	0	2	0	5	1	0	9
Union	0	0	0	0	0	0	0	0	0	0	0	0
Volusia	0	0	0	0	0	1	3	0	0	0	0	4
Wakulla	0	0	0	0	0	0	6	1	24	4	3	38

Table 2-2.—Continued.

	1858-1890s	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	Total
Walton	0	0	0	0	0	0	0	0	1	0	0	1
Washington	0	0	0	0	0	0	1	0	1	1	0	3
	8	11	16	13	34	36	82	44	206	96	275	821

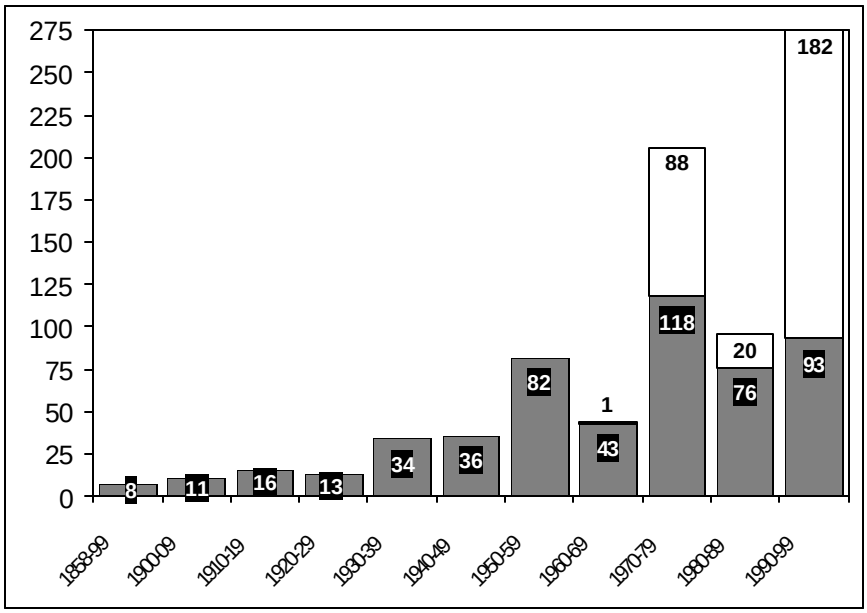

Fig. 2-1. Number of kingsnake, *Lampropeltis getula*, records from 1858 to 1999. Note that top numbers in last four decades correspond to those from two unpublished studies by Means (1960-1990) and Krysko (1993-1995), which specifically targeted collecting large numbers of kingsnakes.

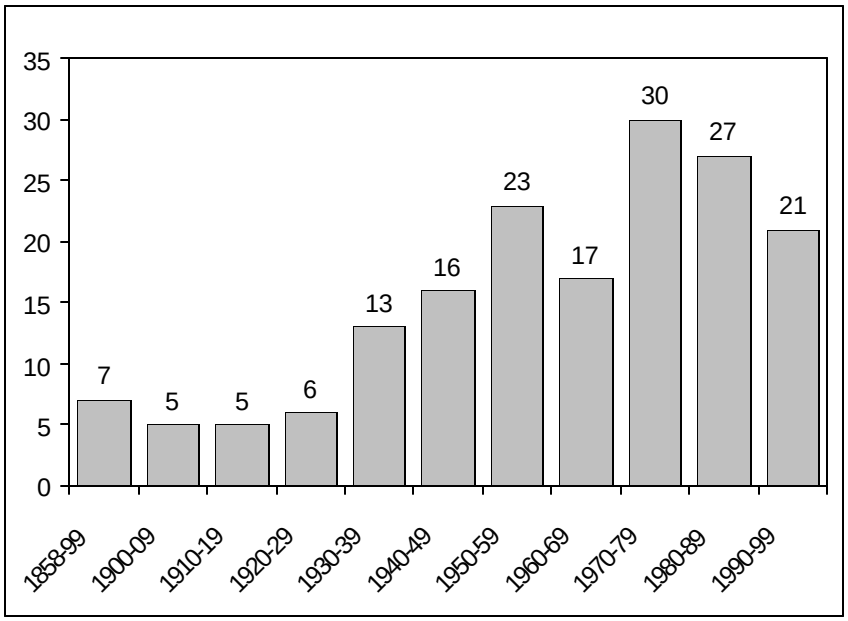

Fig. 2-2. Number of Florida counties with kingsnake, *Lampropeltis getula*, records from 1858 to 1999. Note that the high numbers in last four decades correspond to those from two unpublished studies by Means (1960-1990) and Krysko (1993-1995), which specifically targeted collecting large numbers of kingsnakes.

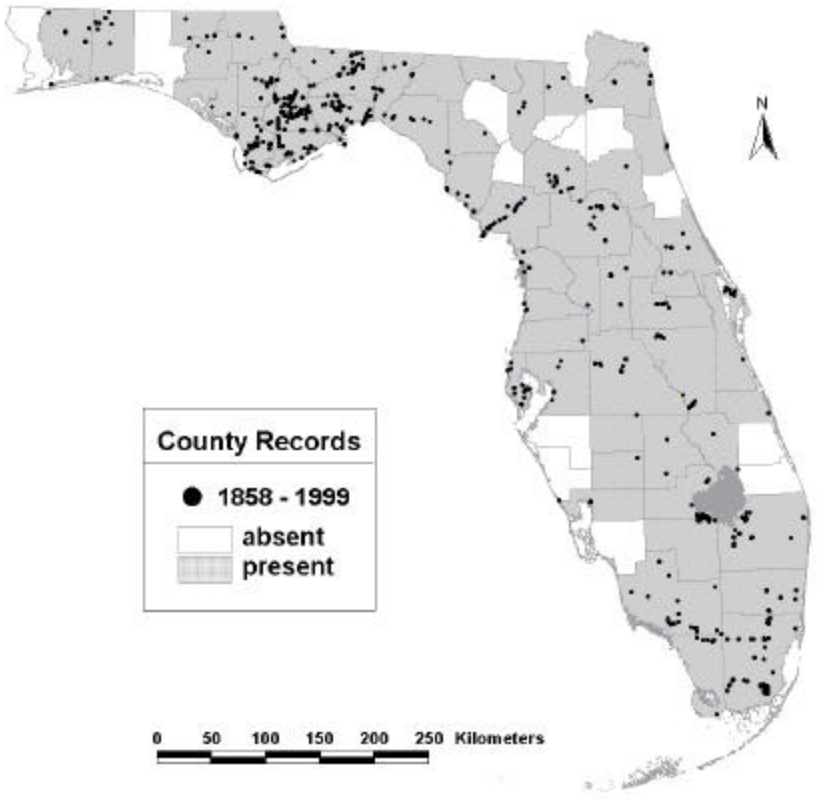

Fig. 2-3. Kingsnake, *Lampropeltis getula*, records from 1858 to 1999 (n = 821). Solid dots correspond to individual records. Fifty-four (80.5%) counties are represented.

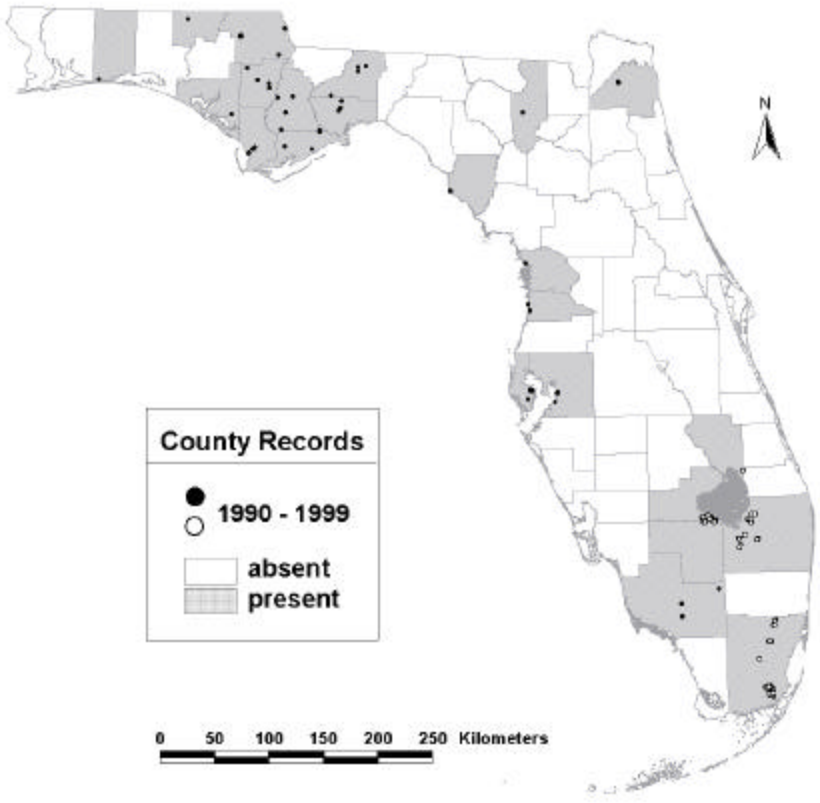

Fig. 2-4. Kingsnake, *Lampropeltis getula*, records from 1990 to 1999 (n = 275). Open circles correspond to 181 individuals recorded in a two-year study in southern Florida from 1993 to 1995. Solid dots correspond to remaining 94 records. Twenty-three (34.3%) counties are represented.

Fig. 2-5. Tate's Hell State Forest, Franklin County, Florida (1997).

CHAPTER 3
SEXUAL AND GEOGRAPHIC VARIATION OF KINGSNAKES (*Lampropeltis getula*) IN FLORIDA

Materials and Methods

I examined morphological characters including scutellation and color pattern of 822 field-collected and museum specimens of *L. getula* from Florida (Appendix B). Of these, 141 were field-collected from 1993 to 1995 in the southern peninsula (Fig. 1-1) and examined alive to evaluate natural color pattern variation. Because *L. getula* populations have drastically declined or been extirpated from Florida (Means, 2000), most specimens demarked KLK (Kenneth L. Krysko, Appendix B) were photographed, marked following Brown and Parker (1976) and released at their capture site after data were collected. Representative voucher specimens were deposited at the Florida Museum of Natural History, University of Florida (FLMNH, UF collection). Morphological data from other areas in the southeastern U.S. were obtained from the scientific literature.

The following standard scale counts and measurements were taken: CROSSBANDS— the number of light body bands from one head length posterior to the head to above the cloaca (after Blaney, 1977). CROSSBAND WIDTH— the number of dorsal scale rows the light crossbands cover mid-dorsally. During embryonic development of individuals from the eastern Apalachicola Lowlands having < 15 crossbands or crossbands > 8 dorsal scales rows wide, their distinct crossbands break up and fuse in two basic ways, forming non-banded (striped and patternless) phenotypes

(Fig. 1-6D, E). First, the light crossbands fuse laterally and divide mid-dorsally, producing a light colored individual with a black mid-dorsal stripe (Fig. 1-6D). This stripe appears to be the remnants of the black interbands because it undergoes ontogenetic lightening. Second, the light crossbands fuse both dorsally and laterally, producing a patternless individual with essentially one crossband from head to tail tip (Fig. 1-6E). Although I consider that both striped and patternless individuals have one crossband whose width is the entire length of the snake, I set this value at 200 dorsal scale rows wide in statistical analyses. VENTRALS— the number using the standard counting system (after Dowling, 1951). SUBCAUDALS— the number of scales from the cloaca to the tail tip, excluding the tail tip. DORSAL SCALE ROWS (DSR)— the maximum number at midbody. SUPRALABIALS and INFRALABIALS— the total number on both sides of the head. TEMPORALS and PRE and POST-OCULARS— the arrangement on both sides of the head. DORSAL PATTERN— the degree of ontogenetic lightening of the normally dark interband (= interspaces between light crossbands) scales was rated on adults with a system of A-D (Fig. 3-1), where interband scales have A = 0% lightening (typical of *L. g. getula*), B = up to 25% of the intensity of the crossbands (typical of *L. g. goini* and *L. g. floridana*), C = 25–75% of the intensity of the crossbands (typical of *L. g. floridana* and Apalachicola Lowlands populations), D = 75–100% of the intensity of the crossbands (typical of *L. g. brooksi* and Apalachicola Lowlands populations). PERCENT OF THE IRIS LIGHTENED— examined on live specimens only. SNOUT-VENT LENGTH (SVL)— measured with a tape from the tip of the snout to the distal edge of the cloaca. HEAD LENGTH— measured with calipers from the posterior tip of the lower jaw to the tip of the snout. HEAD WIDTH—

measured at the widest part on the head. VENTRAL PATTERN— estimated percent of lightened to darkened areas over the entire ventral surface. The ventral pattern (Fig. 3-2) was also scored as A = tight checkerboard, where the alternating light and dark pigment is tightly compressed, typical of *L. g. floridana*; B = loose checkerboard, where the alternating light and dark pigment is loosely compressed, typical of *L. g. getula*; and C = bicolored, where light pigment is confined to the anterior portion and dark pigment is confined to the posterior portion of each ventral scale.

Previous workers defined the ranges of *L. getula* subspecies in Florida based on character distributions (Fig. 3-3; Blanchard, 1921; Conant, 1975; Blaney, 1977). After mapping these same characters in addition to others listed above, I detected similar areas of demarcation. To determine if certain characters differed significantly between regions, I divided Florida into six areas (Fig. 3-4): 1) extreme southern peninsula from the southern tip of Florida north to southern Miami-Dade County, incorporating the range of *L. g. brooksi*; 2) southern and central peninsula, incorporating the range of *L. g. floridana*; 3) northern peninsular intergradation zone between *L. g. floridana* and *L. g. getula* (modified after Krysko, 1995); 4) northern peninsula and panhandle, incorporating the range of *L. g. getula*; 5) western Apalachicola Lowlands on the west side of the Apalachicola River (after Means, 1977); and 6) eastern Apalachicola Lowlands on the east side of the Apalachicola River. In order to determine significant character trends down peninsular Florida as well as to illustrate geographic variation and descriptive statistics, I further separated the peninsula by 0.5°N latitude.

Sexual Dimorphism

Student's *t*-tests were performed to test for sexual dimorphism in crossband numbers, crossband width, ventrals, and subcaudals within each area. A chi-square test for independence was used to determine if males obtain lighter interband dorsal patterns (Fig. 3-1D) more frequently than females in the southern peninsula (area 1, Fig. 3-4).

Geographic Variation

A regression was performed on crossband numbers, crossband width, ventrals, subcaudals, total supralabials and infralabials, and DSR by latitude to see if these characters change significantly north to south in peninsular Florida. I used Analysis of Variance (ANOVA) to determine significance in mean crossband numbers, crossband width, ventrals and subcaudals between each area, and when significance was detected, I used General Linear Models (PROC GLM) with Least Squares Means (LSM) as a multiple comparison tool.

Because the percent of the iris lightened and the ventral pattern do not change with age (pers. obs.), correlation coefficients were calculated to see if these two characters are good indicators for estimating the degree of ontogenetic interband lightening (Fig. 3-1). Because it has been suggested that *L. g. brooksi* is distinguished from *L. g. floridana* by having a smaller head to SVL ratio, I used analysis of covariance (ANCOVA) to compare relationships of head length and head width relative to SVL between individuals from around Lake Okeechobee vs. southern Miami-Dade County. The data were log transformed and a preliminary test was performed to test for homogeneity among slopes between these two populations. Statistical analyses were conducted using Statistical Analysis System (SAS for Windows, ver. 6.12) with $\alpha = 0.05$.

Results

Sexual Dimorphism

Crossband numbers. There were no significant differences in mean crossband numbers between males and females within any areas (all *t* values from 1.985 to 2.131, all *P* values > 0.05) except within the eastern Apalachicola Lowlands (area 6, Fig. 3-4; mean = 9.6 for males, mean = 16.0 for females; $t = 3.400$, df = 89, $P < 0.001$), where a higher frequency of males possess non-banded phenotypes. Only males possessed a patternless phenotype, suggesting that this trait may be sex-linked. Additionally, non-banded individuals are confined to the eastern and southwestern Apalachicola Lowlands (Fig. 3-5). When all non-banded individuals were excluded from the eastern Apalachicola Lowlands population, there was no significant difference in crossbands between males and females ($t = 0.312$, df = 51, $P > 0.05$). Therefore, data from both sexes were combined in all areas except in the eastern Apalachicola Lowlands for analysis of geographic variation.

Crossband width. There were no significant differences in mean crossband width between males and females within any areas (all *t* values from 1.985 to 2.131, all *P* values > 0.05) except within the eastern Apalachicola Lowlands (area 6, Fig. 3-4; mean = 101.0 for males, mean = 33.7 for females; $t = -4.843$, df = 75, $P < 0.001$), where patternless males occur as well as males having wider crossbands than females. Even when all non-banded individuals were excluded from the eastern Apalachicola Lowlands population, a significant difference remained between males and females ($t = -2.149$, df = 37, $P < 0.05$). Therefore, data from both sexes were combined for all areas except within the eastern Apalachicola Lowlands for analysis of geographic variation.

Ventrals. There was no significant difference in mean number of ventrals between males and females within any areas in Florida (all *t* values from 1.989 to 2.178, all *P* values > 0.05). Therefore, data from both sexes were combined in all areas for analysis of geographic variation.

Subcaudals. There was a significant difference in mean number of subcaudals between males and females within all areas in Florida (all *t* values from 1.996 to 2.570, all *P* values < 0.05), due to males having longer tails than females. Males have longer tails, which are required for storage of their hemipenes (Greene, 1997). Therefore, data from both sexes were treated separately in all areas for analysis of geographic variation.

Dorsal pattern. There was no significant difference in the frequency of adult males and females possessing the lightest interband dorsal pattern (Fig. 3-1D) throughout the entire Florida peninsula ($\chi^2 = 1.340$, df = 1, $P > 0.05$). Therefore, males do not obtain lighter interband dorsal patterns more frequently than females.

Geographic Variation

Crossband numbers. A significant regression was detected ($R^2 = 0.031$, $P < 0.001$) for a north to south increase in crossband numbers (Table 3-1). Because crossbands varied drastically from 18-72, there is an overall increase of 6.18 crossbands for every 0.5° latitude. However, this cline terminated at 28° 50' N latitude in the central peninsula. There were significant differences in mean crossband numbers (all *P* values < 0.001) between all areas, except between the 1) extreme southern peninsula and southern and central peninsula (areas 1 and 2, Fig. 3-4), and 2) northern peninsula and panhandle and western Apalachicola Lowlands (areas 4 and 5). The western and eastern Apalachicola Lowlands (areas 5 and 6) are significantly different from each other due to

a higher frequency of patternless males found in the eastern Apalachicola Lowlands. When all non-banded individuals were excluded from the analysis there was no significant difference between these two areas ($P > 0.05$), but the eastern Apalachicola Lowlands was still significantly different from all other areas ($P < 0.05$). Crossband numbers are fewest in the eastern Apalachicola Lowlands (Table 3-1; Fig. 3-4; area 6, Fig. 3-6; mean = 9.6 for males, mean = 16.0 for females, mean = 11.8 combined sexes), followed by western Apalachicola Lowlands (area 5; mean = 18.0), northern peninsula and panhandle (area 4; mean = 22.6), northern peninsula (area 3; mean = 34.0), southern and central peninsula (area 2; mean = 53.0) and extreme southern peninsula (area 1; mean = 54.7). Mean crossband numbers are greatest at 27° 50' N latitude in the central peninsula north of Lake Okeechobee (mean = 56.2; Table 3-1).

Crossband width. A significant regression was detected ($P < 0.001$) for a north to south decrease in crossband width (Table 3-2). However, this is essentially nonsignificant since the fit was poor ($R^2 = 0.023$) and the slope = 0.03, which indicates for every 0.5° latitude there is only a 0.03 decrease in crossband width. This cline terminated at 28° 00' N Latitude in the central peninsula, where from this point south crossband width was invariably 1.5 dorsal scale rows. There were no significant differences in mean crossband width between any areas (Fig. 3-4; all P values > 0.05), except between the western and eastern Apalachicola Lowlands ($P < 0.0001$), as well as both of these areas being significantly different from all other areas (all P values < 0.01). The western and eastern Apalachicola Lowlands are significantly different from each other due to a higher frequency of patternless males found in the eastern Apalachicola Lowlands. When all non-banded individuals were excluded from the analysis, there was

no significant difference in crossband width between these two areas ($P > 0.05$). Crossband width (Table 3-2) was lowest in the southern and central peninsula (areas 1 and 2, Fig. 3-4; mean = 1.5), followed by the northern peninsula (area 3; mean = 1.7), northern peninsula and panhandle (area 4; mean = 2.2), western Apalachicola Lowlands (area 5; mean = 19.1) and eastern Apalachicola Lowlands (Fig. 3-7; area 6, Fig. 3-4, mean = 101.0 for males, mean = 33.7 for females, mean = 71.3 combined sexes).

Ventrals. A significant regression ($P < 0.05$) indicated a change of 0.28 ventrals over latitude (Table 3-3). However, this is essentially nonsignificant since the fit was poor ($R^2 = 0.011$). There were no significant differences in mean number of ventrals between any areas (all P values < 0.001; Table 3-3). Because ventrals are highly variable geographically, this character is not useful for distinguishing populations.

Subcaudals. Although a significant regression was detected ($P < 0.01$) indicating a change of 0.40 subcaudals over latitude, there were no clear geographic trends down the peninsula (Table 3-4). Additionally, this is essentially nonsignificant since the fit was poor ($R^2 = 0.019$). Because subcaudals are sexually dimorphic and highly variable geographically, this character is not useful for distinguishing populations.

Dorsal scale rows. A significant regression was detected ($P < 0.001$) for a north to south increase in number of DSR from 21 to 25 (Table 3-5). However, this is essentially nonsignificant since the fit was poor ($R^2 = 0.031$) and the slope = 0.08, which indicates for every 0.5° latitude there is only a 0.08 increase in DSR. Snakes from both the western and eastern Apalachicola Lowlands (areas 5 and 6, Fig. 3-4) have only 21 DSR, individuals from the panhandle and northern peninsula (area 4) usually have 21 DSR, and

individuals from the southern peninsula (area 2) usually have 23 DSR. One individual from 25° 50’ N latitude in the extreme southern peninsula (area 1) had 25 DSR.

Head scutellation. Supralabials were primarily 14 (Table 3-6) and did not show a significant change over latitude ($P > 0.05$). Although most infralabials were 18 throughout Florida (Table 3-7), this character is highly variable geographically and did not show a significant change over latitude ($P > 0.05$). Most temporals were in the arrangement of 2+3+4 (Table 3-8). Oculars were almost invariably in the arrangement of 1+2 (Table 3-9). Since there were no clear geographic trends in head scutellation within any areas in Florida, these characters are not useful for distinguishing populations.

Dorsal pattern. The dorsal pattern is distinctly narrow banded (1.5 dorsal scale rows) with a degenerate lateral chain in the southern and central peninsula (Fig. 3-7; areas 1, 2, Fig. 3-4), slightly wider banded (1.5-2.5 dorsal scale rows) with both the presence and absence of individuals with a lateral chain in the northern peninsula and panhandle (areas 3, 4), narrow, wide and non-banded (1.5-200 dorsal scale rows) in the western Apalachicola Lowlands (area 5), and wide banded or non-banded (2.5-200 dorsal scale rows) in the eastern Apalachicola Lowlands (area 6).

Adults possessing the lightest interband pattern (Fig. 3-1D) were not confined to *L. g. brooksi* in the southern peninsula (area 1, Fig. 3-4), yet were found scattered throughout the entire peninsula from southern Miami-Dade and Monroe counties north to Collier, Broward, Hendry, Palm Beach, Okeechobee, Pinellas, Hillsborough, Polk, Osceola, Sumter, Orange, Volusia, St. Johns and Baker counties (Fig. 1-1). However, in the panhandle the lightest interbands were confined to the Apalachicola Lowlands (Fig. 3-8). Eighty-nine of 93 (96 %) adults from the eastern Apalachicola Lowlands showed

interband lightening as C or D (Fig. 3-1). Only four (4 %) adults showed interband lightening as B like *L. g. goini* (Fig. 3-1; see Figs. 1-3, Neill and Allen, 1949), and these were peripheral to the eastern Apalachicola Lowlands (Fig. 3-8). Typically patterned *L. g. floridana* (Figs. 1-2B, 3-1C) were found from southern Miami-Dade Co. north to Alachua County. Additionally, newborns within all areas may exhibit reddish crossband scales, previously reported by Neill (1954) for only southern peninsular populations.

The percent of the iris lightened was a good predictor for estimating the degree of ontogenetic interband lightening ($r = 0.812$, $F = 244.7$, $df = 1, 126$, $P < 0.005$), which is fully expressed in adults. Adults with moderately lightened interband patterns (Figs. 3-1B, C) had < 60% of their iris lightened, whereas those with the lightest interband pattern (Fig. 3-1D) had > 60% of their iris lightened. The ventral pattern was not a good predictor for estimating the degree of interband lightening ($r = 0.092$, $F = 1.080$, $df = 1, 126$, $P > 0.05$).

Head to snout-vent length ratio. There were significant relationships between both head length ($F_{2,139} = 1737.03$, $R^2 = 0.961$, $P < 0.001$) and head width ($F_{2,138} = 924.13$, $R^2 = 0.930$, $P < 0.001$) relative to SVL within populations around Lake Okeechobee and southern Miami-Dade County. Slopes of the Lake Okeechobee and southern Miami-Dade Co. populations where homogenous (interaction terms: head length $P = 0.966$ and head width $P = 0.101$ relative to SVL). There was no significant difference between the slopes of the Lake Okeechobee and southern Miami-Dade Co. populations when analyzing both head length ($P = 0.074$) and width ($P = 0.881$) relative to SVL (Fig. 3-9), indicating no significant difference in both head length and width relative to SVL

between snakes occurring around Lake Okeechobee (*L. g. floridana*) versus those in southern Miami-Dade County (*L. g. brooksi*).

Ventral pattern. The ventral pattern is comprised of a tight checkerboard (Fig. 3-2A) in the southern and central peninsula (areas 1 and 2, Fig. 3-4), both a tight and loose checkerboard (Figs. 3-2A, B) in the northern peninsula (area 3), a loose checkerboard in the northern peninsula and panhandle (area 4), both a loose checkerboard and loose checkerboard with interspersed bicolor scales (Figs. 3-2B, C) in the western Apalachicola Lowlands (area 5) and both a bicolored and loose checkerboard with interspersed bicolored scales (Fig. 3-2C) in the eastern Apalachicola Lowlands (area 6).

Discussion

Based on dorsal and ventral patterns and their geographical distributions, I identify three subspecies of *L. getula* in Florida. Two of these subspecies are presently named (*L. g. floridana* and *L. g. getula*) and one is unnamed (eastern Apalachicola Lowlands populations). All three subspecies have zones of intergradation between them due to gene flow. However, gene flow between these populations in Florida is largely a phenomenon of the past, occurring now much less frequently because of isolation from severely declined or extirpated populations.

Populations of *L. g. floridana* (Fig. 1-2B) range from the southern tip of Florida north to Volusia Co. in the central peninsula (Fig. 1-1; areas 1 and 2, Fig. 3-4) and have > 34 narrow (1.5 dorsal scale rows) crossbands, a degenerate lateral chain pattern and tight checkerboard ventral pattern (Fig. 3-2A). Populations of *L. g. getula* (Fig. 1-2A) range from the northern Florida peninsula and panhandle (area 4, Fig. 3-4) north to southeastern Alabama and southern New Jersey and have 19-32 (1.5-2.5 dorsal scale rows)

crossbands, a lateral chain pattern and loose checkerboard ventral pattern (Fig. 3-2B). The eastern Apalachicola Lowlands populations (area 6, Fig. 3-4) have 1-25 wide (up to 200 dorsal scale rows) crossbands (Fig. 1-5A), only 21 DSR, ventral patterns of either bicolor or loose checkerboard with interspersed bicolor scales (Fig. 3-2C), and the presence of non-banded (striped and patternless) individuals (Figs. 1-5B, C). Although these Apalachicola morphs are found mainly in the eastern Apalachicola Lowlands in Franklin and Liberty counties, others have been found in the southwestern Apalachicola Lowlands in Franklin and southern Gulf counties (Figs. 3-5 to 3-8).

Relationship between *L. g. floridana* and *L. g. brooksi*

Soon after the description of *L. g. brooksi* (Barbour, 1919), its validity was questioned (Blanchard, 1920, 1921; Barbour, 1920; Wright, 1935). Duellman and Schwartz (1958) and Blaney (1977) invalidated *L. g. brooksi* because they found no differences in scutellation between *L. g. floridana* (Fig. 1-2B) and *L. g. brooksi* (Fig. 1-4A), as well as because both morphs occur together from southern Miami-Dade Co. north to Osceola and Polk counties in the central peninsula (Fig. 1-1). Christman (1980) reported individuals with the light interband pattern of *L. g. brooksi* (Fig. 3-1D) much farther to the north around eastern Tampa Bay and the extreme northeastern peninsula. I have also found both *L. g. floridana* and *L. g. brooksi* (Figs. 1-2B, 1-4A) together from southern Miami-Dade Co. to Volusia Co. (Fig. 1-1), as well as individuals with the light interband pattern of *L. g. brooksi* (Fig. 3-1D) as far north as the northeastern peninsula in Duval and Baker counties. Therefore, I am unable to distinguish specimens from southern Miami-Dade Co. (= *L. g. brooksi*) from those to the north in the southern and central peninsula (= *L. g. floridana*). All scutellation characters (Tables 3-1 to 3-9), as

well as meristics (Fig. 3-9) and dorsal (Figs. 1-2B, 1-4A, 3-1B, C, D) and ventral patterns (Fig. 3-2A) are the same for both named taxa. Because Blanchard's (1919) description of *L. g. floridana* preceded Barbour's description of *L. g. brooksi* by one month, *L. g. brooksi* is confirmed as a junior synonym of *L. g. floridana*. Because individuals with the light interband pattern (Fig. 3-1D) have been found more frequently around prairies and in areas with exposed oolitic limestone, they are considered an ecotype.

Relationship between *L. g. floridana* and *L. g. getula*

Blaney (1977) reported that *L. g. getula* has 21 DSR from southern New Jersey south to peninsular Florida and used this character to define the ranges of *L. g. floridana* and *L. g. getula* in peninsular Florida (Fig. 3-3C). Like Blaney (1977), I found this character in different frequencies within these two taxa in Florida (Table 3-5; *L. g. floridana* usually has 23 DSR and *L. g. getula* usually 21 DSR). However, since it is a polymorphic character represented in both taxa it should not be used to define these forms in the peninsula. Auffenberg (1963) hypothesized that ancestral *L. getula* utilized the Gulf Coast Corridor as a dispersal route from the west into Florida during the Pliocene when sea levels were > 100 meters (m) lower than present day. I found an individual from the extreme southern peninsula with 25 DSR, which provides support for an historical relationship with *L. g. splendida* in Texas.

Blanchard (1919, 1921) and Van Hyning (1933) reported occasional morphological intermediates (i.e., intergrades) between *L. g. floridana* and *L. g. getula* from Orange Co. in the central peninsula north to Alachua Co. in the northern peninsula (Fig. 1-1). Blaney (1977) believed a disjunct population of *L. g. floridana* existed in the northeastern peninsula in Duval and Baker counties (Fig. 3-3C), as well as two intergradation zones in

the peninsula between these two taxa: from eastern Miami-Dade Co. north to Alachua Co., and in the northeastern peninsula surrounding his putative disjunct population of *L. g. floridana*. Additionally, many subsequent faunal treatments have perpetuated this view (Conant, 1975; Behler and King, 1979; Ashton and Ashton, 1988; Conant and Collins, 1991, 1998). I recognize one intergradation zone between *L. g. floridana* and *L. g. getula* from Pinellas Co. in the central peninsula northeast to Baker, Duval, and Nassau counties in the northern peninsula (Fig. 1-1; area 3, Fig. 3-4). Here, individuals possess intermediate characters between these two taxa. Blaney (1977:72) stated that individuals from Baker and Duval counties at 30° 50' N latitude "exhibit all the characters of *L. g. floridana"*, yet claimed that they were distinguished from *L. g. floridana* by having fewer crossbands, similar to *L. g. getula*. I examined many of the specimens examined by Blaney in addition to others not available to him, and these snakes are clearly intermediate by exhibiting 18-28 crossbands and a lateral chain pattern like *L. g. getula*, yet undergo interband lightening like *L. g. floridana*. Therefore, this is not a disjunct population of *L. g. floridana*, rather it extends the previously recognized intergradation zone from Alachua Co. to the northeast by 45 km.

Relationships among *L. g. getula, L. g. goini*, and Eastern Apalachicola Lowlands Populations

Blanchard (1921) and Blaney (1977) claimed that the southwestern portion of the range of *L. g. getula* included southeastern Alabama and panhandle Florida. Neill and Allen (1949) claimed that *L. g. goini* was found only on the western side of the Apalachicola River in the northwestern Apalachicola Lowlands in Calhoun and northern Gulf counties (Figs. 1-1, 1-3). Neill and Allen (1949), however, did not examine any

specimens from the eastern side of the Apalachicola River, and like Blaney (1977), appeared to be unaware of non-banded morphs. All specimens examined by Neill and Allen possessed 15-17 crossbands of 4-8 dorsal scale rows wide, nearly black interbands in adults and ventral patterns intermediate between *L. g. getula* and individuals in the eastern Apalachicola Lowlands (*see* Figs. 1-3, Neill and Allen, 1949). Their description did not include snakes with < 15 crossbands (Fig. 3-6), crossbands > 8 dorsal scale rows wide (Fig. 3-7), extensively lightened interbands (Fig. 3-8), nor striped nor patternless phenotypes (Fig. 3-5). Because the color pattern and locality of *L. g. goini* are intermediate between *L. g. getula* and populations in the eastern Apalachicola Lowlands, *L. g. goini* is relegated to intergrade status.

Blaney (1977) invalidated *L. g. goini* solely by speculating that the Apalachicola populations were relict intergrades from the Pleistocene between panhandle *L. g. getula* and now disjunct peninsular *L. g. floridana*. Although Blaney (1977) acknowledged that the Apalachicola variants were morphologically unique, he provided no data to support his conclusion. Means (2000) mistakenly stated that patternless individuals occur in both the Apalachicola region and the southern peninsula. However, other than for rare aberrant pattern abnormalities, there are no truly patternless individuals found anywhere within the range of *L. getula* other than in the Apalachicola Lowlands. Neonate peninsular *L. g. floridana* are boldly crossbanded with black interbands (Fig. 1-6A) and only after extensive ontogenetic interband lightening do crossbands become obscured (Fig. 3-1D). However, crossbands can always be distinguished on peninsular snakes, simply by examining the snake's body in sufficient light. Adult speckled *L. g. holbrooki* from the midwestern U.S. have also been confused with truly patternless individuals from

the Apalachicola Lowlands, yet newborn *L. g. holbrooki* are also distinctly banded and undergo ontogenetic interband lightening. Ontogenetically lightened interbands are not restricted to Florida populations in the eastern U.S., as individuals from the Outer Banks of North Carolina (= *L. g. sticticeps* Barbour and Engels, 1942) and coastal Georgia (both populations = *L. g. getula* x *L. g. floridana sensu* Blaney, 1977) may also exhibit this trait (Lazell and Musick, 1973; Blaney, 1977; Palmer and Braswell, 1995).

Striped individuals have been commonly found in the eastern Apalachicola Lowlands and in *L. g. californiae* from the western U.S., as well as in rare pattern abnormalities in *L. g. floridana* from eastern Tampa Bay in peninsular Florida (K. M. Enge, pers. comm.) and *L. g. getula* from Georgia (D. B. Means, pers. comm.). However, Apalachicola Lowlands snakes are black striped whereas all others are light striped (Figs. 1-5B, 1-6D). To determine if the gene for light striping is the same in both California and Georgia populations, a cross between striped *L. g. californiae* and *L. g. getula* was performed. All offspring were boldly banded (D. B. Means, pers. comm.) suggesting that the light striping gene in the two populations are on different loci. I therefore presume that the gene for black striping in the Apalachicola Lowlands is also different from these light striping genes.

Crossband numbers are fewest (1-25) in the eastern Apalachicola Lowlands population (Table 3-1; area 6, Fig. 3-4; Fig. 3-6), intermediate (18-63) between *L. g. getula* and *L. g. floridana* within their northern peninsular intergradation zone (area 3), and greatest (35-72) in peninsular Florida (areas 1 and 2). Crossband width is greatest (2.5-200 dorsal scale rows) in the eastern Apalachicola Lowlands (Table 3-2; area 6, Fig. 3-4; Fig. 3-7), intermediate (1.5-2.5 dorsal scale rows) between *L. g. getula* and *L. g.*

floridana within their intergradation zone in the northern peninsula (area 3), and least (1.5 dorsal scale rows) in the central and southern peninsula (areas 1 and 2). Wide crossbands (up to 4 DSR) are not restricted to Apalachicola Lowlands populations in the eastern U.S., as occasional *L. g. getula* have been found on Edisto Island of South Carolina exhibiting this trait (K. M. Enge, pers. comm.). Ventral patterns (Fig. 3-2) in the eastern Apalachicola Lowlands are more similar to those in the western Apalachicola Lowlands and surrounding panhandle, and remarkably different from peninsular *L. g. floridana*. The eastern Apalachicola Lowlands population displays no intermediacy in crossband numbers, crossband width, nor ventral patterns between *L. g. getula* and *L. g. floridana*, rather it represents the extreme for each of these characters and appears to be more closely related to *L. g. goini* and *L. g. getula* in the surrounding panhandle. Therefore, I believe that Blaney's (1977) hypothesis that the Apalachicola Lowlands populations are intergrades between *L. g. getula* and *L. g. floridana* is not supported.

The Apalachicola River drainage in the Florida panhandle is renowned for its historical biogeography and high diversity of endemic flora and fauna (James, 1961; Clewell, 1977; Means, 1977; Yerger, 1977; Ward, 1979; Judd, 1982; Gilbert, 1987; Coile, 1996; Chafin, 2000; Chaplin et al., 2000). The majority of these endemic species have been known for more than 150 years from the Apalachicola Bluffs and Ravines (Fig. 1-3), which were utilized by many species as refugia during the Pleistocene. Within the last few decades, many other endemic species have been recognized from the Apalachicola Lowlands (Table 3-10), nested between the Apalachicola Bluffs and Ravines to the north and the Gulf of Mexico to the south. Three ancient barrier islands have been identified within the Apalachicola Lowlands: two in the eastern Apalachicola

Lowlands ca. 26.5-30 km NE Apalachicola, and one in the southwestern Apalachicola Lowlands ca. 15 km NE Apalachicola. These ancient islands presently exist as elevated sand bodies, each being 11-15 km long and up to 10 m above sea level (Brenneman, 1957; Brenneman and Tanner, 1958). During high sea levels in the Pleistocene, it is speculated that these sand bodies would have been surrounded by saltwater and could have served as isolated areas allowing for the evolution of the Apalachicola Lowlands endemic species (Ward, 1979).

Table 3-1. Geographic variation in crossband numbers in *Lampropeltis getula* from Florida. Data are given for each of the six areas defined in Fig. 2. Areas 1, 2 and 3 are further separated by latitude. Males (M) and females (F) were treated separately within only the eastern Apalachicola Lowlands due to a higher frequency of males exhibiting a non- banded phenotype.

	Crossbands				
Area	Mean	S.E.	Range		n
6 = E. Apalachicola Lowlands	9.6 = M	0.82	1 – 23		65
	16.0 = F	1.31	1 – 25		26
5 = W. Apalachicola Lowlands	18.0	0.97	1 – 24		45
4 = N. Peninsula and Panhandle	22.6	0.47	14 – 31		174
3 = N. Peninsula	34.0	0.50			206
30° 50’ N Latitude	24.8	1.68	18 – 28	n = 19	
30° 00’ N Latitude	40.6	2.57	21 – 62	n = 17	
29° 50’ N Latitude	29.9	0.89	19 – 63	n = 54	
29° 00’ N Latitude	29.4	1.26	24 – 46	n = 32	
28° 50’ N Latitude	40.3	1.68	32 – 50	n = 13	
28° 00’ N Latitude	38.4	0.74	29 – 48	n = 71	
2 = S. and C. Peninsula	53.0	0.50			175
29° 00’ N Latitude	52.2	3.15	45 – 60	n = 4	
28° 50’ N Latitude	53.6	1.48	40 – 70	n = 19	
28° 00’ N Latitude	49.0	2.10	44 – 56	n = 9	
27° 50’ N Latitude	56.2	1.26	44 – 78	n = 25	
27° 00’ N Latitude	51.5	1.15	35 – 65	n = 30	
26° 50’ N Latitude	53.5	1.08	41 – 65	n = 34	
26° 00’ N Latitude	52.7	0.85	42 – 66	n = 54	
1 = Extreme S. Peninsula					
25° 50’ N Latitude	54.7	0.72	44 – 72		76
Total					767

Table 3-2. Geographic variation in crossband width in *Lampropeltis getula* from Florida. Arrangement and abbreviations as in Table 3-1.

	Crossband Width				
Area	Mean	S.E.	Range		n
6 = E. Apalachicola Lowlands	101.0 = M	4.09	2.5 – 200		51
	33.7 = F	6.57	2.5 – 200		26
5 = W. Apalachicola Lowlands	19.1	5.06	1.5 – 200		49
4 = N. Peninsula and Panhandle	2.2	2.50	1.5 – 8		189
3 = N. Peninsula	1.7	2.73	1.5 – 2.5		189
30° 50’ N Latitude	1.7	0.15	1.5 – 2.5	n = 13	
30° 00’ N Latitude	1.6	0.08	1.5 – 2	n = 9	
29° 50’ N Latitude	1.5	0.02	1.5 – 2	n = 53	
29° 00’ N Latitude	1.6	0.04	1.5 – 2.5	n = 32	
28° 50’ N Latitude	1.5	0.00	1.5	n = 10	
28° 00’ N Latitude	1.5	0.02	1.5 – 2.5	n = 72	
2 = S. and C. Peninsula	1.5	0.00	1.5		170
29° 00’ N Latitude	1.5	0.00	1.5	n = 4	
28° 50’ N Latitude	1.5	0.00	1.5	n = 20	
28° 00’ N Latitude	1.5	0.00	1.5	n = 9	
27° 50’ N Latitude	1.5	0.00	1.5	n = 24	
27° 00’ N Latitude	1.5	0.00	1.5	n = 24	
26° 50’ N Latitude	1.5	0.00	1.5	n = 34	
26° 00’ N Latitude	1.5	0.00	1.5	n = 55	
1 = Extreme S. Peninsula	1.5	0.00	1.5		
25° 50’ N Latitude	1.5	0.00	1.5		83
Total					757

Table 3-3. Geographic variation in ventral scales in *Lampropeltis getula* from Florida. Arrangement as in Table 1.

	Ventral Scales			
Area	Mean	S.E.	Range	n
6 = E. Apalachicola Lowlands	212.7	0.47	206 – 222	60
5 = W. Apalachicola Lowlands	211.7	0.09	208 – 217	15
4 = N. Peninsula and Panhandle	216.1	0.29	208 – 225	153
3 = N. Peninsula	216.8	0.28	204 – 231	169
30° 50’ N Latitude	216.4	1.03	213 – 220	n = 4
30° 00’ N Latitude	218.6	1.52	216 – 222	n = 8
29° 50’ N Latitude	217.8	0.52	209 – 231	n = 51
29° 00’ N Latitude	216.4	0.76	208 – 223	n = 32
28° 50’ N Latitude	216.2	1.00	204 – 223	n = 12
28° 00’ N Latitude	216.3	0.47	208 – 225	n = 62
2 = S. and C. Peninsula	216.0	0.29	206 – 227	164
29° 00’ N Latitude	216.0	2.64	213 – 219	n = 2
28° 50’ N Latitude	216.4	0.90	212 – 222	n = 19
28° 00’ N Latitude	214.5	1.24	208 – 219	n = 9
27° 50’ N Latitude	216.8	0.74	209 – 225	n = 25
27° 00’ N Latitude	216.0	0.78	207 – 227	n = 23
26° 50’ N Latitude	217.8	0.65	211 – 226	n = 33
26° 00’ N Latitude	214.6	0.51	206 – 225	n = 53
1 = Extreme S. Peninsula				
25° 50’ N Latitude	216.1	0.42	210 – 225	76
Total				637

Table 3-4. Geographic variation in subcaudal scales in *Lampropeltis getula* from Florida. Arrangement and abbreviations as in Table 1.

	Subcaudal Scales				
Area	Mean	S.E.	Range		n
6 = E. Apalachicola Lowlands	M: 50.6	0.43	47 – 53		31
	F: 45.5	0.59	42 – 53		17
5 = W. Apalachicola Lowlands	M: 51.2	0.73	49 – 55		11
	F: 46.6	1.41	45 – 48		2
4 = N. Peninsula and Panhandle	M: 51.7	0.29	47 – 57		61
	F: 45.4	0.40	41 – 50		36
3 = N. Peninsula	M: 51.4	0.32	45 – 59		65
	F: 45.6	0.30	41 – 55		63
30° 50’ N Latitude	M: 49.6	0.66	49 – 51	n = 3	
	F: 45.5	0.50	45 – 46	n = 2	
30° 00’ N Latitude	M: 52.0	3.00	49 – 55	n = 2	
	F: 44.4	0.57	43 – 45	n = 3	
29° 50’ N Latitude	M: 51.1	0.45	47 – 54	n = 15	
	F: 45.5	0.95	41 – 55	n = 16	
29° 00’ N Latitude	M: 51.6	0.47	48 – 54	n = 16	
	F: 46.2	0.96	43 – 48	n = 5	
28° 50’ N Latitude	M: 50.0	0.70	49 – 52	n = 4	
	F: 45.8	1.46	42 – 50	n = 5	
28° 00’ N Latitude	M: 51.9	0.62	45 – 59	n = 25	
	F: 45.4	0.36	42 – 49	n = 32	
2 = S. and C. Peninsula	M: 51.3	0.26	46 – 58		75
	F: 45.8	0.30	40 – 53		63
29° 00’ N Latitude	M: 51	0.00	51	n = 1	
	F: 47	0.00	47	n = 1	
28° 50’ N Latitude	M: 51.4	0.80	48 – 56	n = 10	
	F: 46.0	0.82	42 – 49	n = 8	
28° 00’ N Latitude	M: 52.4	0.92	50 – 55	n = 5	
	F: 46.5	0.64	45 – 48	n = 4	
27° 50’ N Latitude	M: 52.0	0.69	47 – 56	n = 14	
	F: 46.4	0.52	44 – 49	n = 9	
27° 00’ N Latitude	M: 51.7	0.63	48 – 58	n = 14	
	F: 46.2	0.54	44 – 50	n = 9	
26° 50’ N Latitude	M: 50.6	0.65	47 – 55	n = 18	
	F: 45.5	0.66	40 – 48	n = 14	
26° 00’ N Latitude	M: 51.2	0.58	46 – 57	n = 23	
	F: 45.6	0.84	41 – 53	n = 18	
1 = Extreme S. Peninsula					
25° 50’ N Latitude	M: 52.9	0.45	47 – 57		39
	F: 47.0	0.61	40 - 52		29
Total					492

Table 3-5. Geographic variation in dorsal scales rows in *Lampropeltis getula* from Florida. Arrangement as in Table 1.

	Dorsal Scale Rows					
Area	21	23	24	25		n
6 = E. Apalachicola Lowlands	58 (100%)	0 (0.00%)	0 (0.00%)	0 (0.00%)		58
5 = W. Apalachicola Lowlands	15 (100%)	0 (0.00%)	0 (0.00%)	0 (0.00%)		15
4 = N. Peninsula and Panhandle	128 (80.0%)	32 (20.0%)	0 (0.00%)	0 (0.00%)		160
3 = N. Peninsula	28 (15.4%)	152 (83.9%)	1 (0.55%)	0 (0.00%)		181
30° 50’ N Latitude	8 (57.1%)	6 (42.8%)	0 (0.00%)	0 (0.00%)	n = 14	
30° 00’ N Latitude	1 (11.1%)	8 (88.8%)	0 (0.00%)	0 (0.00%)	n = 9	
29° 50’ N Latitude	11 (22.0%)	39 (78.0%)	0 (0.00%)	0 (0.00%)	n = 50	
29° 00’ N Latitude	6 (18.1%)	27 (81.8%)	0 (0.00%)	0 (0.00%)	n = 33	
28° 50’ N Latitude	0 (0.00%)	12 (100%)	0 (0.00%)	0 (0.00%)	n = 12	
28° 00’ N Latitude	2 (3.17%)	60 (95.2%)	1 (1.58%)	0 (0.00%)	n = 63	
2 = S. and C. Peninsula	10 (5.91%)	159 (94.0%)	0 (0.00%)	0 (0.00%)		169
29° 00’ N Latitude	0 (0.00%)	4 (100%)	0 (0.00%)	0 (0.00%)	n = 4	
28° 50’ N Latitude	0 (0.00%)	20 (100%)	0 (0.00%)	0 (0.00%)	n = 20	
28° 00’ N Latitude	0 (0.00%)	9 (100%)	0 (0.00%)	0 (0.00%)	n = 9	
27° 50’ N Latitude	3 (12.0%)	22 (88.0%)	0 (0.00%)	0 (0.00%)	n =25	
27° 00’ N Latitude	2 (8.30%)	22 (91.6%)	0 (0.00%)	0 (0.00%)	n =24	
26° 50’ N Latitude	1 (3.03%)	32 (96.9%)	0 (0.00%)	0 (0.00%)	n =33	
26° 00’ N Latitude	4 (7.40%)	50 (92.5%)	0 (0.00%)	0 (0.00%)	n =54	
1 = Extreme S. Peninsula						
25° 50’ N Latitude	14 (18.4%)	61 (80.2%)	0 (0.00%)	1 (1.30%)		76
Total						659

Table 3-6. Geographic variation in the total number of supralabial scales in *Lampropeltis getula* from Florida. Arrangement as in Table 1.

	Supralabials				
Area	14	15	16		n
6 = E. Apalachicola Lowlands	46 (100%)	0 (0.00%)	0 (0.00%)		46
5 = W. Apalachicola Lowlands	10 (100%)	0 (0.00%)	0 (0.00%)		10
4 = N. Peninsula and Panhandle	89 (94.6%)	5 (5.31%)	0 (0.00%)		94
3 = N. Peninsula	172 (97.1%)	5 (2.82%)	0 (0.00%)		177
30° 50’ N Latitude	14 (100%)	0 (0.00%)	0 (0.00%)	n = 14	
30° 00’ N Latitude	6 (100%)	0 (0.00%)	0 (0.00%)	n = 6	
29° 50’ N Latitude	48 (97.9%)	1 (2.04%)	0 (0.00%)	n = 49	
29° 00’ N Latitude	32 (100%)	0 (0.00%)	0 (0.00%)	n = 32	
28° 50’ N Latitude	9 (90.0%)	1 (10.0%)	0 (0.00%)	n = 10	
28° 00’ N Latitude	63 (95.4%)	3 (4.54%)	0 (0.00%)	n = 66	
2 = S. and C. Peninsula	148 (94.8%)	7 (4.48%)	1 (0.64%)		156
29° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	n = 0	
28° 50’ N Latitude	16 (88.8%)	1 (5.55%)	1 (5.55%)	n = 18	
28° 00’ N Latitude	8 (88.8%)	1 (11.1%)	0 (0.00%)	n = 9	
27° 50’ N Latitude	24 (100%)	0 (0.00%)	0 (0.00%)	n = 24	
27° 00’ N Latitude	21 (87.5%)	3 (12.5%)	0 (0.00%)	n = 24	
26° 50’ N Latitude	30 (96.7%)	1 (3.22%)	0 (0.00%)	n = 31	
26° 00’ N Latitude	49 (98.0%)	1 (2.00%)	0 (0.00%)	n = 50	
1 = Extreme S. Peninsula					
25° 50’ N Latitude	64 (90.1%)	5 (7.06%)	2 (2.84%)		71
Total					554

Table 3-7. Geographic variation in the total number of infralabial scales in *Lampropeltis getula* from Florida. Arrangement and abbreviations as in Table 1.

	Infralabials							
Area	16	17	18	19	20	21		n
6 = E. Apalachicola Lowlands	0 (0.00%)	0 (0.00%)	18 (40.0%)	12 (26.6%)	15 (33.3%)	0 (0.00%)		45
5 = W. Apalachicola Lowlands	0 (0.00%)	0 (0.00%)	7 (70.0%)	3 (30.0%)	0 (0.00%)	0 (0.00%)		10
4 = N. Peninsula and Panhandle	0 (0.00%)	1 (1.07%)	47 (50.5%)	25 (26.8%)	19 (20.4%)	1 (1.07%)		93
3 = N. Peninsula	1 (0.57%)	6 (3.44%)	87 (50.0%)	43 (24.7%)	31 (17.8%)	6 (3.44%)		174
30° 50’ N Latitude	0 (0.00%)	0 (0.00%)	7 (50.0%)	2 (14.2%)	2 (14.2%)	3 (21.4%)	n = 14	
30° 00’ N Latitude	0 (0.00%)	0 (0.00%)	1 (14.2%)	2 (28.5%)	3 (42.8%)	1 (14.2%)	n = 7	
29° 50’ N Latitude	1 (2.21%)	2 (4.25%)	19 (40.4%)	13 (27.6%)	11 (23.4%)	1 (2.21%)	n = 47	
29° 00’ N Latitude	0 (0.00%)	1 (3.33%)	13 (43.3%)	10 (33.3%)	6 (20.0%)	0 (0.00%)	n = 30	
28° 50’ N Latitude	0 (0.00%)	0 (0.00%)	4 (40.0%)	3 (30.0%)	3 (30.0%)	0 (0.00%)	n = 10	
28° 00’ N Latitude	0 (0.00%)	3 (4.54%)	43 (65.1%)	13 (19.6%)	6 (9.09%)	1 (1.51%)	n = 66	
2 = S. and C. Peninsula	0 (0.00%)	1 (6.49%)	83 (53.8%)	34 (22.0%)	33 (21.4%)	3 (1.94%)		154
29° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	n = 0	
28° 50’ N Latitude	0 (0.00%)	0 (0.00%)	11 (61.1%)	1 (5.55%)	5 (27.7%)	1 (5.55%)	n = 18	
28° 00’ N Latitude	0 (0.00%)	0 (0.00%)	6 (75.0%)	2 (25.0%)	0 (0.00%)	0 (0.00%)	n = 8	
27° 50’ N Latitude	0 (0.00%)	0 (0.00%)	11 (45.8%)	9 (37.5%)	3 (12.5%)	1 (4.16%)	n = 24	
27° 00’ N Latitude	0 (0.00%)	0 (0.00%)	7 (30.4%)	6 (26.0%)	9 (39.1%)	1 (4.34%)	n = 23	
26° 50’ N Latitude	0 (0.00%)	1 (3.22%)	12 (38.7%)	7 (22.5%)	11 (35.4%)	0 (0.00%)	n = 31	
26° 00’ N Latitude	0 (0.00%)	0 (0.00%)	36 (72.0%)	9 (18.0%)	5 (10.0%)	0 (0.00%)	n = 50	
1 = Extreme S. Peninsula								
25° 50’ N Latitude	0 (0.00%)	0 (0.00%)	42 (60.0%)	11 (15.7%)	16 (22.8%)	1 (1.42%)		70
Total								546

Table 3-8. Geographic variation in the arrangement of temporal scales in *Lampropeltis getula* from Florida. Counts are from one head-side and are not always symmetrical. Arrangement as in Table 1.

	Temporal Scales					
Area	1+1+3	1+2+4	1+3+3	1+3+4	2+2+3	2+2+4
6 = E. Apalachicola Lowlands	0 (0.00%)	0 (0.00%)	1 (1.09%)	1 (1.09%)	4 (4.39%)	4 (4.39%)
5 = W. Apalachicola Lowlands	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
4 = N. Peninsula and Panhandle	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	5 (2.85%)	3 (1.71%)
3 = N. Peninsula	3 (0.86%)	1 (0.28%)	0 (0.00%)	0 (0.00%)	1 (0.28%)	7 (2.01%)
30° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	3 (10.3%)
30° 00’ N Latitude	1 (8.33%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
29° 50’ N Latitude	0 (0.00%)	1 (1.03%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	1 (1.03%)
29° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	2 (3.63%)
28° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
28° 00’ N Latitude	2 (1.55%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	1 (0.77%)	1 (0.77%)
2 = S. and C. Peninsula	0 (0.00%)	1 (0.32%)	0 (0.00%)	1 (0.32%)	0 (0.00%)	3 (0.97%)
29° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
28° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
28° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
27° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	2 (5.55%)
27° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)
26° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	1 (1.63%)
26° 00’ N Latitude	0 (0.00%)	1 (1.01%)	0 (0.00%)	1 (1.01%)	0 (0.00%)	0 (0.00%)
1 = Extreme S. Peninsula						
25° 50’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	0 (0.00%)	2 (1.41%)
	3	2	1	2	10	19

Table 3-9. Geographic variation in the arrangement of pre-ocular and post-ocular scales in *Lampropeltis getula* from Florida. Counts are from one head-side and are not always symmetrical. Arrangement as in Table 1.

	Ocular Scales				
Area	1+2	1+3	2+3		n
6 = E. Apalachicola Lowlands	92 (100%)	0 (0.00%)	0 (0.00%)		92
5 = W. Apalachicola Lowlands	20 (100%)	0 (0.00%)	0 (0.00%)		20
4 = N. Peninsula and Panhandle	192 (100%)	0 (0.00%)	0 (0.00%)		168
3 = N. Peninsula	339 (100%)	0 (0.00%)	0 (0.00%)		339
30° 50’ N Latitude	14 (100%)	0 (0.00%)	0 (0.00%)	n = 14	
30° 00’ N Latitude	12 (100%)	0 (0.00%)	0 (0.00%)	n = 12	
29° 50’ N Latitude	97 (100%)	0 (0.00%)	0 (0.00%)	n = 97	
29° 00’ N Latitude	64 (100%)	0 (0.00%)	0 (0.00%)	n = 64	
28° 50’ N Latitude	20 (100%)	0 (0.00%)	0 (0.00%)	n = 20	
28° 00’ N Latitude	132 (100%)	0 (0.00%)	0 (0.00%)	n = 132	
2 = S. and C. Peninsula	314 (100%)	0 (0.00%)	0 (0.00%)		314
29° 00’ N Latitude	0 (0.00%)	0 (0.00%)	0 (0.00%)	n = 0	
28° 50’ N Latitude	36 (100%)	0 (0.00%)	0 (0.00%)	n = 36	
28° 00’ N Latitude	18 (100%)	0 (0.00%)	0 (0.00%)	n = 18	
27° 50’ N Latitude	48 (100%)	0 (0.00%)	0 (0.00%)	n = 48	
27° 00’ N Latitude	48 (100%)	0 (0.00%)	0 (0.00%)	n = 48	
26° 50’ N Latitude	62 (100%)	0 (0.00%)	0 (0.00%)	n = 62	
26° 00’ N Latitude	102 (100%)	0 (0.00%)	0 (0.00%)	n = 102	
1 = Extreme S. Peninsula					
30° 50’ N Latitude	102 (96.2%)	2 (1.88%)	2 (1.88%)		106
Total					1039

Table 3-10. List of endemic (E) and relict (R) plants and animals whose geographic distribution is confined to or centered on the Apalachicola Lowlands.

Species	Endemic or Relict	Confined	Centered
Angiosperms			
Southern milkweed (*Asclepias viridula*)	R		X
Pinewoods aster (*Aster spinulosus*)	E	X	
Scare-weed (*Baptisia simplicifolia*)	E	X	
Apalachicola rosemary (*Conradina glabra*)	E	X	
Chipola dye-flower (*Coreopsis integrifolia*)	R		X
Florida waxweed (*Cuphea aspera*)	E	X	
Dark-headed hatpins (*Eriocaulon nigrobracteatum*)	E	X	
Telephus spurge (*Euphorbia telephioides*)	E	X	
Harper's beauty (*Harperocallis flava*)	E	X	
Henry's spiderlily (*Hymenocallis henryae*)	E		X
Thick-leaved water willow (*Justicia crassifolia*)	E		X
Godfrey's blazing star (*Liatris provincialis*)	E	X	
West's flax (*Linum westii*)	R		X
White birds-in-a-nest (*Macbridea alba*)	E		X
Ashe's magnolia (*Magnolia ashei*)	R		X
Florida beargrass (*Nolina atopocarpa*)	E		X
Giant water dropwort (*Oxypolis filiformes greenmanii*)	E	X	
Carolina grass of parnassus (*Parnassia caroliniana*)	R	X	
Large flowered grass of parnassus (*Parnassia grandifolia*)	R	X	
Narrow-leaved Phoebanthus (*Phoebanthus tenuifolia*)	E	X	
Apalachicola Dragonhead (*Physostegia godfreyi*)	E		X
Violet butterwort (*Pinguicula ionantha*)	E		X
Chapman's butterwort (*Pinguicula planifolia*)	E		X
Small-flowered meadow beauty (*Rhexia parviflora*)	E		X

Table 3-10.—Continued.

	Species	Endemic or Relict	Confined	Centered
	Chapman's rhododendron (*Rhododendron chapmanii*)	R		X
	St. John's black-eyed Susan (*Rudbeckia nitida*)	R		X
	Florida skullcap (*Scutellaria floridana*)	E	X	
	Mock pennyroyal (*Stachyedeoma graveolens*)	E		X
	Chapman's crownbeard (*Verbesina chapmanii*)	E		X
	Quillwort yellow-eyed grass (*Xyris isoetifolia*)	E		X
Serpentes				
	Brown-chinned racer (*Coluber constrictor helvigularis*)	E		X
	Apalachicola Lowlands kingsnake (*Lampropeltis getula* ssp.)	E	X	

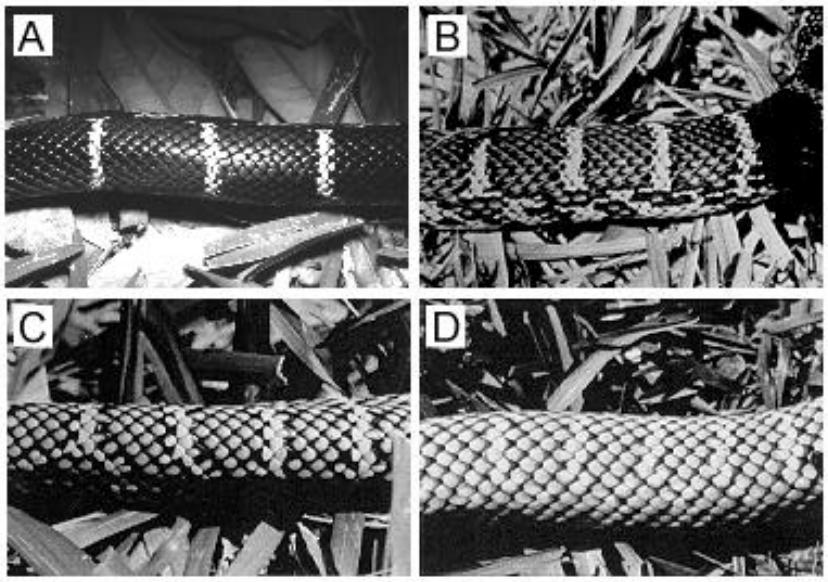

Fig. 3-1. Note interbands (areas between light crossbands) only. Interband scale rating system on adult *Lampropeltis getula* (modified after Krysko, 1995), A = 0% lightening (typical of *L. g. getula*), B = up to 25% of the intensity of the crossbands (typical of *L. g. goini* and *L. g. floridana*), C = 25–75% of the intensity of the crossbands (typical of *L. g. floridana* and Apalachicola Lowlands populations), D = 75–100% of the intensity of the crossbands (typical of *L. g. brooksi* and Apalachicola Lowlands populations).

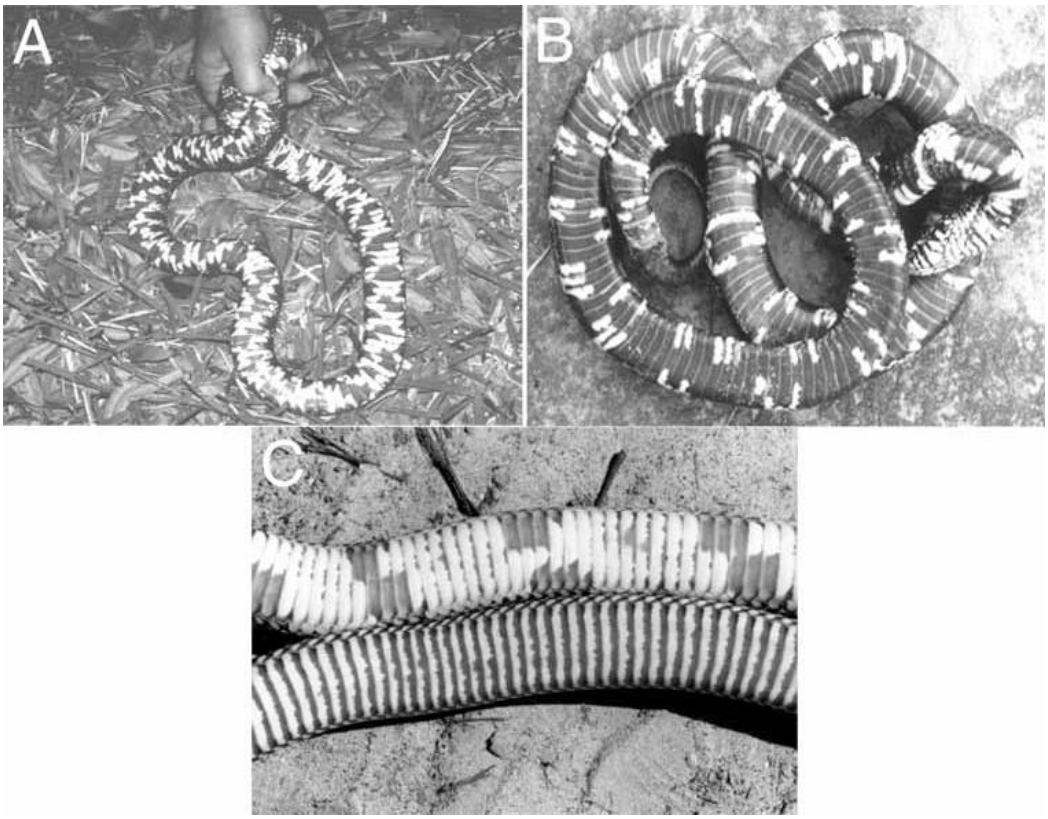

Fig. 3-2. Ventral patterns of *Lampropeltis getula*, A = tight checkerboard where the alternating light and dark pigment is tightly compressed, typical of *L. g. floridana*; B = loose checkerboard where the alternating light and dark pigment is loosely compressed, typical of *L. g. getula*; C = bicolored where light pigment is confined to the anterior portion and the dark pigment is confined to the posterior portion of each ventral scale (bottom), loose checkerboard with interspersed bicolored scales (top).

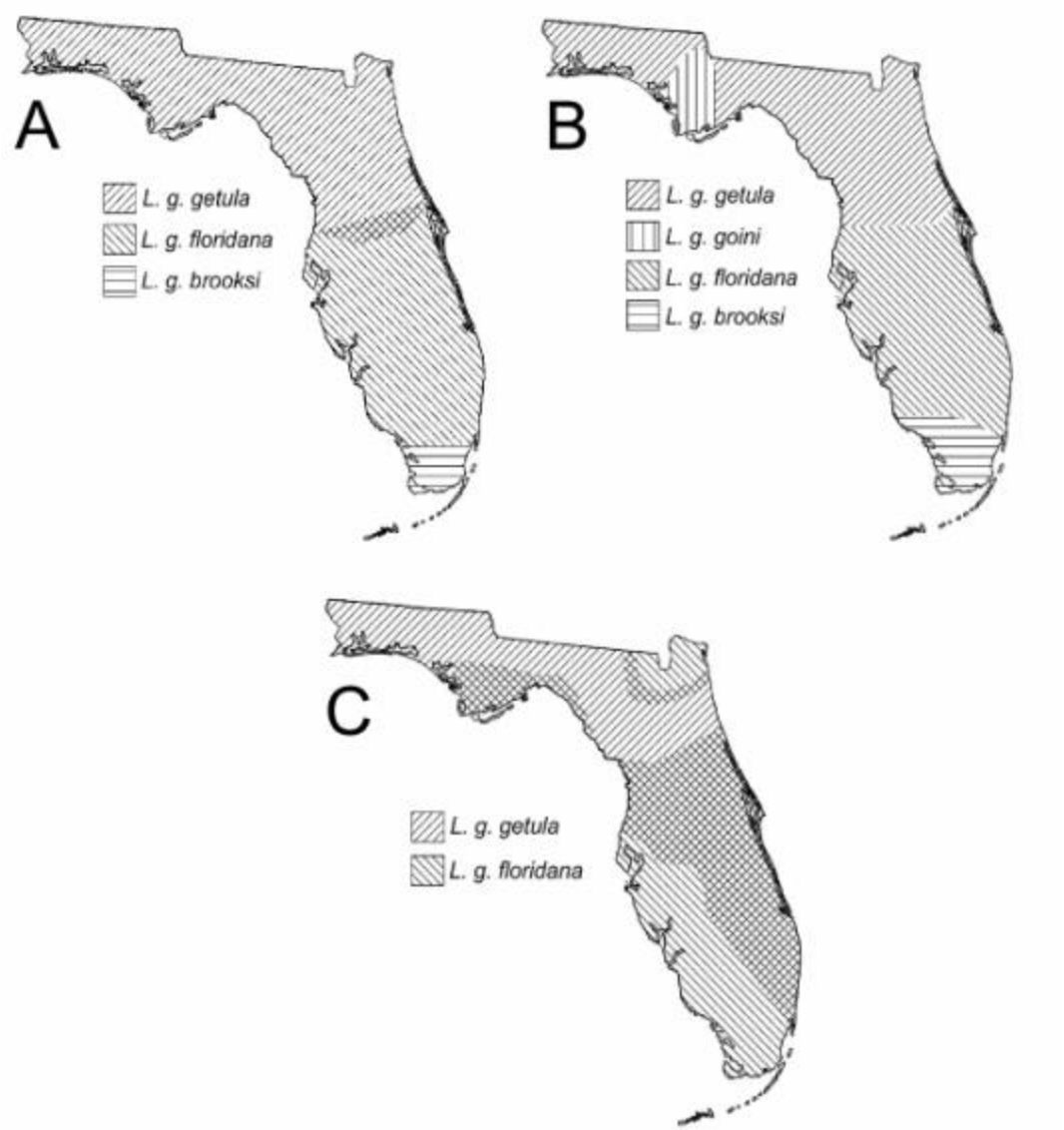

Fig. 3-3. Distribution hypotheses of *Lampropeltis getula* subspecies in Florida after A = Blanchard (1921), B = Conant (1975), C = Blaney (1977).

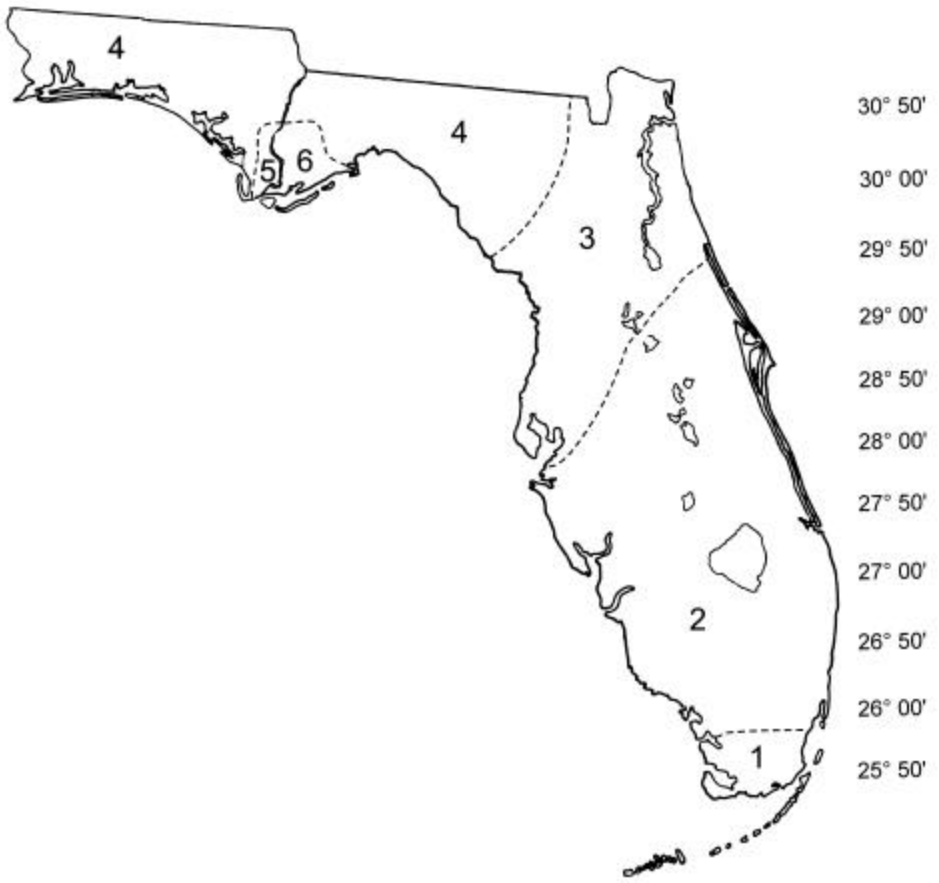

Fig. 3-4. Six areas in Florida used to analyze geographic variation of *Lampropeltis getula*. 1 = southern peninsula, 2 = southern and central peninsula, 3 = central and northern peninsula, 4 = northern peninsula and panhandle, 5 = western Apalachicola Lowlands, 6 = eastern Apalachicola Lowlands. Degrees latitude are shown in the column on right.

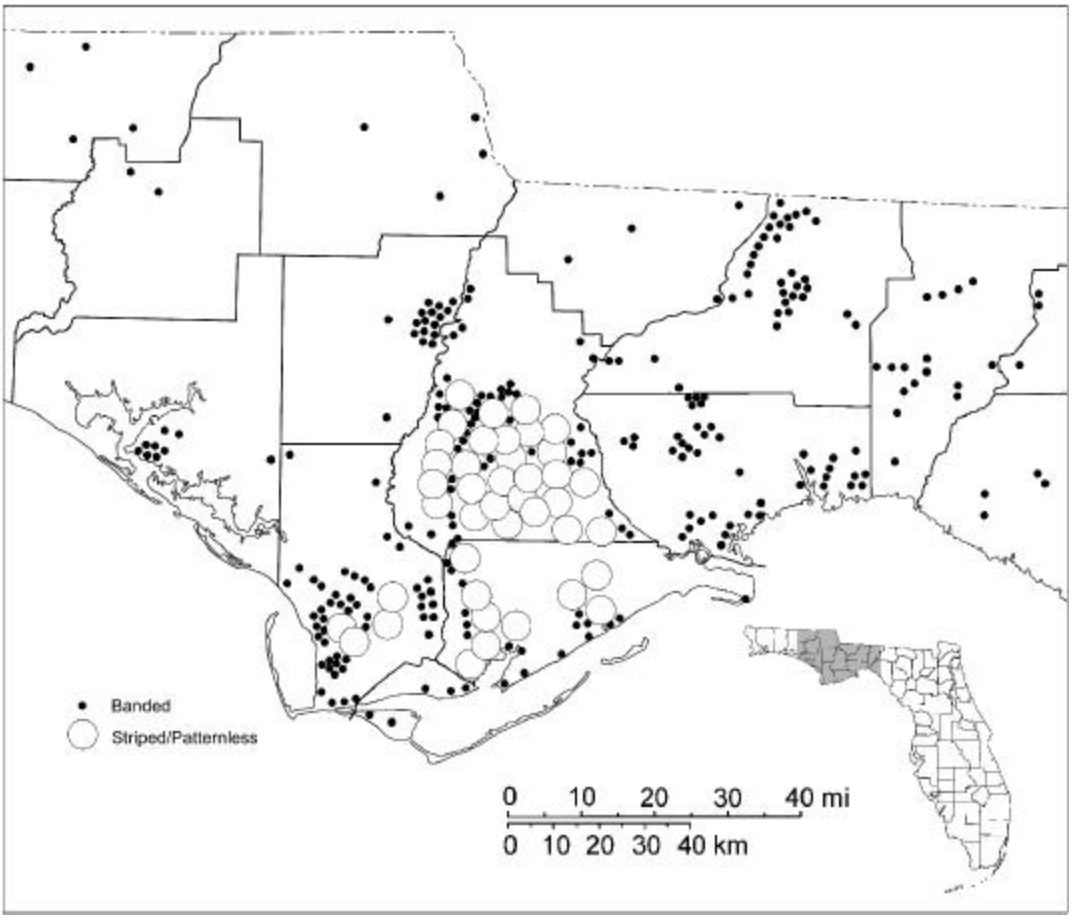

Fig. 3-5. Geographic distribution of non-banded (striped and patternless) phenotypes of *Lampropeltis getula* across the Apalachicola region of Florida.

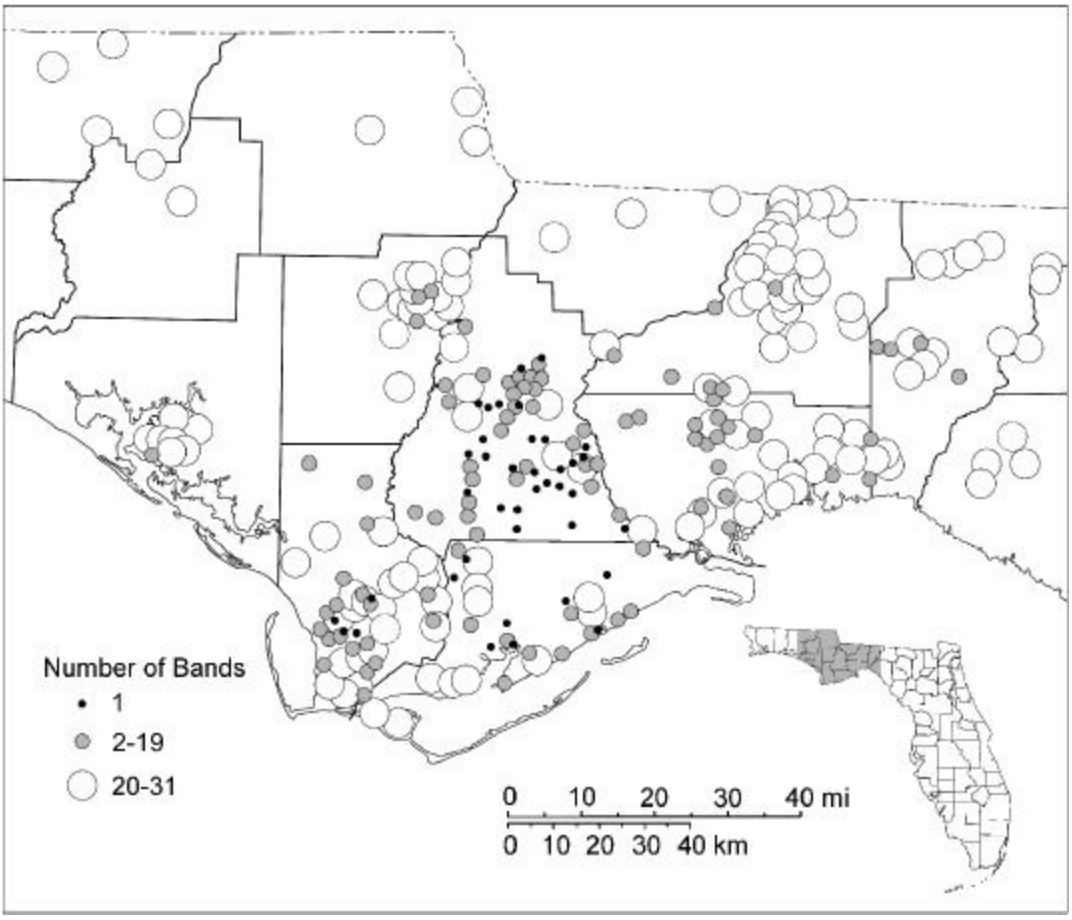

Fig. 3-6. Geographic variation in the number of light crossbands in *Lampropeltis getula* across Apalachicola region of Florida.

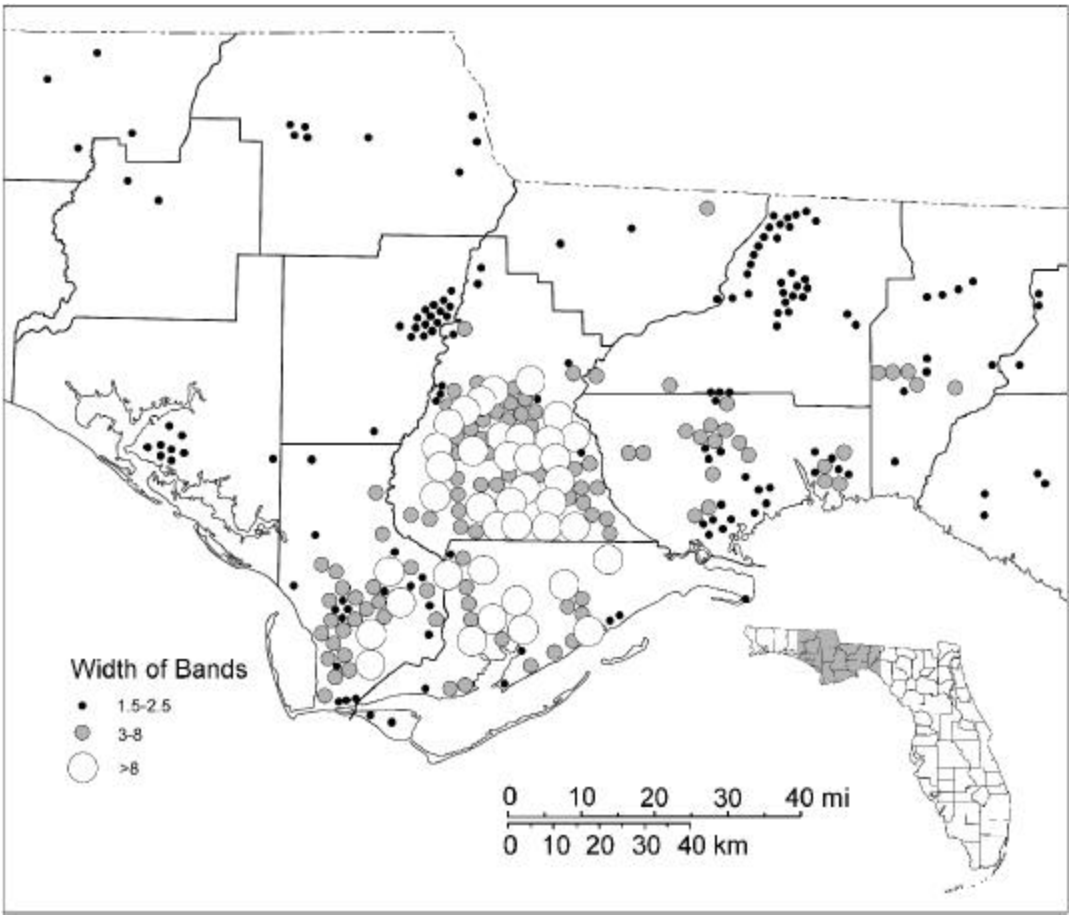

Fig. 3-7. Geographic variation in the width of light crossbands in *Lampropeltis getula* across the Apalachicola region of Florida.

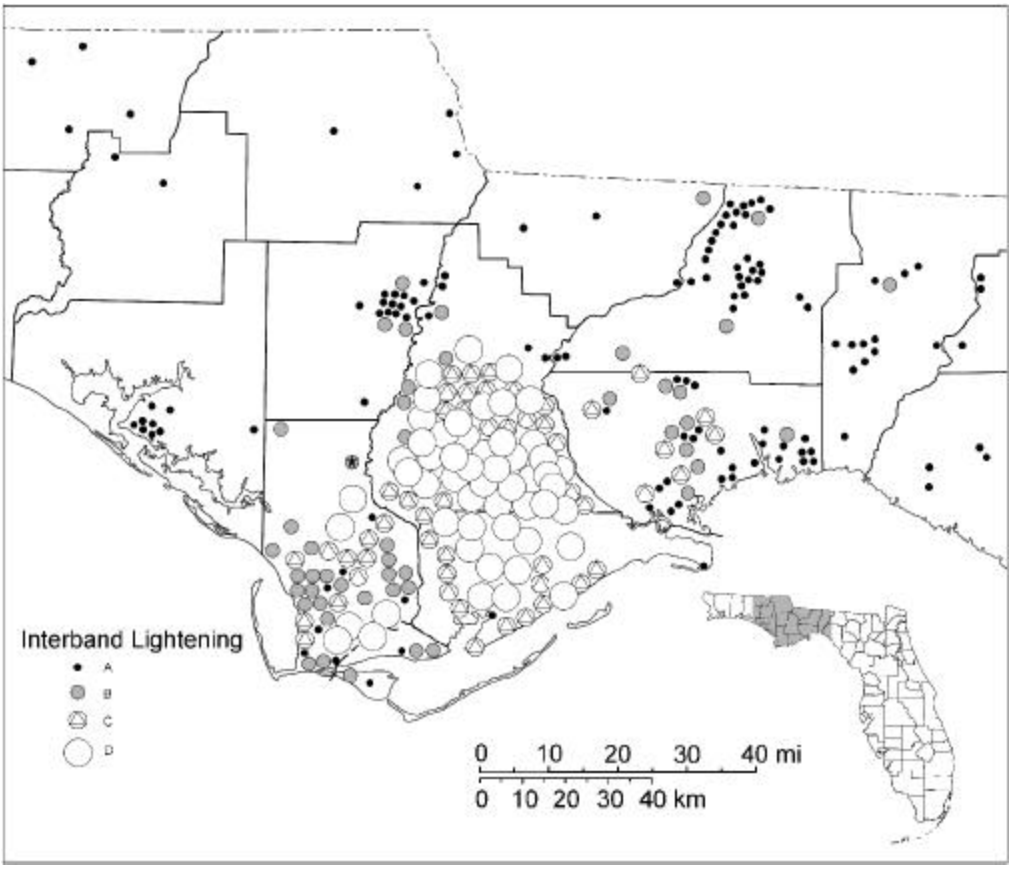

Fig. 3-8. Geographic variation in the degree of ontogenetic interband lightening in *Lampropeltis getula* across the Apalachicola region of Florida. A = 0% lightening typical of *L. g. getula*, B = up to 25% of the intensity of the crossbands typical of *L. g. goini*, C = 25–75% of the intensity of the crossbands, D = 75–100% of the intensity of the crossbands. Non-banded (striped and patternless) individuals were as D.

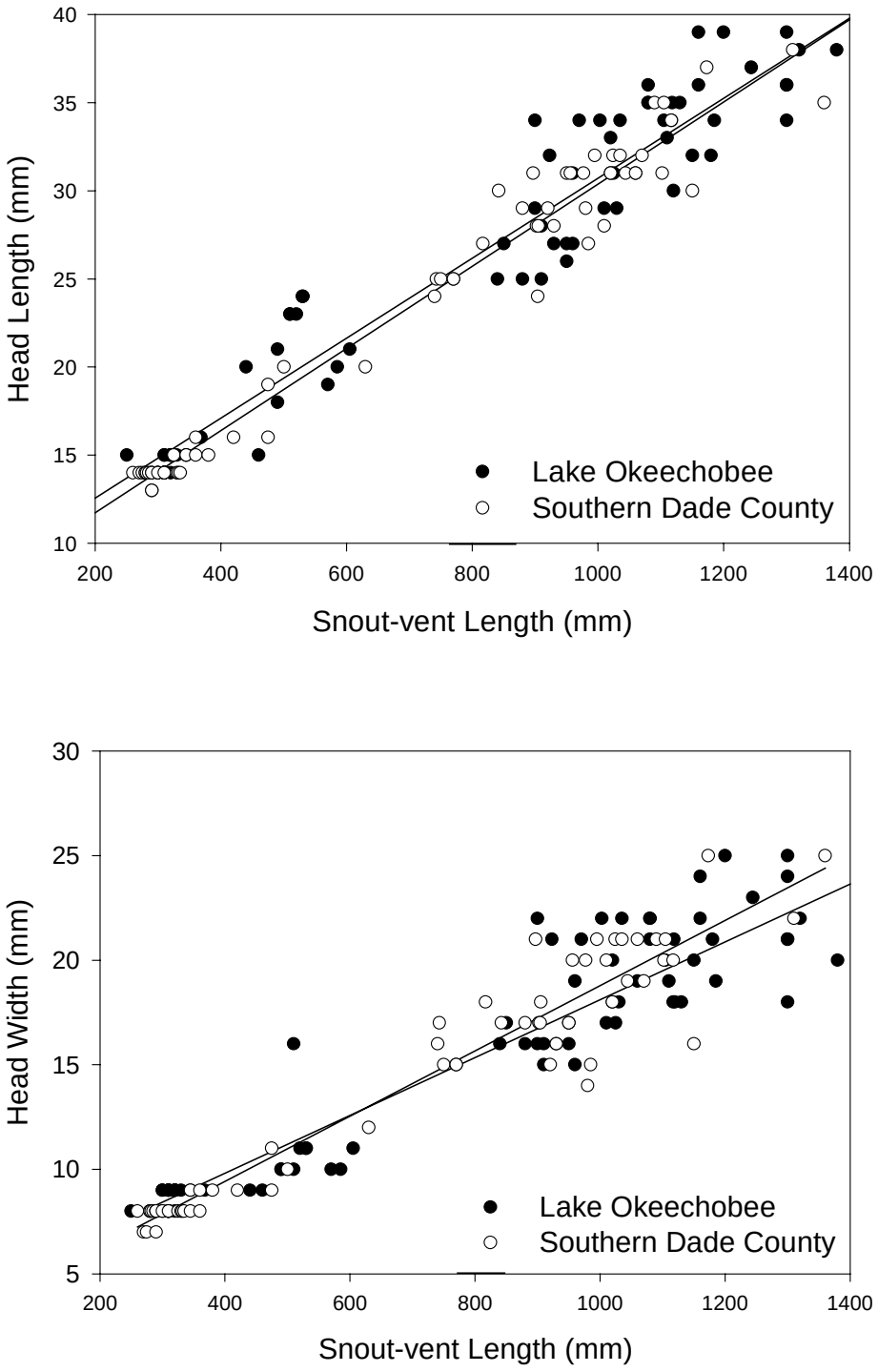

Fig. 3-9. A = Head Length/SVL and B = Head Width/SVL in *Lampropeltis getula* from southern Florida, modified after Krysko (1995).

CHAPTER 4
MORPHOLOGICAL SYSTEMATICS OF KINGSNAKES (*Lampropeltis getula)*

Materials and Methods

I examined color pattern and external morphology from 52 individuals of the *L. getula* complex (Table 4-1): 1) 10 from the Florida peninsula as defined by Enge (1994), 2) 9 from the eastern Apalachicola Lowlands in panhandle Florida as defined by Means (1977), 3) 13 from the surrounding panhandle, 4) 12 from the Atlantic U.S. border, and 5) 1-2 individuals of each remaining subspecies of the *L. getula* complex west to northern Mexico and California. In order to facilitate comparison of morphological and molecular phylogenetic results, most of these individuals were the same as those used in DNA analyses. For some missing localities replacement specimens with a similar morphology from and nearby geographic area were used.

Morphological Characters

Supralabial, infralabial, loreal, temporal, ocular and ventral scales were reviewed, but determined to be uninformative and omitted from the analyses. Twelve variable and potentially phylogenetically informative characters (Table 4-2) were used in cladistic analyses and plesiomorphic (0) and apomorphic (1-4) conditions (Tables 4-2, 4-3) were determined using western and midwestern individuals as functional outgroups (Maddison et al., 1984). Because not every individual could be examined throughout its entire life, coding for juvenile and adult characters was inferred from other specimens (juvenile or

adult) collected in close geographic proximity. Characters are listed and discussed below. When ordering of characters is used in the analysis, it follows the progression stated for each character.

Dorsal scale rows (DSR). Maximum number at midbody (Fig. 4-1). Examined individuals had either 25, 23, or 21 (Table 4-2).

Ventral pattern as juvenile. Primary ventral patterns are illustrated in Fig. 4-2. The ventral pattern is typically A = ringed in extreme western North America or B = light with dark lateral margins in the San Diego region of California (A and B = *L. g. californiae*), D = tight checkerboard south into northern Mexico and east to peninsular Florida (= *L. g. nigrita, L. g. splendida, L. g. holbrooki, L. g. nigra, and L. g. floridana*), E = loose checkerboard north along the Atlantic U.S. border (*L. g. getula*), G = bicolored in the eastern Apalachicola Lowlands of Florida, and F = loose checkerboard with interspersed bicolored scales in the eastern Apalachicola Lowlands and surrounding Florida panhandle. There is a progression from A and B to D to E to G (Table 4-2).

Ventral pattern as adult. Although the ventral pattern does not typically change ontogenetically, individuals from northern Mexico (= *L. g. nigrita*) gain dark pigment until becoming completely black (Fig. 4-2C). There may be considerable variation within a single clutch of eggs in *L. g. nigrita*, where some newborns might exhibit a tight checkerboard ventral pattern (Fig. 4-2D) like those of neighboring populations of *L. g. splendida*, while other siblings might exhibit a completely black venter (Fig. 4-2C). After only a few periods of ecdysis following hatching, all pattern remnants are usually lost. Because this evidence suggests that the ventral pattern may be genetically controlled ontogenetically and there appears to be a progression like that in the juvenile

stage described above, this character was treated as an ordered transformation series (Table 4-2).

Dorsal pattern as juvenile. Primary dorsal patterns are illustrated in Fig. 4-2. The dorsal pattern is typically A = ringed in extreme western North America or B = light striped in the San Diego region of California (A and B = *L. g. californiae*), D and E = narrow banded south into northern Mexico and east to the Atlantic U.S. border (= *L. g. nigrita, L. g. splendida, L. g. holbrooki, L. g. nigra, L. g. floridana, and L. g. getula*), F = wide banded in the eastern Apalachicola Lowlands and surrounding Florida panhandle, and dark striped (not illustrated), and G = patternless in the eastern Apalachicola Lowlands. See above for explanation regarding *L. g. nigrita* and introduction regarding dark striped eastern Apalachicola Lowlands. There is a progression from A and B to D and E to F to G (Table 4-2).

Ontogenetic dorsal pattern change. The dorsal pattern changes in certain geographic areas including the juvenile's 1) light bands becoming black (Fig. 4-2C) in northern Mexico (= *L.g. nigrita*) and in the midwestern U.S. on the western side of the Appalachian Mountains (= *L. g. nigra*), 2) black interbands becoming lightened laterally in the Texas area (= *L. g. splendida*), or 3) lightened over the entire dorsum east to Florida (= *L. g. holbrooki, L. g. floridana*). Individuals of *L. g. getula* from the Outer Banks, Dare Co., North Carolina, as well as individuals in the Apalachicola region of Florida, also undergo interband lightening over the dorsum.

Band or ring formation as juvenile. Formations include 1) ringed around body or light-striped in extreme western North America or light-striped in the San Diego region of California (Fig. 4-2A, B = *L. g. californiae*), 2) narrow bands that fork laterally

east to the Atlantic U.S. border (Fig. 4-2E = *L. g. splendida, L. g. nigrita, L. g holbrooki, L. g. nigra, L. g. floridana, and L. g. getula*) and 3) bands that fuse laterally and/or dorsally in the Apalachicola region of Florida (Fig. 4-2F, G). There is a progression from 1 to 2 to 3 (Table 4-2).

Placement of light pigment within band or ring scales as juvenile. Pigment is either A = located on the entire scale, B = centered, or C = anterior (Fig. 4-3). There is a progression from A to B to C (Table 4-2).

Placement of ontogenetically lightened pigment within dark interband or ring scales. There is either 1) no light pigment, or light pigment is 2) centered, or 3) anterior (Fig. 4-4). There is a progression from 1 to 2 to 3 (Table 4-2).

Red tipping of dorsal scales as juvenile. Although previously reported by Neill (1954) for only southern peninsular Florida populations, newborns from the entire eastern U.S. populations may exhibit reddish crossband scales. There may be considerable variation within a single clutch of eggs as different proportions of siblings may or may not exhibit this trait. It appears that the brightest red bands usually change ontogenetically into an off-white, beige, or dull light brown color (K. M. Enge and H. Sherman, pers. comm.). Bands without reddish scales usually remain brilliant white or yellow.

Number of light bands or rings as juvenile. On body starting one head-length posterior to the head and ending above the cloaca (Fig. 4-5). A = 0, B = 1, C = 16-34, and D = 44-65. Note that the light striped individual (San Diego, CA1) has no bands (Figs. 4-2B, 4-5A) and individuals from the eastern Apalachicola Lowlands are considered to have only one band (Fig. 4-5B, see Chapter 3 for explanation).

Fraction of light pigment within band or ring scales as juvenile. As a fraction, light pigment incorporates entire = 1.00, half = 0.50, or one-third = 0.33 of entire scale (Fig. 4-6).

Band or ring width as juvenile. Mean scale width (= # mid-dorsal scale rows) on body: A = 0, B = 0.33, C = 1.5-2, D = 2.5-8, E = 200 (Fig. 4-7). Character state delimitation of D is somewhat subjective because it incorporates a relatively wide range of values, however, this variation is found almost exclusively in the eastern Apalachicola Lowlands and surrounding region. Note that the light striped individual (San Diego, CA1) has no bands.

Cladistic Analyses

Relationships among individuals are investigated using the maximum-parsimony (MP) method using PAUP* (ver. 4.08b, Swofford, 2000). MP analyses were performed with heuristic search using 500 repetitions of random stepwise additions with subtree pruning and regrafting (SPR), with limits set to 25 trees (30 steps) per random addition replicate. Both unordered and ordered character analyses were performed (Table 4-2). Confidence limits for phylogenetic groupings in both approaches were assessed with bootstrapping (Felsenstein, 1985) with full heuristic search using 500 repetitions of random stepwise additions with SPR and limits set to 5 trees per random addition replicate. Nonparametric bootstrapping generally yields conservative measures of the probability that a group represents a true evolutionary clade (Zharkikh and Li, 1992; Hillis and Bull, 1993; Rodriguez-Robles et al., 1999c).

Results

Cladistic Analyses

MP analysis using unordered characters (Table 4-2) resulted in 69 most parsimonious trees of 44 steps (CI = 0.795, RI = 0.954) from 15 parsimony-informative characters. Strict and majority rule consensus trees were produced (Fig. 4-8). The midwestern/western and eastern U.S. samples form separate monophyletic groups. The eastern clade is further divided into three subclades. The strict consensus tree (Fig. 4-8) illustrates a primarily eastern Apalachicola Lowland subclade nested within a predominately Atlantic, SW Georgia and Panhandle sample subclade. Peninsular individuals are most closely related to the predominately Atlantic, SW Georgia and Panhandle subclade. A random representative of the 69 shortest trees was selected, illustrating the number of character differences between individuals and bootstrap support above 50% (Fig. 4-8). Major nodes are statistically supported: California individuals of the western clade (100%), midwest/western clade (87%) and eastern U.S. clade (63%). Most nodes within the eastern clade are less supported, with fewer character differences, illustrating their close relationships to each other. The primarily eastern Apalachicola Lowland samples exist within the only well supported subclade (85%). The MP tree demonstrates the relationships of the outgroups indicating that the midwestern/western clade is the sister group to the eastern clade rather than California individuals of the western clade (with 100% bootstrap support).

MP analysis using ordered characters (Table 4-2) resulted in 171 most parsimonious trees of 46 steps (CI = 0.761, RI = 0.952) from 15 parsimony-informative characters. Strict and majority rule consensus trees were created, which yield similar

results as the unordered MP analysis, but give less resolution of ingroup relationships (Fig. 4-9). The strict consensus tree illustrates that the eastern U.S. samples form a monophyletic group. The eastern clade is divided into three subclades: a primarily eastern Apalachicola Lowlands subclade and a predominately Atlantic, SW Georgia and Panhandle sample subclade. There is no information regarding how the Florida peninsula and two Outer Banks, NC, samples relate each other. The majority rule consensus tree (Fig. 4-9) is more similar to the unordered MP analysis, where the midwestern/western samples also form a monophyletic group. Additionally, there is more resolution of the ingroup; the primarily eastern Apalachicola Lowland subclade is most closely related to a predominately Atlantic, SW Georgia and Panhandle sample subclade. A randomly selected representative of the 171 shortest trees in Fig. 4-9 illustrates the number of character differences between individuals and bootstrap support above 50%. Certain major nodes are well supported: California individuals of the western clade (100%) and eastern U.S. clade (81%). Certain nodes within the ingroup (eastern clade) are also statistically supported, illustrating their close relationship to each other. The eastern Apalachicola Lowland samples exist within the only well supported subclade (93%). The Apalachicola and a predominately Atlantic, SW Georgia and Panhandle sample subclade are supported together (57%). Like the unordered MP analysis, the ordered MP analysis demonstrate the relationships of the outgroups indicating that the midwestern/western individuals are the sister group to the eastern clade rather than California individuals of the western clade with 100% bootstrap support.

Character Evolution

Although many characters used in the analysis were homoplasious, synapomorphies were identified, supporting the monophyly of particular clades. There were three characters supporting the monophyly of *L. g. holbrooki*, *L. g. nigra*, *L. g. nigrita*, and *L. g. splendida* in the midwestern/western clade (Fig. 4-8). These include centered light pigment within band scales as juvenile (character 7-1, Table 4-2, Fig. 4-3B), light pigment incorporating 33% of band scales as juvenile (character 11-2, Table 4-2, Fig. 4-6), and 33% mean band width as juvenile (character 12-1, Table 4-2, Fig. 4-7). Centered ontogenetically lightened pigment within dark interband scales (character 8-1, Table 4-2, Fig. 4-4B) is the only character supporting the monophyly of *L. g. splendida* and *L. g. holbrooki* from Duval Co., TX, Terrebonne Parish, LA, and Perry, MS, within the midwestern/western clade (Fig. 4-8). Ontogenetically darkened dorsal and ventral patterns in the adult stage (characters 3b-1, 5-2, Table 4-2, Fig. 4-2C) were the two characters supporting the monophyly of *L. g. nigrita* from Sonora, Mexico (Fig. 4-8). However, it is noted that an ontogenetically darkened dorsal pattern (character 5-2, Fig. 4-2C) is homoplasious, because it is also found on the western edge of the Appalachian Mountains (= *L. g. nigra*). There were three characters supporting the monophyly of the eastern clade with *L. g. floridana*, *L. g. getula*, and populations in the Apalachicola Lowlands (Fig. 4-8). These include anterior light pigment within band scales as a juvenile (character 7-2, Table 4-2, Fig. 4-3C), red tipping of dorsal scales as juvenile (character 9-1, Table 4-2), and light pigment incorporating 50% of band scales as a juvenile (character 11-1, Table 4-2, Fig. 4-6). There are five synapomorphies supporting the monophyly of the eastern Apalachicola Lowlands snakes with individuals from the

surrounding panhandle (Fig. 4-8): a ventral pattern of loose checkerboard with interspersed bicolored scales as a juvenile (character 2-3, Table 4-2, Fig. 4-2F), ventral patterns of loose checkerboard with interspersed bicolored scales or bicolored as an adult (character 3d-1, Table 4-2, Fig. 4-2F, G), wide banded dorsal pattern (character 4-2, Table 4-2, Fig. 4-2F), band formation fused laterally and/or dorsally as a juvenile (character 6-2, Table 4-2, Fig. 4-2F, G), and band width of 2.5-8 DSR as a juvenile (character 12-3, Table 4-2, Fig. 4-7). There are six autapomorphies found within the eastern Apalachicola Lowlands (Fig. 4-8), including bicolored ventral patterns as a juvenile and an adult (characters 2-4, 3e-1, Table 4-2, Fig. 4-2G), dark striped and patternless dorsal patterns as a juvenile (characters 4-3, 4-4, Table 4-2, Fig. 4-2G), one light dorsal band as a juvenile (character 10-1, Table 4-2, Fig. 4-5), and band width of >200 DSR as a juvenile (character 12-4, Table 4-2, Fig. 4-7). There are two synapomorphies supporting the monophyly of *L. g. getula* in the Atlantic/panhandle clade (Fig. 4-8): a loose checkerboard ventral pattern as a juvenile (character 2-2, Table 4-2,Fig. 4-2E) and a banded dorsal pattern with no ontogenetic change (character 5-1, Table 4-2, Fig. 4-2E). There are two characters supporting the monophyly of eastern Apalachicola Lowlands snakes and *L. g. getula* from the surrounding region and the Atlantic (Fig. 4-8), including a loose checkerboard, loose checkerboard with interspersed bicolor scales or bicolored ventral patterns (character 3c-1, Table 4-2, Fig. 4-2E, F, G) and laterally forked banded dorsal pattern (character 6-1, Table 4-2, Fig. 4-2E). The monophyly of *L. g. floridana* from the peninsula (Fig. 4-8) is weakly supported by a single homoplasious character of a band width of 1.5 DSR (character 12-2, Table 4-2, Fig. 4-2).

Discussion

Based on previous morphological work by Keogh (1996), a terrestrial behavior was the single synapomorphy defining the monophyly of *L. getula*. Although some clades (or subspecies) within the *L. getula* complex may be weakly supported by homoplasious characters, at least one synapomorphy supports the monophyly of each of the major clades. Midwestern/western individuals of *L. g. holbrooki, L. g. nigra, L. g. nigrita* and *L. g. splendida* represent sister taxa to the eastern clade of *L. g. floridana, L. g. getula* and eastern Apalahicola Lowlands snakes (Fig. 4-8). This evidence supports the two nearly identical hypotheses of Blanchard (1921) and Blaney (1977), in which the eastern subspecies were derived from midwestern/western individuals.

The three identified geographic races in the east, *L. g. getula, L. g. floridana*, and eastern Apalachicola Lowlands populations (chapter 3) are not completely discrete because of intermediates through interbreeding with members of adjacent subspecies. It is quite interesting that the unnamed highly polymorphic and very distinctive eastern Apalachicola Lowlands populations are identified by more synapomorphies than any other recognized subspecies (Fig. 4-8). Because these populations overlap in distribution with a number of endemic plants and animals (Table 3-10), I suggest that these snakes evolved locally and deserve taxonomic recognition. There is no evidence supporting the recognition of *L. g. brooksi* from the extreme southern Florida peninsula (Dade and Monroe counties) as there are no characters distinguishing *L. g. brooksi* from *L. g. floridana*. There is no evidence supporting the recognition of *L. g. sticticeps* from the Outer Banks of North Carolina (Dare Co.) as they exhibit characters of both *L. g. getula* from the adjacent mainland and *L. g. floridana* from the Florida peninsula.

Table 4-1. Sample, voucher number and locality of kingsnakes, *Lampropeltis getula* complex, used in this study for morphological analyses. Number next to sample indicates that more than one sample was used from the same general locality. Asterisk next to number in parentheses indicates that identical sample was used in DNA analyses.

Sample	Voucher No., Locality
San Diego, CA[1]	UF 116020; U.S.: California, San Diego Co.
San Diego, CA[2]	UF 116023; U.S.: California, San Diego Co.
Sonora, Mexico	UF 123994, Mexico: Sonora
Duval, TX	UF 116062; U.S.: Texas, Duval Co., Hwy 59, 9.5 km N of Freer
Terrebonne	KLK-xx519 (*Lg 59); U.S.: Louisiana, Terrebonne Parish, Houma
Perry, MS	KLK-xx259 (*Lg 90); U.S.: Mississippi, Perry Co.
Calloway, KY	KLK-xx232 (*Lg 56); U.S.: Kentucky, Calloway Co.
Trigg, KY	KLK-xx262 (*Lg 93); U.S.: Kentucky, Trigg Co.
Dare, NC[1]	KLK-xx530 (*Lg 121); U.S.: North Carolina, Dare Co., Hatteras Island
Dare, NC[2]	KLK-xx525 (*Lg 111); U.S.: North Carolina, Dare Co., Hatteras Island
Watauga, NC	KLK-xx520 (*Lg 29); U.S.: North Carolina, Watauga Co., Triplett
Charleston, SC[1]	KLK-xx521 (*Lg 37); U.S.: South Carolina, Charleston Co., Adams Run
Charleston, SC[2]	KLK-xx528 (*Lg 120); U.S.: South Carolina, Charleston Co., Edisto Island
Greenwood, SC	KLK-xx522 (*Lg 129;) U.S.: South Carolina, Greenwood Co., US 221, 2.6 km W of Hwy 10
Jasper, SC	KLK-xx526 (*Lg 99); U.S.: South Carolina, Jasper Co.
Banks, GA	KLK-xx350 (*Lg 117); U.S.: Georgia, Banks Co., Yonah Church Rd, 9.8 km W of Homer
Echols, GA	KME-m10 (*Lg 18); U.S.: Georgia, Echols Co., Statenville
Randolph, GA	KLK-xx523 (*Lg 133); U.S.: Georgia, Randolph Co.
Thomas, GA	KLK-xx524 (*Lg 134); U.S.: Georgia, Thomas Co., Ochlockonee River
Walton, GA	UF 121162 (*Lg 119); U.S.: Georgia, Walton Co., Loganville
Bay, FL	KLK-xx227 (*Lg 52); U.S.: Florida, Bay Co., SR 22, 32.1 km W of Wewahitchka
Dade, FL	UF 19675; U.S.: Miami-Dade Co., Krome Ave ca. 10 mi S of Tamiami Trail
Calhoun, FL	UF 114321 (*Lg 5, KLK-xx031); U.S.: Florida, Calhoun Co., Blountstown
Dixie, FL	KLK-xx316 (*Lg 115); U.S.: Florida, Dixie Co., CR 361, 5.7 km S of Rocky Creek
Duval, FL	KME-f11 (*Lg 16); U.S.: Florida, Duval Co., Jacksonville
Franklin, FL[1]	KLK-xx220 (*Lg 45); U.S.: Florida, Franklin Co., US 98, 7 km E of C30
Franklin, FL[2]	KLK-xx221 (*Lg 46); U.S.: Florida, Franklin Co., US 98, 9.5 km W of Carrabelle
Franklin, FL[3]	KLK-xx231 (*Lg 55); U.S.: Florida, Franklin Co., Tates Hell Swamp near New River
Gadsden, FL	KLK-xx222 (*Lg 47); U.S.: Florida, Gadsden Co., US 90 5.7 km W of Quincy
Gulf, FL[1]	KME-m25 (*Lg 11); U.S.: Florida, Gulf Co., Port St. Joe
Gulf, FL[2]	KME-m26 (*Lg 15); U.S.: Florida, Gulf Co., Port St. Joe
Hernando, FL	UF 111101 (*Lg 23, KLK-xx230); U.S.: Florida, Hernando Co., Hernando Beach
Hillsborough, FL	KLK-xx238; U.S.: Florida, Hillsborough Co., Brandon
Holmes, FL	KLK-xx257 (*Lg 65); U.S.: Florida, Holmes Co., Rt 179A, 3.8 km SW of SR 2
Jackson, FL	KLK-xx491 (*Lg 107); U.S.: Florida, Jackson Co., CR 271
Jefferson, FL	KLK-xx225 (*Lg 50); U.S.: Florida, Jefferson Co., Goosepasture Rd, 1.9 km S of Tram Rd
Lee, FL	KLK-xx527 (*Lg 35); U.S.: Florida, Lee Co., Gasparilla Island, Boca Grande
Leon, FL[1]	KME-m3 (*Lg 13); U.S.: Florida, Leon Co., Bloxham cutoff

Table 4-1—Continued.

Sample	Voucher No., Locality
Leon, FL[2]	KLK-xx226 (* Lg 51); U.S.: Florida, Leon Co., Meridian Rd, 0.2 km S of Meridian Hills Rd
Levy, FL	UF 95556; U.S.: Florida, Levy Co., 6 mi E of Cedar Key
Liberty, FL[1]	UF 105383 (* Lg 10, KLK-xx211); U.S.: Florida, Liberty Co., SR 67, 3.7 km S of SR 20
Liberty, FL[2]	KLK-xx213 (* Lg 26); U.S.: Florida, Liberty Co., SR 67, just N of Liberty-Franklin Co. line
Liberty, FL[3]	KLK-xx239 (* Lg 27); U.S.: Florida, Liberty Co., near junction of NFR 103 and 116
Liberty, FL[4]	KLK-xx240 (* Lg 28); U.S.: Florida, Liberty Co., near junction of NFR 103 and 116
Liberty, FL[5]	DBM-104 (*Lg 30); U.S.: Florida, Liberty Co.
Liberty, FL[6]	DBM-50 (* Lg 32); U.S.: Florida, Liberty Co., NFR 110 2.9 km S of jct 111
Liberty, FL[7]	KLK-xx247 (* Lg 58); U.S.: Florida, Liberty Co., NFR 139
Monroe, FL	UF 123777 (* Lg 36, KLK-xx490); U.S.: Florida, Monroe Co., Key Largo
Palm Beach, FL	UF 99739 (KLK-94005); U.S.: Florida, Palm Beach Co., Pahokee
Pinellas, FL	KLK-xx050; U.S.: Florida, Pinellas Co.
Wakulla, FL[1]	KME-m13 (*Lg 12); U.S.: Florida, Wakulla Co., junction of NFR 313 and 312
Wakulla, FL[2]	KME-f3 (* Lg 14); U.S.: Florida, Wakulla Co., Arren

Table 4-2. Morphological characters of kingsnakes, *Lampropeltis getula* complex, used for cladistic analyses. Note plesiomorphic (0) and apomorphic (1-4) conditions.

#	Character	Character State (Coding)
1	*Dorsal scale rows* (Fig. 4-1).	25 (0), 23 (1), 21 (2)
2	*Ventral pattern as juvenile* (Fig. 4-2).	(Ordered) Ringed or light with dark lateral margins (0), tight checkerboard (1), loose checkerboard (2), loose checkerboard with interspersed bicolored scales (3), bicolored (4)
3	*Ventral pattern as adult* (Fig. 4-2).	(Ordered transformation series) Ringed or light with dark lateral margins = A, tight checkerboard = B, solid dark = C, loose checkerboard = D, loose checkerboard with interspersed bicolored scales = E, bicolored = F 3a. A (0), not A (1) 3b. C (1), not C (0) 3c. A, B or C (0); D, E or F (1) 3d. A, B, C or D (0); E or F (1) 3e. A, B, C, D or E (0); F (1)
4	*Dorsal pattern as juvenile* (Fig. 4-2).	(Ordered) Ringed or light striped (0), narrow banded (1), wide banded (2), dark striped (3), patternless (4)
5	*Ontogenetic dorsal pattern change*.	Ringed or light striped with no change (0), banded with no change (1), bands becoming solid dark (2), interband lightening laterally (3), interband lightening over dorsum (4)
6	*Band or ring formation as juvenile* (Fig. 4-2).	(Ordered) Ringed around body or light striped (0), forked laterally (1), fused laterally and/or dorsally (2)
7	*Placement of light pigment within band or ring scales as juvenile* (Fig. 4-3).	(Ordered) Entire scale (0), centered (1), anterior (2)
8	*Placement of ontogenetically lightened pigment within dark interband or ring scales* (Fig. 4-4).	(Ordered) No lightening (0), centered (1), anterior (2)
9	*Red tipping of dorsal scales as juvenile*.	(Ordered) Absent (0), present (1)
10	*Number of light bands or rings as juvenile* (Fig. 4-5).	A (0), B (1), C (2), D (3)
11	*Fraction of light pigment within band or ring scales as juvenile* (Fig. 4-6).	1.00 (0), 0.50 (1), 0.33 (2)
12	*Band or ring width as juvenile* (Fig. 4-7).	A (0), B (1), C (2), D (3), E (4)

Table 4-3. Data matrix of kingsnakes, *Lampropeltis getula* complex, used for cladistic analyses. See Table 4-2 for character descriptions. Number next to sample indicates that more than one sample was used from the same general locality.

Sample	Character State															
	1	2	3a	3b	3c	3d	3e	4	5	6	7	8	9	10	11	12
San Diego, CA[1]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
San Diego, CA[2]	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Sonora, Mexico	1	1	1	1	0	0	0	1	2	1	1	0	0	3	2	1
Duval, TX	1	1	1	0	0	0	0	1	3	1	1	1	0	3	2	1
Terrebonne	2	1	1	0	0	0	0	1	4	1	1	1	0	3	2	1
Perry, MS	2	1	1	0	0	0	0	1	4	1	1	1	0	3	2	1
Calloway, KY	2	1	1	0	0	0	0	1	2	1	1	0	0	3	2	1
Trigg, KY	2	1	1	0	0	0	0	1	2	1	1	0	0	3	2	1
Dare, NC[1]	2	2	1	0	1	0	0	1	4	1	2	2	1	2	1	2
Dare, NC[2]	2	2	1	0	1	0	0	1	4	1	2	2	1	2	1	2
Watauga, NC	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Charleston, SC[1]	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Charleston, SC[2]	2	2	1	0	1	0	0	2	1	1	2	0	1	2	1	3
Greenwood, SC	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Jasper, SC	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Banks, GA	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Echols, GA	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Randolph, GA	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Thomas, GA	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Walton, GA	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Bay, FL	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Dade, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	3	1	2
Calhoun, FL	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Dixie, FL	2	1	1	0	0	0	0	1	4	1	2	2	1	2	1	2
Duval, FL	2	2	1	0	1	0	0	1	4	1	2	2	1	2	1	2
Franklin, FL[1]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Franklin, FL[2]	2	4	1	0	1	1	1	3	4	2	2	2	1	1	1	4
Franklin, FL[3]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Gadsden, FL	1	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Gulf, FL[1]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Gulf, FL[2]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Hernando, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	2	1	2
Hillsborough, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	3	1	2
Holmes, FL	1	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Jackson, FL	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Jefferson, FL	2	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Lee, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	3	1	2
Leon, FL[1]	2	3	1	0	1	0	0	1	1	1	2	0	1	2	1	3
Leon, FL[2]	1	2	1	0	1	0	0	1	1	1	2	0	1	2	1	2
Levy, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	2	1	2
Liberty, FL[1]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Liberty, FL[2]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Liberty, FL[3]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Liberty, FL[4]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Liberty, FL[5]	2	4	1	0	1	1	1	4	4	2	2	2	1	1	1	4
Liberty, FL[6]	2	4	1	0	1	1	1	3	4	2	2	2	1	1	1	4
Liberty, FL[7]	2	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3

Table 4-3—Continued.

Sample	Character State															
	1	2	3a	3b	3c	3d	3e	4	5	6	7	8	9	10	11	12
Monroe, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	3	1	2
Palm Beach, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	3	1	2
Pinellas, FL	1	1	1	0	0	0	0	1	4	1	2	2	1	2	1	2
Wakulla, FL[1]	1	3	1	0	1	1	0	2	4	2	2	2	1	2	1	3
Wakulla, FL[2]	2	3	1	0	1	1	0	2	4	1	2	2	1	2	1	3

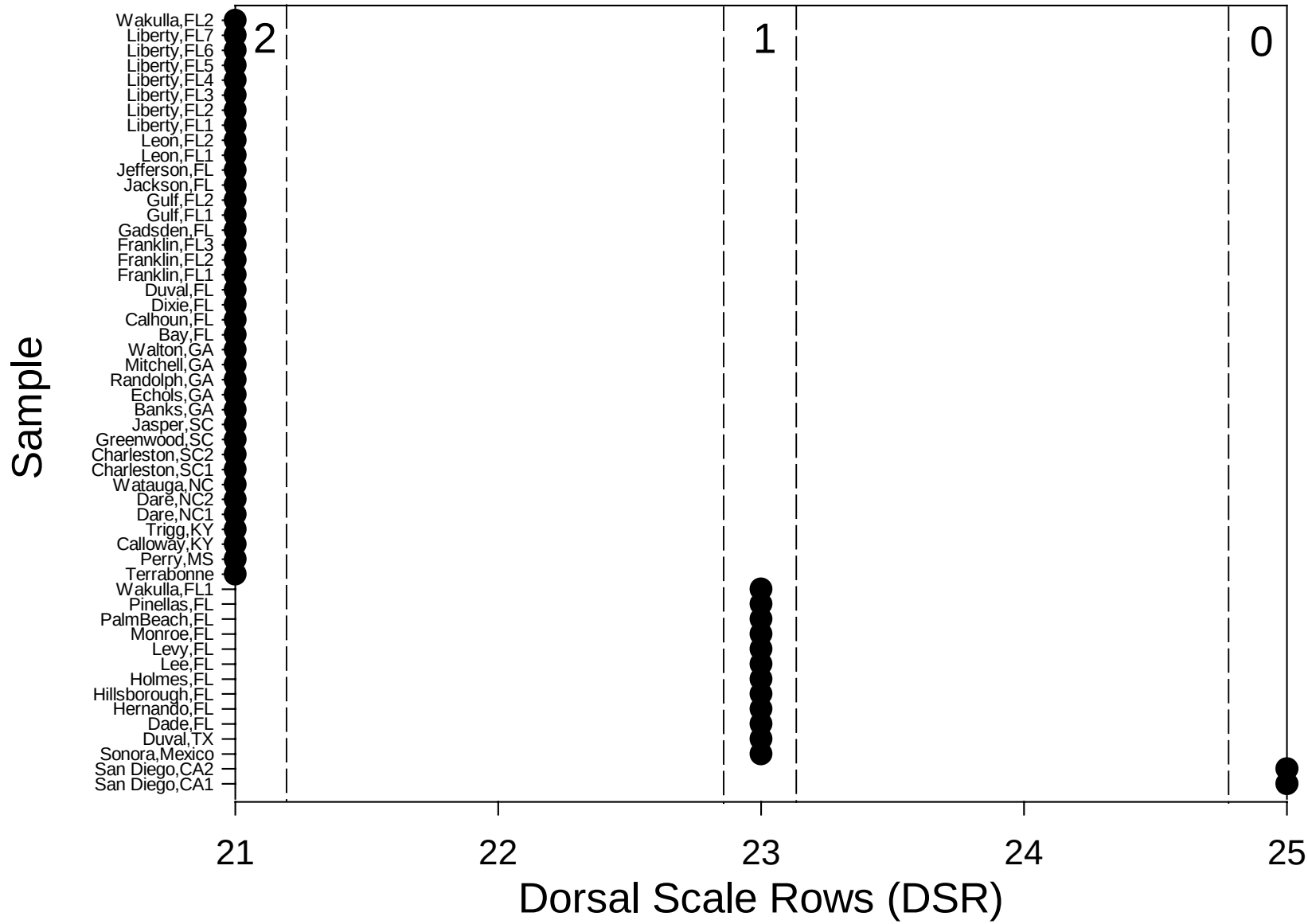

Fig. 4-1. Dorsal scale rows (DSR) at midbody in *Lampropeltis getula* complex. Note plesiomorphic (0) and apomorphic (1-2) conditions.

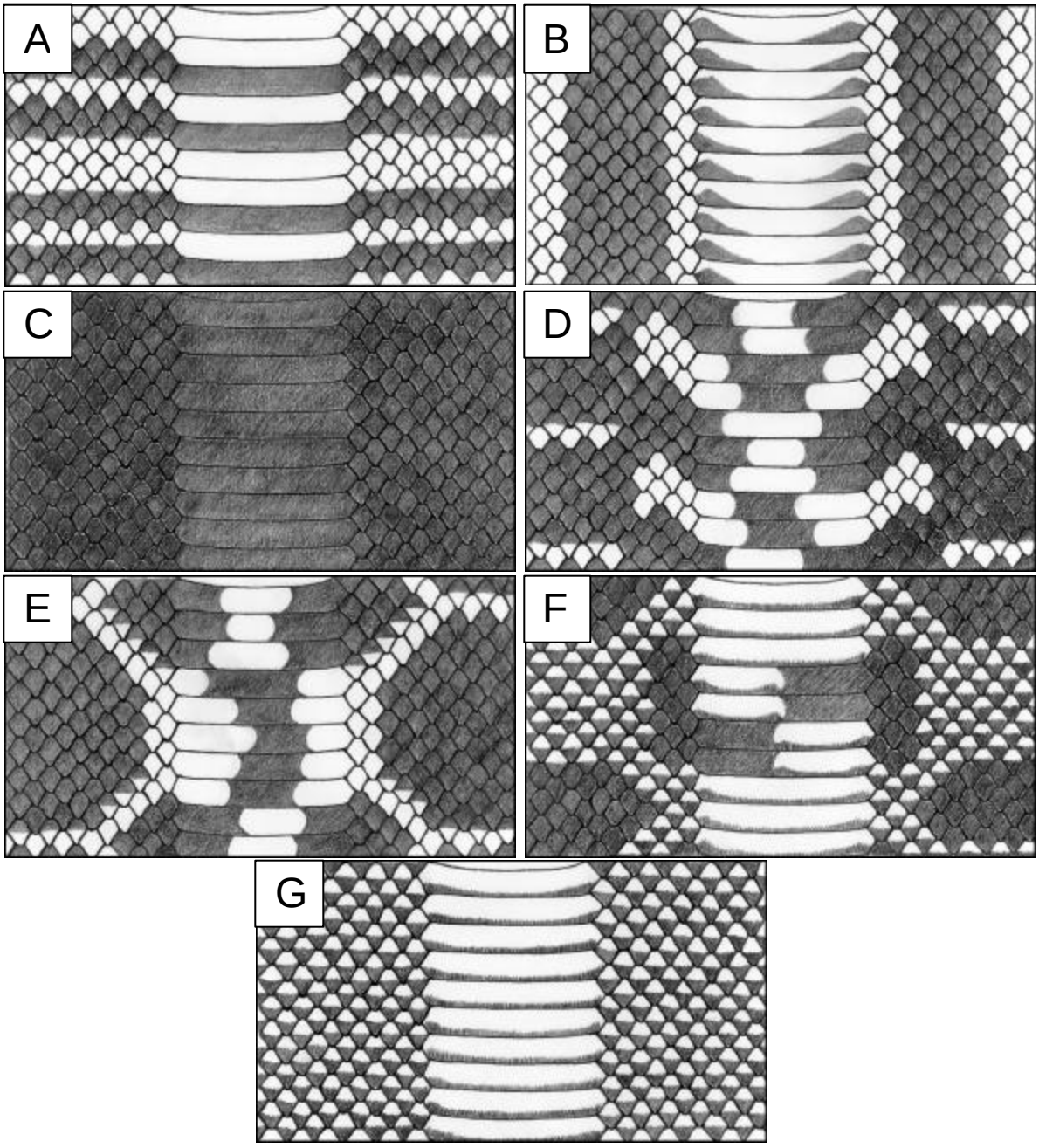

Fig. 4-2. Primary dorsal and ventral patterns of kingsnakes, *Lampropeltis getula* complex. Note that dorsal or ventral patterns might be referred to separately in text.

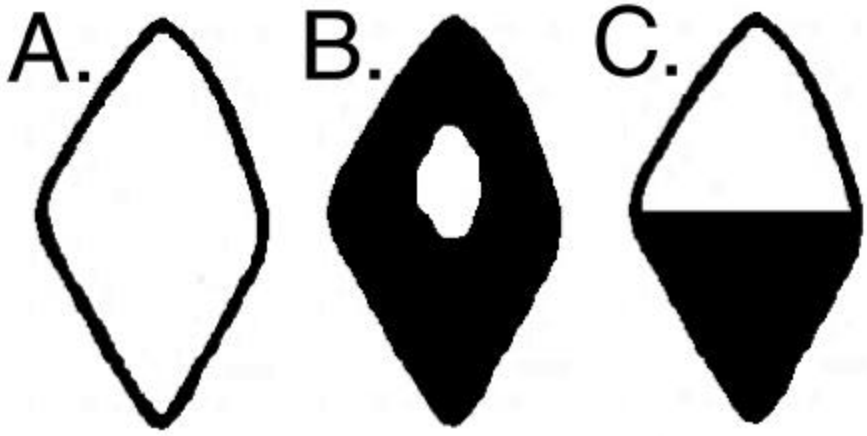

Fig. 4-3. Placement of light pigment within light band or ring scales in *Lampropeltis getula* complex. Pigment is either A = located on the entire scale, B = centered or C = anterior. See Table 4-2 for character state coding.

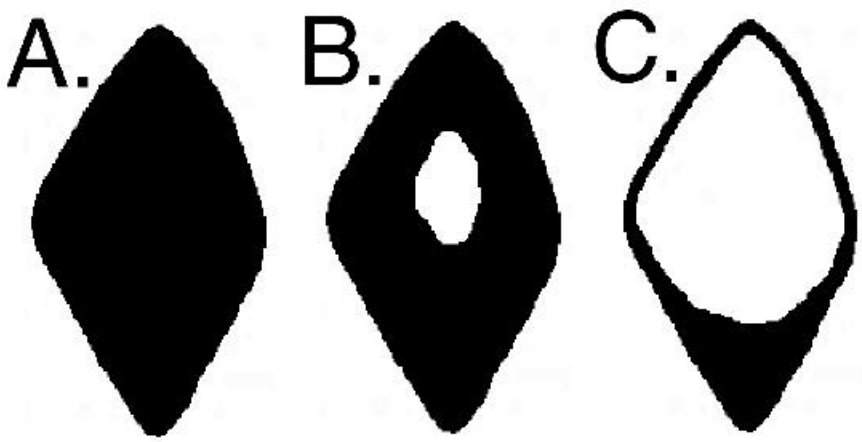

Fig. 4-4. Placement of ontogenetically lightened pigment within dark interband or ring scales in *Lampropeltis getula* complex. Their is either A = no pigment, or pigment is B = centered or C = anterior. See Table 4-2 for character state coding.

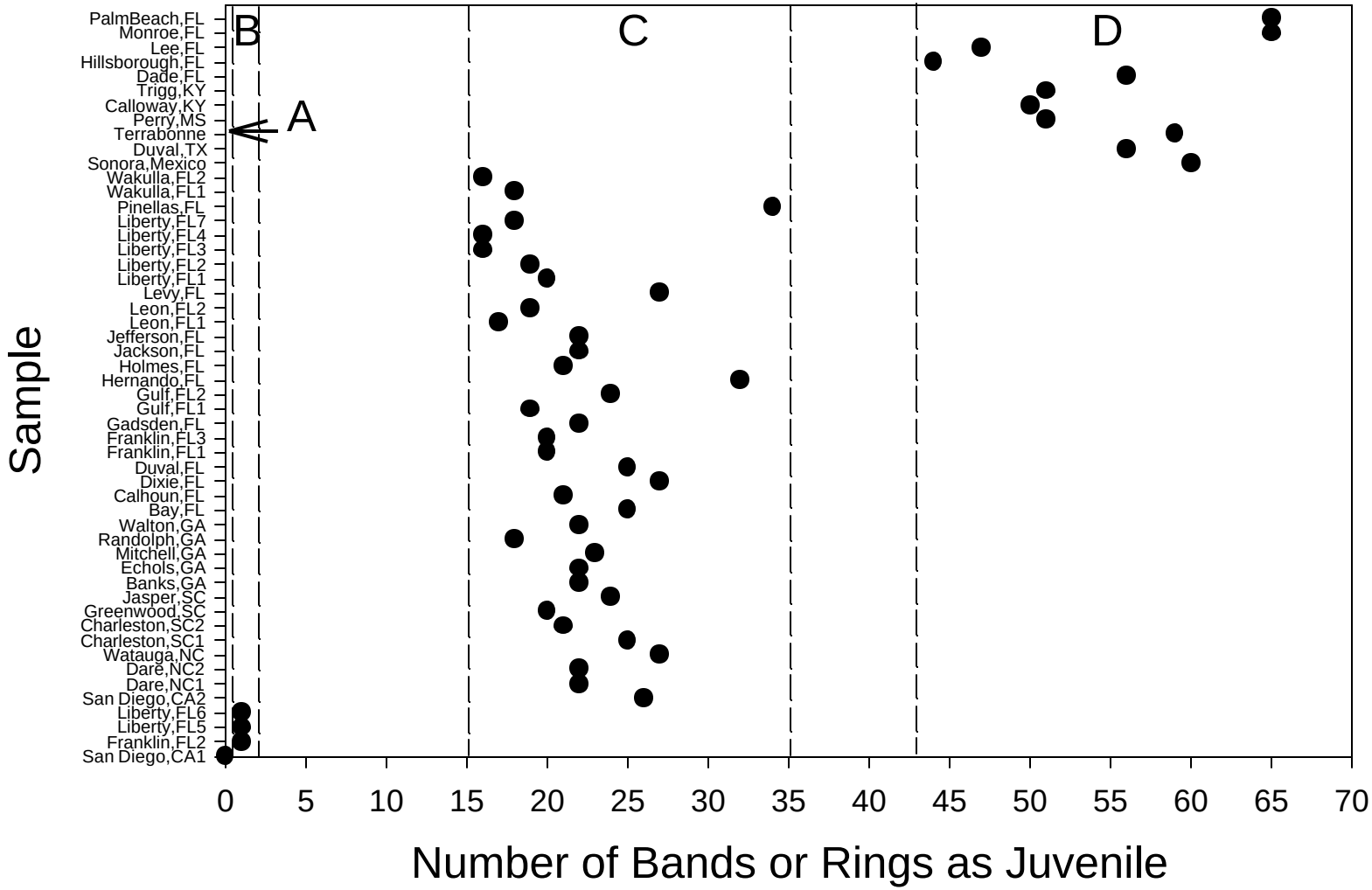

Fig. 4-5. Number of light bands or rings in juveniles of *Lampropeltis getula* complex. See Table 4-2 for character state coding.

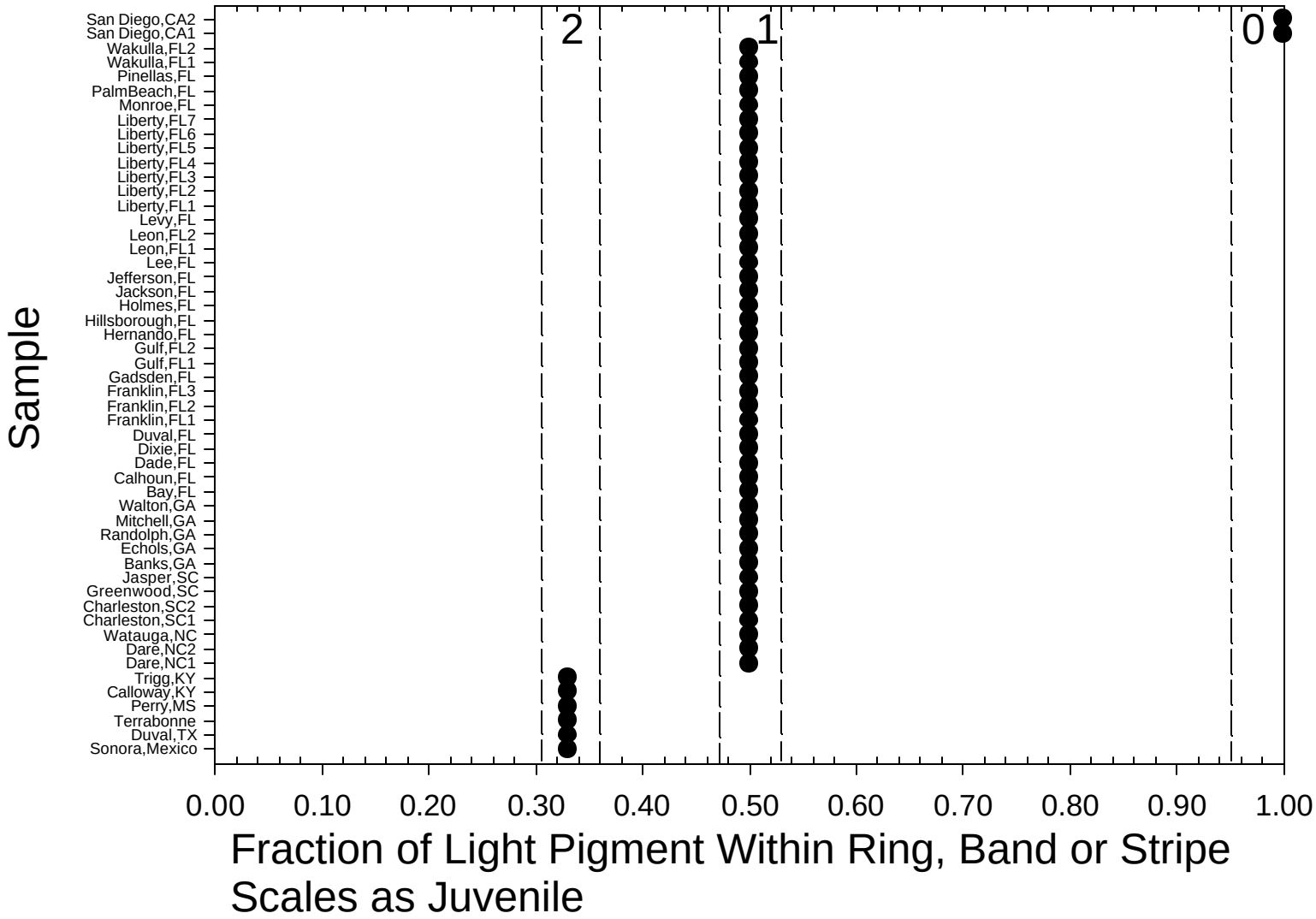

Fig. 4-6. Fraction of light pigment within band or ring scales in juveniles of *Lampropeltis getula* complex. Note plesiomorphic (0) and apomorphic (1-2) conditions.

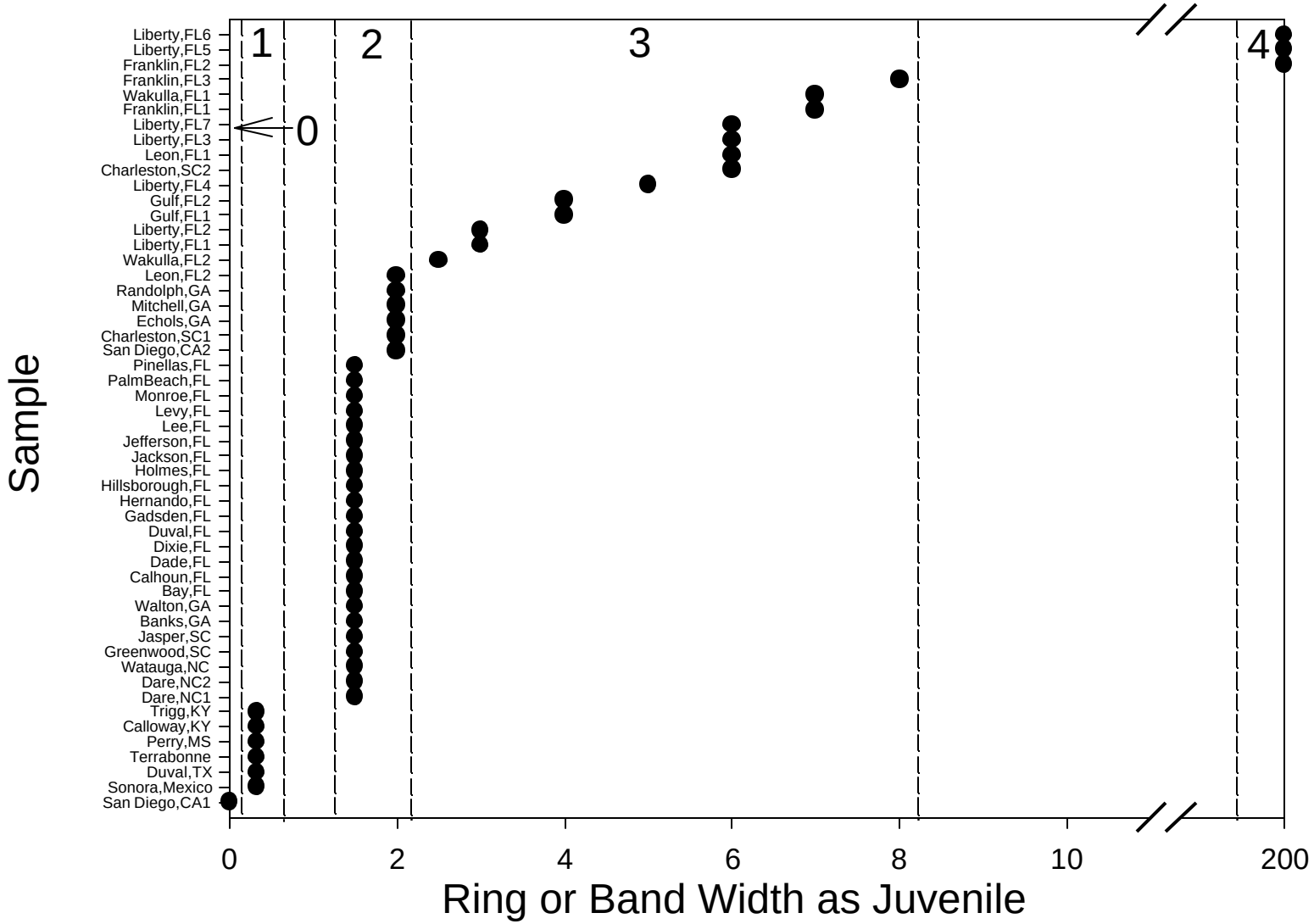

Fig. 4-7. Band or ring width in juveniles of *Lampropeltis getula* complex. plesiomorphic (0) and apomorphic (1-4) conditions.

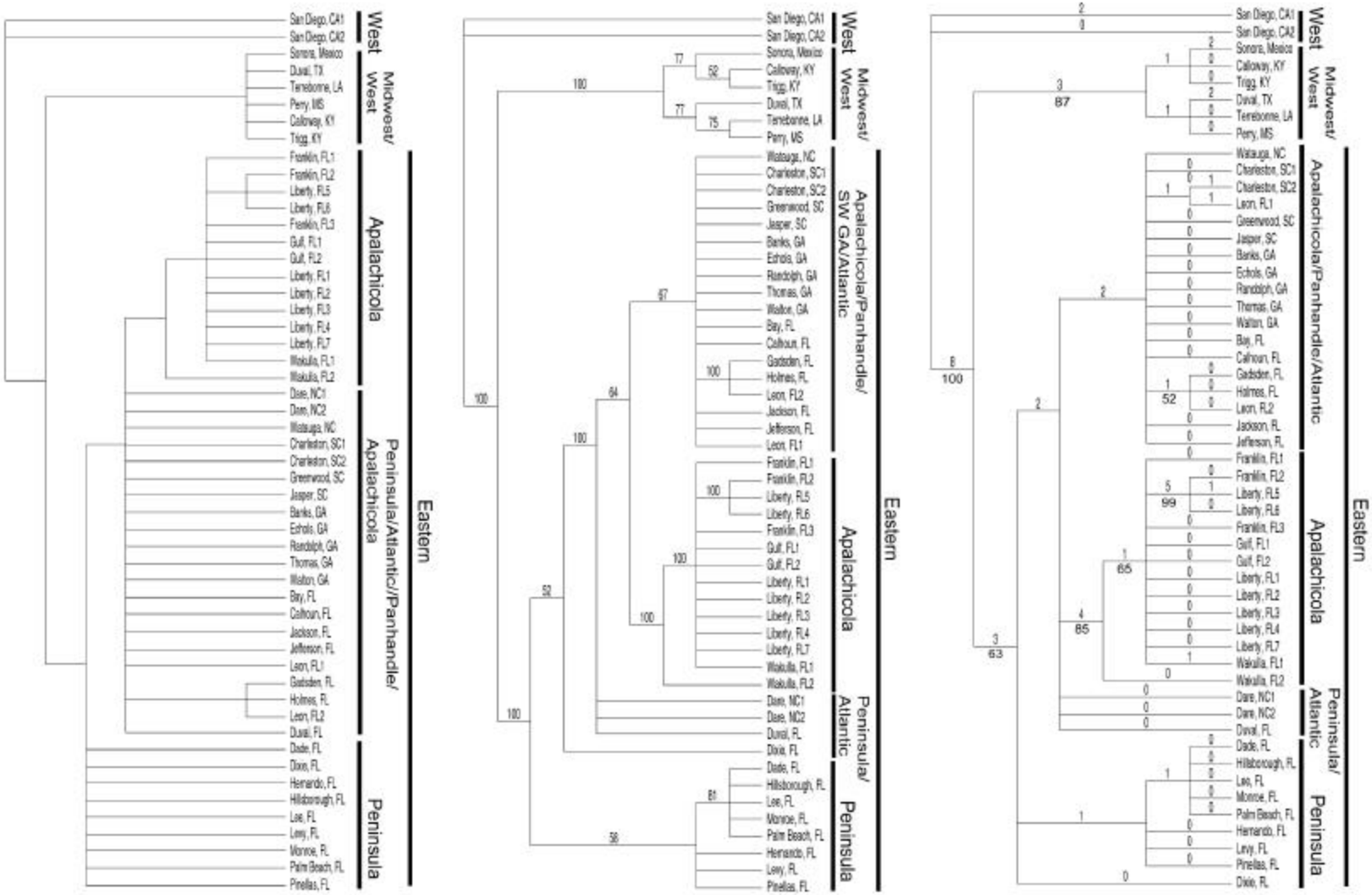

Fig. 4-8. Strict consensus (left), majority rule (center) and random single representative of 69 trees (right) from unordered maximum-parsimony analysis of morphological data in *Lampropeltis getula*. Majority rule (center) illustrates the percentage that nodes are found. Random tree (right) illustrates the number of steps (above) and bootstrap values (> 50%, below).

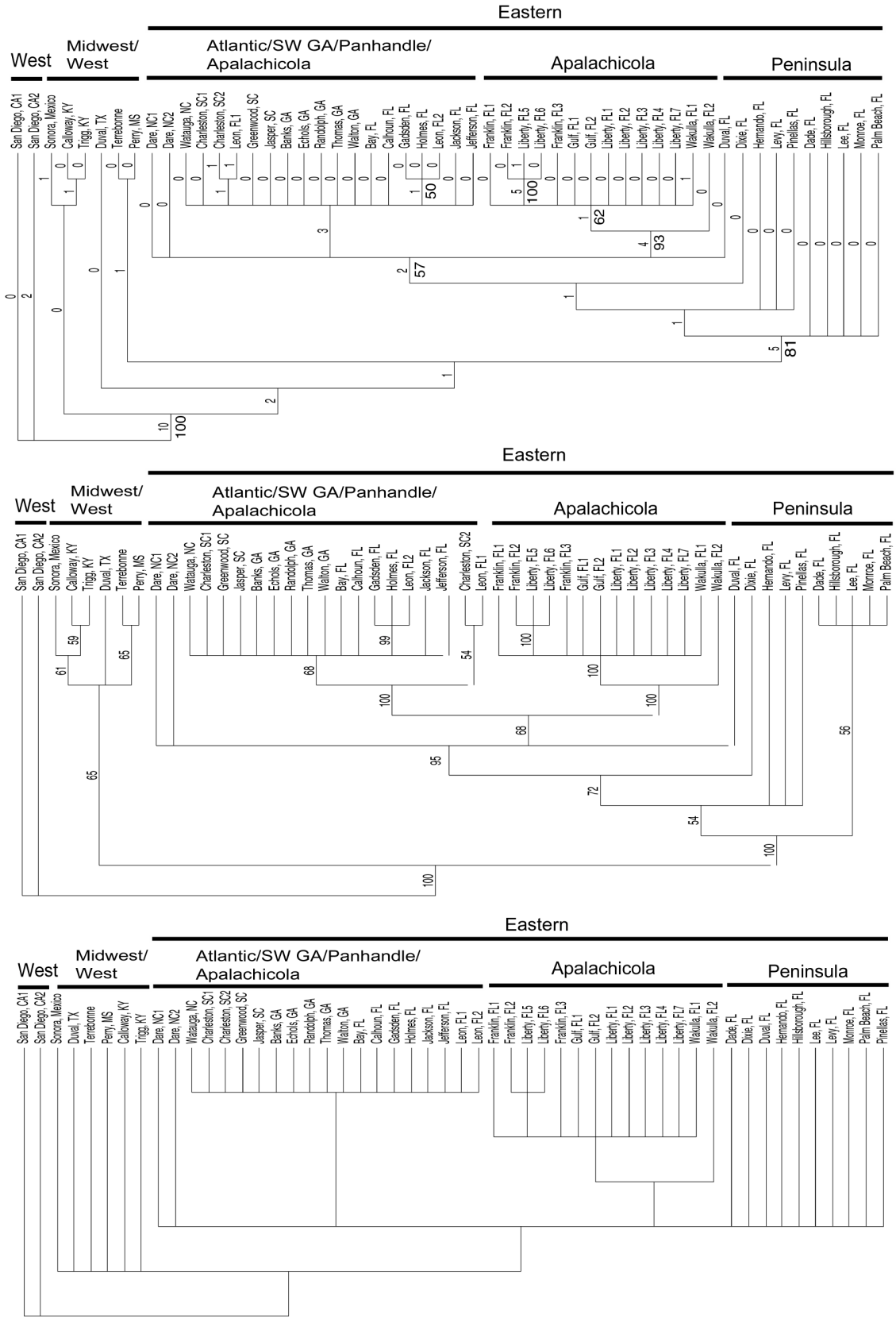

Fig. 4-9. Strict consensus (left), majority rule (center) and random single representative of 171 trees (right) from ordered maximum-parsimony analysis of morphological data in *Lampropeltis getula*. Majority rule (center) illustrates the percentage that nodes are found. Random tree (right) illustrates the number of steps (above) and bootstrap values (> 50%, below).

CHAPTER 5
MOLECULAR SYSTEMATICS OF KINGSNAKES (*Lampropeltis getula*)

Materials and Methods

I sequenced mitochondrial DNA (mtDNA) from a total of 55 *L. getula* from the following three eastern U.S. areas: 1) 15 from Atlantic coast, 2) 25 from panhandle Florida and 3) 15 from peninsular Florida (Table 5-1). Additionally, I sequenced mtDNA from five midwestern and three western U.S. *L. getula* to be used as functional outgroups to eastern U.S. snakes. In order to facilitate comparison of molecular and morphological phylogenetic results, most of these individuals were the same as those used in morphological analyses (Table 4-1).

Laboratory Techniques

Mitochondrial DNA samples were obtained from blood, muscle tissue, shed skins and bone. Between 0.5 and 1.0 ml of blood was taken from the caudal vein of live specimens and stored in lysis buffer (100 mM Tris-HCl, pH 8: 100 mM EDTA, ph 8; 10 mM NaCl; 1.0% sodium dodecyl sulfate) in approximately 1:10 blood to buffer ratio (White and Densmore, 1992). Muscle tissue was taken from salvaged dead on road (DOR) specimens and stored in SED buffer (saturated NaCl; 250 mM EDTA, pH 7.5; 20% DMSO; Amos and Hoelzel, 1991; Proebstel et al., 1993). Both lysis buffer and saturated salt solution preserve tissues for genetic analysis for at least one year without refrigeration and are nontoxic and nonflammable. Shed skins were taken from live

specimens and stored in ziplock plastic bags at room temperature. Bone samples were obtained from the skeletal collection in the Division of Herpetology, Florida Museum of Natural History (FLMNH), University of Florida. DNA isolations were obtained following protocols of Hillis et al. (1990) for blood and muscle tissue, Clark (1998) for shed skins and Iudica et al. (2001) for bone.

Using total cellular DNA as a template and polymerase chain reaction (PCR) methodology (Saiki et al., 1988), I amplified and sequenced mtDNA from the cytochrome *b* (cyt *b*) gene and the nicotinamide adenine dinucleotide dehydrogenase subunit 4 (ND4) region (Figs. 5-1, 5-2). Cytochrome *b* (Table 5-2, Fig. 5-2) was sequenced using the primers LGL765 (Bickham et al., 1995) and H15919 (Fetzner, 1999). For degraded samples, I used cyt *b* primer CYB 2 (Kessing et al., 1989), along with designed internal primers using OLIGO software (ver. 4.06): CYB 1L, CYB 2L, CYB 1H, CYB 2H. PCR was conducted in a Biometra thermal cycler in 50 µl reactions: 25.9 µl H_2O, 5.0 µl 10 x PCR reaction buffer (Sigma®), 8.0 ul deoxynucleotide triphophates (800 µM), 6.0 µl $MgCl_2$ (25 mM, Sigma®), 1.2 µl each primer (10 µM), 0.2 µl *Taq* DNA polymerase (Sigma®, 5 U / µl), and 2.5 µl template DNA. PCR parameters included initial denaturing at 96°C for 3 min, followed by 45 cycles of amplification: denaturing at 95°C for 25 sec, annealing at 53°C for 1 min, and extension at 72°C for 2 min, followed by a final extension at 72°C for 5 min (J. W. Fetzner, pers. comm.). The ND4 region (Table 5-2, Figs. 5-1, 5-2) included a section of the 3' end of the ND4 gene, and the three following transfer ribonucleic acids ($tRNA^{His}$, $tRNA^{Ser}$, $tRNA^{Leu}$), which were sequenced using the primers ND4 and Leu (Arevalo et al., 1994; Rodriguez-Robles and De Jesus-Escobar, 1999b), along with designed internal primers: ND4 1L, ND4 1H.

PCR was conducted in 50 µl reactions as above. PCR parameters included initial denaturing at 96°C for 2 min, followed by 45 cycles of amplification: denaturing at 95°C for 10 sec, annealing at 52°C for 25 sec, and extension at 72°C for 45 min, followed by a final extension at 72°C for 7 min (Rodriguez-Robles and De Jesus-Escobar, 1999b).

Five µl of each PCR product were electrophoresed on a 1% agarose gel, visualized with ethidium bromide staining, and compared with a DNA standard. Double-stranded PCR products were cleaned with 30,000 MW Millipore filters. Cleaned PCR products were sequenced with Big Dye® terminator reagents (Applied Biosystems, Foster City, CA) according to manufacturer's instructions, except that reactions were scaled down to 1/8 volume in 20 µl reactions: 1 µl of terminator mix, 3.5 µl 5x buffer (400 mM Tris, pH 9.0, 10 mM $MgCl_2$), 1 µl primer (10 µM), and H_2O (13.5 - 10.5 µl) and PCR products (1-4 µl) for a total volume of 20 µl. Single stranded sequence products were analyzed with automated DNA sequencers (Applied Biosystems models 373 and 377). New haplotypes were confirmed by comparing complimentary DNA strands and ambiguities that could not be resolved were resequenced. Initial sequences were screened for the presence of mitochondrial-like pseudogenes (from the nuclear genome) using patterns of nucleotide substitution, stringency tests and primer redesign (Zhang and Hewitt, 1996). Sequence files from the automated sequencer were assembled and edited as necessary with Sequencher (ver. 3.1, Genes Codes Corp., Ann Arbor, MI) and aligned manually.

Phylogenetic Analyses

Relationships among mtDNA haplotypes were described with maximum-parsimony (MP) and Neighbor-joining (NJ) distance (Saitou and Nei, 1987) methods using PAUP*

(ver. 4.0b8; Swofford, 2000). MP cladograms were constructed with an heuristic search using 500 repetitions of random stepwise additions with subtree pruning and regrafting (SPR), with limits set to 25 trees (30 steps) per random addition replicate. Both equal weighting and weighting of transistions (TS) and transversions (TV) were considered based on an observed 3:1 (TS:TV) ratio (Table 5-3). Genetic distances (*d*) between haplotypes were related using a NJ tree with Kimura two-parameter model (Saitou and Nei, 1987) in PAUP* (Swofford, 2000). Support for phylogenetic groupings in both approaches were assessed with bootstrapping (Felsenstein, 1985) with full heuristic search using 500 repetitions of random stepwise additions, with SPR and limits set to 5 trees per random addition replicate. Nonparametric bootstrapping generally yields conservative measures of the probability that a group represents a true evolutionary clade (Zharkikh and Li, 1992; Hillis and Bull, 1993; Rodriguez-Robles et al., 1999c).

Population Structure

Mitochondrial DNA variation was described with the nucleotide diversity (p; equation 10.5 in Nei, 1987) and haplotype diversity (*h*; equation 8.4 in Nei, 1987) in Arlequin (ver. 2.000; Schneider et al., 2000). Tests of population structure within and among sampling regions were estimated with Φ_{st} (a molecular analog of the conventional F_{ST}; Wright, 1951) using analysis of molecular variance (AMOVA; Excoffier et al., 1992) with 1000 permutations in Arlequin. Pairwise estimates of gene flow within and among sampling regions (*Nm*; number of migrants per generation) were determined using the formula $Nm = (1/\Phi_{st} - 1) / 4$ (Slatkin, 1993). Sampling regions with sample sizes less than five were excluded in pairwise calculations of Φ_{st} and *Nm* values, yet were included for estimates of genetic diversity.

Results

Cytochrome *b* (Figs. 5-1, 5-2) consisted of 1117 base pairs (bp) in *Lampropeltis getula* and 1083 bp were resolved for these analyses. The analyzed ND4 region consisted of 783 bp, including a 669 bp section of the 3' end of the ND4 gene and a 114 bp section of the subsequent tRNAs. Sequence comparisons revealed a total of 216 polymorphic sites containing a TS:TV ratio of 172:48, and 137 parsimony-informative characters within the 1886 bp sequenced (Table 5-3). Forty-nine unique haplotypes were resolved from 63 total individuals including the midwestern and western individuals (Tables 5-1, 5-4), differing by a mean sequence divergence of d = 1.36% (range d = 0.05-7.2%). Shared haplotypes included (Table 5-1): Lee Co., FL (haplotype hh) = Pinellas Co, FL2; Palm Beach Co., FL (jj) = Hendry Co., FL; Calhoun Co., FL 1 (J) = Bay Co., FL, Calhoun Co., FL2, Leon Co., FL1 and Franklin Co., FL2; Wakulla Co., FL1 (S) = Wakulla Co., FL2; Liberty Co., FL3 (C) = Liberty Co., FL4; Dare Co., NC2 (bb) = Mitchell Co., GA and Randolph Co., GA; Watauga Co., NC (cc) = Charleston Co., SC1, Dare Co., NC1 and Dare Co., NC3; Stewart Co., TN (uu) = Calloway Co., KY.

Maximum Parsimony

There were 84 parsimony-informative characters within the 1083 bp sequenced from cyt *b*. MP analysis using equally weighted TS:TV resulted in 44 most parsimonious trees of 171 steps (CI = 0.836, RI = 0.899). There were 53 parsimony-informative characters within the 783 bp fragment of ND4 region. MP analysis using equally weighted TS:TV resulted in 209 most parsimonious trees of 101 steps (CI = 0.822, RI = 0.895). MP analysis using combined genes with equally weighted TS:TV resulted in

2474 most parsimonious trees of 277 steps (CI = 0.816, RI = 0.887). Strict consensus trees were created for individual and combined genes (Fig. 5-3). ND4 produced more resolution within the ingroup (eastern U.S. samples) than cyt *b*, where there are three recognizable subclades: Peninsula, Atlantic and Apalachicola/Panhandle/SW Georgia (A/P/SWGA). When analyzing both cyt *b* and ND4 together there is much better resolution within the ingroup. Because a combined cyt *b*-ND4 data set provides a larger number of characters and more robust estimate of matrilineal phylogeny (Wiens and Reeder, 1997; Soltis et al., 1998; Pook et al., 2000), I used combined genes throughout the rest of the study. The midwestern and eastern samples formed separate monophyletic groups. As with ND4 only, the eastern clade is further divided into three subclades: Peninsula, Atlantic and A/P/SWGA. The Atlantic subclade is most closely related to the A/P/SWGA subclade, which consists primarily of eastern Apalachicola Lowlands and panhandle samples. There is no information regarding how the majority of peninsular samples relate to each other. A random single representative of the 2474 shortest trees was created illustrating the number of base differences between haplotypes and bootstrap support above 50% (Fig. 5-4). Major nodes representing the west, midwest and eastern clades are extremely well supported (100%) with relatively large genetic breaks between them. Nodes within the eastern clade are less supported and there are fewer base differences between subclades and individuals, illustrating their close relationships to each other. The A/P/SWGA subclade has 60% bootstrap support and its close relationship to the Atlantic subclade has 55% bootstrap support. The unweighted MP tree further indicates that the midwestern clade is the sister group to the eastern clade rather than the western clade, a relationship supported by a 100% boostrap.

MP analysis using an empirical 3:1 (TS:TV) ratio found 5143 most parsimonious trees of 385 steps (CI = 0.831, RI = 0.893). A strict consensus tree was created and as in the unweighted MP analysis, the midwestern and eastern samples form separate monophyletic groups (Fig. 5-5). However, there is much less resolution within the eastern clade and only the A/P/SWGA subclade is identified. Additionally, this analysis also indicates that the midwestern clade is the sister group to the eastern clade rather than the western clade.

Neighbor-Joining

The NJ tree produced a very similar topology to the unweighted MP strict consensus tree (Fig. 5-6), with greater resolution within the eastern clade. The midwestern and eastern clades form separate monophyletic groups with 100% bootstrap support. The eastern clade is further differentiated into the same three subclades. The Atlantic and A/P/SWGA subclades are most closely related to each other with 56% bootstrap support. The A/P/SWGA subclade alone has 55% bootstrap support. As in the MP analyses, the NJ tree demonstrates that the midwestern clade is the sister group to the eastern clade rather than the western clade with 100% bootstrap support.

Population Structure

The minumum sequence divergences between the eastern clade and the outgroups are d = 2.18% for the midwestern clade and d = 5.56% for the western clade, as compared with the maximum divergence within the eastern clade at d = 0.91%. Genetic diversities for the eastern clade as well as each subclade and its sampling regions are presented in Table 5-4. Significant population structure existed within the eastern clade

(Φ_{ST} = 0.550, P < 0.001), illustrating that this is not a single panmictic population. Relatively low and nonsignificant population structure was found within the Atlantic (Φ_{ST} = 0.102, P > 0.05) and peninsula (Φ_{ST} = 0.072, P > 0.05) subclades. However, relatively moderate and significant population structure (Φ_{ST} = 0.181, P < 0.05) existed in the A/P/SWGA subclade, perhaps because this subclade does not actually represent a panmictic population illustrated by the few base differences between haplotypes, or the samples were distributed over a large geographic area (Avise, 1994). Pairwise comparisons of Φ_{ST} values and estimates of migrants per generation (Nm) between subclades and sampling regions (with n ≥ 5) are presented in Table 5-5. The three consistently identified subclades illustrate significant populations structure as well as extremely limited gene flow between each other indicating that they may be separate populations.

Discussion

MP and NJ methods recovered identical well-supported (100%) major monophyletic groups of *L. getula*: western, midwestern, and eastern (Figs. 5-3 ? 5-6). The minumum divergences between the eastern clade and both the midwestern and western clades is 2.18% and 5.56%, respectively. My genetic distances between clades are within the range reported between many other closely related snake species (Johns and Avise, 1998, Pook et al., 2000; Burbrink et al., 2000). Because there exists a clear genetic separation of *L. getula* populations from east and west of the Appalachian Mountains along with the fact that these populations can be distinguished using morphology, the eastern and midwestern clades may represent separate evolutionary

lineages, and may be recognizable at the species level. However, I hesitate at this time to propose nomenclatural rearrangements at this time using a limited sampling of individuals for determining species. Although I believe the opportunity for gene flow may exist between the eastern and midwestern clades on the southwestern side of the Appalachian Mountains, further investigation is required to clarify their relationships.

MP and NJ analyses consistently produced the same three subclades within the eastern clade: Atlantic, A/P/SWGA and peninsula. A shallow tree with few diagnostic substitutions between subclades indicates a relatively high degree of gene flow among these populations and/or their divergence has been recent (Rodriguez-Robles et al., 1999c). Yet, congruence among data sets is probably the best arbiter of the accuracy of phylogenetic results (Miyamoto and Cracraft, 1991; Slowinski, 1993; Slowinski and Keogh, 2000), thus these subclades probably are the results of past geological and evolutionary events. Very high and significant population genetic structure was found throughout the eastern clade (Table 3-5), suggesting that this is not a single panmictic population. Additionally, the number of migrants per generation is extremely low ($Nm < 0.23$) suggesting that gene flow is severely restricted between these subclades. This low Nm value further demonstrates the high degree of isolation between sampling regions because an excess of four migrants per generation ($Nm \geq 4$) is required to homogenize populations at mitochondrial loci and offset the effects of drift (Birky et al., 1983; Avise, 1994).

Table 5-1. Haplotype, sample, voucher number and locality of kingsnakes, *Lampropeltis getula* complex used in this study for DNA analyses. Number next to sample indicates that more than one sample was used from the same general locality. Asterisk next to number in parentheses indicates that identical sample was used in morphological analyses.

Haplotype	Sample	Voucher No., Locality
A	Liberty, FL[1]	UF 105383 (*Lg 10, KLK-xx211); U.S.: Florida, Liberty Co., SR 67, 3.7 km S SR 20
B	Liberty, FL[2]	KLK-xx213 (*Lg 26); U.S.: Florida, Liberty Co., SR 67, just N Liberty-Franklin Co. line
C	Liberty, FL[3]	KLK-xx239 (*Lg 27); U.S.: Florida, Liberty Co., near junction NFR 103 and 116
C	Liberty, FL[4]	KLK-xx240 (*Lg 28); U.S.: Florida, Liberty Co., near junction NFR 103 and 116
D	Liberty, FL[5]	DBM-104 (*Lg 30); U.S.: Florida, Liberty Co.
E	Liberty, FL[6]	DBM-50 (*Lg 32); U.S.: Florida, Liberty Co., NFR 110 2.9 km S jct 111
F	Liberty, FL[7]	KLK-xx247 (*Lg 58); U.S.: Florida, Liberty Co., NFR 139
G	Liberty, FL[8]	KLK-xx537 (Lg 31); U.S.: Florida, Liberty Co.
H	Franklin, FL[1]	KLK-xx220 (*Lg 45); U.S.: Florida, Franklin Co., US 98, 7 km E C30
I	Franklin, FL[3]	KLK-xx231 (*Lg 55); U.S.: Florida, Franklin Co., Tates Hell Swamp near New River
J	Bay, FL	KLK-xx227 (*Lg 52); U.S.: Florida, Bay Co., SR 22, 32.1 km W Wewahitchka
J	Calhoun, FL[1]	UF 114321 (*Lg 5, KLK-xx031); U.S.: Florida, Calhoun Co., Blountstown
J	Calhoun, FL[2]	KLK-xx032 (Lg 6); U.S.: Florida, Calhoun Co., Blountstown
J	Franklin, FL[2]	KLK-xx221 (*Lg 46); U.S.: Florida, Franklin Co., US 98, 9.5 km W Carrabelle
J	Leon, FL[1]	KME-m3 (*Lg 13); U.S.: Florida, Leon Co., Bloxham cutoff
K	Gadsden, FL	KLK-xx222 (*Lg 47); U.S.: Florida, Gadsden Co., US 90 5.7 km W Quincy
L	Gulf, FL[1]	KME-m25 (*Lg 11); U.S.: Florida, Gulf Co., Port St. Joe
M	Gulf, FL[2]	KME-m26 (*Lg 15); U.S.: Florida, Gulf Co., Port St. Joe
N	Holmes, FL	KLK-xx257 (*Lg 65); U.S.: Florida, Holmes Co., Rt 179A, 3.8 km SW SR 2
O	Jackson, FL	KLK-xx491 (*Lg 107); U.S.: Florida, Jackson Co., CR 271
P	Jefferson, FL[1]	KLK-xx225 (*Lg 50); U.S.: Florida, Jefferson Co., Goosepasture Rd, 1.9 km S Tram Rd
Q	Jefferson, FL[2]	KLK-xx538 (Lg 105); U.S.: Florida, Jefferson Co.
R	Leon, FL[2]	KLK-xx226 (*Lg 51); U.S.: Florida, Leon Co., Meridian Rd, 0.2 km S Meridian Hills Rd
S	Wakulla, FL[1]	KME-m13 (*Lg 12); U.S.: Florida, Wakulla Co., junction of NFR 313 and 312
S	Wakulla, FL[2]	KME-f3 (*Lg 14); U.S.: Florida, Wakulla Co., Arren
T	Banks, GA	KLK-xx350 (*Lg 117); U.S.: Georgia, Banks Co., Yonah Church Rd, 9.8 km W Homer
U	Echols, GA	KME-m10 (*Lg 18); U.S.: Georgia, Echols Co., Statenville
V	Thomas, GA	KLK-xx524 (*Lg 134); U.S.: Georgia, Thomas Co., Ochlockonee River
W	Walton, GA	UF 121162 (*Lg 119); U.S.: Georgia, Walton Co., Loganville

Table 5-1—Continued.

Haplotype	Sample	Voucher No., Locality
X	Charleston, SC[2]	KLK-xx528 (* Lg 120); U.S.: South Carolina, Charleston Co., Edisto Island
Y	Greenwood, SC	KLK-xx522 (* Lg 129); U.S.: South Carolina, Greenwood Co., US 221, 2.6 km W Hwy 10
Z	McCormick, SC	KLK-xx531 (Lg 24); U.S.: Florida, South Carolina, McCormick Co., Long Cane Creek, junction SR 81 and SR 28
aa	Jasper, SC	KLK-xx526 (* Lg 99); U.S.: South Carolina, Jasper Co.
bb	Mitchell, GA	KME-m27 (* Lg 17); U.S.: Georgia, Mitchell Co., Cotton
bb	Randolph, GA	KLK-xx523 (* Lg 133); U.S.: Georgia, Randolph Co.
bb	Dare, NC[2]	KLK-xx525 (* Lg 111); U.S.: North Carolina, Dare Co., Hatteras Island
cc	Dare, NC[1]	KLK-xx530 (* Lg 121); U.S.: North Carolina, Dare Co., Hatteras Island
cc	Dare, NC[3]	KLK-xx532 (Lg 104); U.S.: North Carolina, Dare Co., Hatteras Island
cc	Watauga, NC	KLK-xx520 (* Lg 29); U.S.: North Carolina, Watauga Co., Triplett
cc	Charleston, SC[1]	KLK-xx521 (* Lg 37); U.S.: South Carolina, Charleston Co., Adams Run
dd	Charlotte, FL	KLK-xx533 (Lg 34); U.S.: Florida, Charlotte Co., SR 776, S Englewood
ee	Dade, FL[1]	KLK-94021 (Lg 3); U.S.: Florida, Dade Co., C-111 basin
ff	Dade, FL[2]	KLK-xx161 (Lg 7); U.S.: Florida, Dade Co., Krome Ave, 2 km S Tamiami Trail
gg	Hendry, FL	KLK-xx534 (Lg 19); U.S.: Florida, Hendry Co., Hwy 80A, 18 km SE Clewiston
hh	Lee, FL	KLK-xx527 (* Lg 35); U.S.: Florida, Lee Co., Gasparilla Island, Boca Grande
hh	Pinellas, FL[2]	UF 121121 (* Lg 4, KLK-xx030); U.S.: Florida, Pinellas Co., Pinellas Park
ii	Monroe, FL	UF 123777 (* Lg 36, KLK-xx490); U.S.: Florida, Monroe Co., Key Largo
jj	Palm Beach, FL	KLK-xx535 (Lg 20); U.S.: Florida, Palm Beach Co., King Ranch S South Bay
kk	Dixie, FL	KLK-xx316 (* Lg 115); U.S.: Florida, Dixie Co., CR 361, 5.7 km S Rocky Creek
ll	Duval, FL	KME-f11 (* Lg 16); U.S.: Florida, Duval Co., Jacksonville
mm	Hernando, FL	UF 111101 (* Lg 23, KLK-xx230); U.S.: Florida, Hernando Co., Hernando Beach
nn	Hillsborough, FL	KLK-xx195 (Lg 8); U.S.: Florida, Hillsborough Co., Gibsonton
oo	Levy, FL[1]	KLK-xx536 (Lg 22); U.S.: Florida, Levy Co., just N Cedar Key
pp	Levy, FL[2]	KLK-xx539 (Lg 116); U.S.: Florida, Levy Co., Cedar Key
qq	Pinellas, FL[1]	KLK-xx160 (Lg 2); U.S.: Florida, Pinellas Co., Gandy Blvd
rr	Terrebonne, LA	KLK-xx519 (* Lg 59); U.S.: Louisiana, Terrebonne Parish, Houma
ss	Perry, MS	KLK-xx259 (* Lg 90); U.S.: Mississippi, Perry Co.
tt	Trigg, KY	KLK-xx262 (* Lg 93); U.S.: Kentucky, Trigg Co.
uu	Stewart, TN	KLK-xx529 (Lg 96); U.S.: Tennessee, Stewart Co.
uu	Calloway, KY	KLK-xx232 (* Lg 56); U.S.: Kentucky, Calloway Co.
vv	Graham, AZ	JF25sY; U.S.: Graham Co., AZ
ww	Sonora, Mexico	JF14sY; Mexico: Sonora
xx	Borrego Desert, CA	JF23sY; U.S.: Borrego Desert, CA

Table 5-2. Oligonucleotide primers used for amplification and sequencing of kingsnakes, *Lampropeltis getula* complex. Primers are listed from left to right in the 5' to 3' direction. Reference position corresponds to location when aligned with *Dinodon semicarinatus* (Kumazawa et al., 1996).

Primer	Reference Position	Primer Sequence
Cytochrome *b*		
LGL765	14895-14919	GAA AAA CCA YCG TTG TWA TTC AAC T
H15919	16097-16072	GAC CCA KCT TTG RYT TAC AAG GAC AA
CYB 1L	15271-15292	CTT ATA GCA ACA GCC TTC TTC G
CYB 2L	15670-15688	TTC TCA AAG GCT AAT CCA C
CYB 1H	15786-15766	GAG GGC TAC AGT TCC ACC AAG
CYB 2	15340-15307	AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A
ND4 Region		
ND4	11671-11702	CAC CTA TGA CTA CCA AAA GCT CAT GTA GAA GC
Leu	12594-12569	CAT TAC TTT TAC TTG GAT TTG CAC CA
ND4 1L	12086-12105	TCC TAC CAA TAC TCA CAA CC
ND4 1H	12182-12163	GAT GCA ATT AGT AGT TCT CC

Table 5-3. Variable sites observed in Cytochrome b and ND4 sequences of *Lampropeltis getula*. The 49 haplotypes are indicated as letters A through ww. Vertical numbers at top indicate locations of polymorphic sites within the 1864 bp sequence.

	2	11	26	32	44	47	50	53	59	76	77	116	122	125	128	137	146	170	186	188	200	206	215	221	227	233	242	245	254	257	278	281	293	317	332	347
Consensus	C	A	A	A	A	T	A	G	C	T	C	T	T	A	T	T	T	G	C	T	C	C	T	T	C	T	A	A	C	A	A	G	C	A	T	A
A	A																																			
B	A																																			
C	A																																			
D	A																																			
E	A																																			
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Table 5-3—Continued.

	2	11	26	32	44	47	50	53	59	76	77	116	122	125	128	137	146	170	186	188	200	206	215	221	227	233	242	245	254	257	278	281	293	317	332	347
Consensus	C	A	A	A	A	T	A	G	C	T	C	T	T	A	T	T	T	G	C	T	C	C	T	T	C	T	A	A	C	A	A	G	C	A	T	A
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uu					G		G									C											C		T			A	T			
vv		G	T	G	G			A	A	C			C	C	C		C		A	A		T	C	C	T	C	C	G	T		G	A	T			
ww	A	G		G	G			A	A	C			C	C	C		C	A		A	A	T		C	T	C	C		T			A		G		G
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Table 5-3—Continued.

	359	390	397	401	404	407	434	437	440	443	458	461	479	482	488	503	509	512	521	527	530	531	534	549	560	567	576	578	582	587	608	620	632	638	650	655
Consensus	A	C	C	A	A	C	C	A	C	G	C	A	C	C	C	C	T	C	C	C	C	A	G	G	T	T	A	T	G	C	G	C	T	T	A	T
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Table 5-3—Continued.

	359	390	397	401	404	407	434	437	440	443	458	461	479	482	488	503	509	512	521	527	530	531	534	549	560	567	576	578	582	587	608	620	632	638	650	655
Consensus	A	C	C	A	A	C	C	A	C	G	C	A	C	C	C	C	T	C	C	C	C	A	G	G	T	T	A	T	G	C	G	C	T	T	A	T
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xx		T	T	G	G		T	G	G		T		T	T	T	T	T	C				T	G	A	A		C	C			T	A		A		C	C

Table 5-3—Continued.

	656	657	658	660	662	665	667	668	671	695	697	716	722	725	728	743	755	758	765	776	779	783	791	797	805	814	818	823	826	827	830	842	843	854	860	866
Consensus	A	C	T	T	C	C	T	T	A	T	A	G	T	A	A	C	A	G	T	C	A	C	G	A	T	C	C	G	A	G	A	C	C	A	T	C
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Table 5-3—Continued.

	656	657	658	660	662	665	667	668	671	695	697	716	722	725	728	743	755	758	765	776	779	783	791	797	805	814	818	823	826	827	830	842	843	854	860	866
Consensus	A	C	T	T	C	C	T	T	A	T	A	G	T	A	A	C	A	G	T	C	A	C	G	A	T	C	C	G	A	G	A	C	C	A	T	C
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vv					T	A										T	G		C				A		C		A	A				T		C	
ww	G				T	A				C		A				T	G		C	T	T		A	G	C		A	A						C	
xx		A	C	C	T	T	A		C	C		A	G		G	T	G	A	C	T	T	T	A		G	G	A	A	G				G		C	

Table 5-3—Continued.

	869	872	873	875	893	899	905	911	923	924	929	935	941	958	959	968	977	986	995	999	1019	1028	1046	1049	1071	1075	1076	1080	1081	1086	1095	1097	1100	1103	1109	1140
Consensus	C	C	T	T	T	A	G	C	T	C	A	C	T	C	T	C	A	C	T	G	C	C	G	C	A	C	T	A	C	T	C	A	G	A	C	A
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Table 5-3—Continued.

	869	872	873	875	893	899	905	911	923	924	929	935	941	958	959	968	977	986	995	999	1019	1028	1046	1049	1071	1075	1076	1080	1081	1086	1095	1097	1100	1103	1109	1140
Consensus	C	C	T	T	T	A	G	C	T	C	A	C	T	C	T	C	A	C	T	G	C	C	G	C	A	C	T	A	C	T	C	A	G	A	C	A
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vv			C	C		G	A	T		T		A			C			T								C			C	T	C		G	T	
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xx	G	G	C				A			T			C		C			T	C					T		C	G		C			A			

Table 5-3—Continued.

	141	175	176	178	188	196	205	241	256	259	265	268	271	278	280	292	307	313	334	337	343	355	364	367	368	379	385	397	415	421	424	433	439	457	461	468
Consensus	T	T	G	C	G	A	A	T	C	T	A	G	A	G	T	C	T	A	T	T	G	C	C	C	C	T	C	A	T	C	A	T	A	G	T	T
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Table 5-3—Continued.

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4
	4	7	7	7	8	9	0	4	5	5	6	6	7	7	8	8	9	0	1	3	3	3	4	5	6	6	6	7	8	9	1	2	2	3	3	5	6	6
	1	5	6	8	8	6	5	1	6	9	5	8	1	8	0	2	7	3	4	7	3	5	4	7	8	8	9	5	7	5	1	1	4	3	9	7	1	8
Consensus	T	T	G	C	G	A	A	T	C	T	A	G	A	G	T	C	T	A	T	T	G	C	C	C	C	T	C	A	T	C	A	T	A	G	T	T
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uu										C		C		T							A			T					G						
vv		A		T				C		C		C	G		A	T	C		C	C		T	T				T	G	C	A		G	A	C	C
ww			T	T				C				C	G		A	T	C		C	C		T	T		T		T			G	G		G	A	C	C
xx	C			T				C	T	C		C	G		A	T			C	C	A	T	T		T		T			G	G		G	A	C	C

Table 5-3—Continued.

	1473	1481	1493	1526	1543	1547	1550	1562	1575	1586	1593	1604	1607	1610	1617	1628	1630	1640	1641	1645	1652	1658	1659	1702	1703	1710	1736	1739	1749	1779	1798	1819	1820	1821	1843	1846
Consensus	C	T	A	T	A	A	T	C	C	C	G	C	A	T	C	A	T	T	C	T	T	T	C	T	T	T	G	A	G	C	A	G	T	G	C	C
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Table 5-3—Continued.

	1473	1481	1493	1526	1543	1547	1550	1562	1575	1586	1593	1604	1607	1610	1617	1628	1630	1640	1641	1645	1652	1658	1659	1702	1703	1710	1736	1739	1749	1779	1798	1819	1820	1821	1843	1846
Consensus	C	T	A	T	A	A	T	C	C	C	G	C	A	T	C	A	T	T	C	T	T	T	C	T	T	T	G	A	G	C	A	G	T	G	C	C
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vv	T						C	T	T			T		C					T					C			A			T	G				T	T
ww	T			C	G		C		T			T												C	C		A		A	T	G		C		T	T
xx	T		G		G		C		T			T						C						C	C		A	G	A	T	G		C		T	T

Table 5-4. Genetic diversities and haplotypes of kingsnakes, *Lampropeltis getula*, for the eastern U.S. clade, and three main subclades and sampling regions. A/P/SW GA = Apalachicola/Panhandle/SW Georgia subclade, EAL and WAL = eastern and western Apalachicola Lowlands respectively, SW GA = SW Georgia, C&N Intergrade Zone = hypothesized intergradation zone in the central and northern peninsula between *L. g. getula* and *L. g. floridana*, *N*= No. of individuals, Φ_{ST} = levels of genetic exchange, p = nucleotide diversity, *h* = haplotype diversity, number in parentheses indicates the number of samples with each haplotype. Asterisk next to Φ_{ST} value indicates significant genetic structure: $*P < 0.05$, $**P < 0.001$.

Clade/Subclade	Region	*N*	Φ_{ST}	p	*h*	Haplotypes
Atlantic		**11**	**0.102**	**<0.000**	**0.890**	
	Atlantic Mainland	8		0.001	0.964	T, W, X, Y, Z, aa, cc(2)
	Outer Banks	3		<0.000	0.666	bb, cc(2)
A/P/SW GA		**29**	***0.181**	**0.001**	**0.968**	
	EAL	10		0.002	0.977	A, B, C(2), D, E, F, G, I, J
	WAL	5		0.001	0.900	H, J(2), L, M
	N&E of EAL	8		0.001	0.964	J, K, R, P, S(2), O, Q
	N&W of WAL	2		<0.000	1.000	J, N
	SW GA	4		0.001	0.833	U, V, bb(2)
Peninsula		**15**	**0.072**	**0.002**	**0.981**	
	C&N Intergrade Zone	7		0.003	1.000	hh, jj, kk, ll, nn, oo, pp
	Central and Southern	5		0.001	0.900	dd, gg(2), hh, mm
	Extreme Southern	3		0.001	1.000	ee, ff, ii
All eastern U.S.		**55**	****0.562**	**0.003**	**0.984**	

Table 5-5. Population structure and levels of genetic exchange, Φ_{ST} (below diagonal) and *Nm* (above diagonal), between the three main subclades and sampling regions (with n ≥ 5) in the eastern U.S. for kingsnakes, *Lampropeltis getula*. 1 = Atlantic, 2 = Apalachicola/Panhandle/SW Georgia and 3 = Peninsula subclades; 4 = Atlantic mainland, 5 = eastern Apalachicola Lowlands (EAL), 6 = western Apalachicola Lowlands, 7 = N&E of EAL, 8 = central and northern peninsular intergradation zone, 9 = Central and Southern peninsula. Dashed line for Φ_{ST} or *Nm* indicate n < 5.

	1	2	3	4	5	6	7	8	9
1	——	0.223	0.227	——	0.174	0.123	0.153	0.219	0.135
2	0.528	——	0.175	0.212	——	——	——	0.179	0.15
3	0.524	0.587	——	0.231	0.181	0.174	——	——	——
4	——	0.540	0.519	——	0.179	0.122	0.153	0.234	0.140
5	0.589	——	0.579	0.582	——	2.623	3.782	0.202	0.152
6	0.670	——	0.589	0.672	0.087	——	3.596	0.191	0.106
7	0.619	——	——	0.619	0.062	0.065	——	0.196	0.125
8	0.533	0.582	——	0.516	0.553	0.566	0.560	——	249.7
9	0.649	0.625	——	0.640	0.621	0.702	0.666	0.001	——

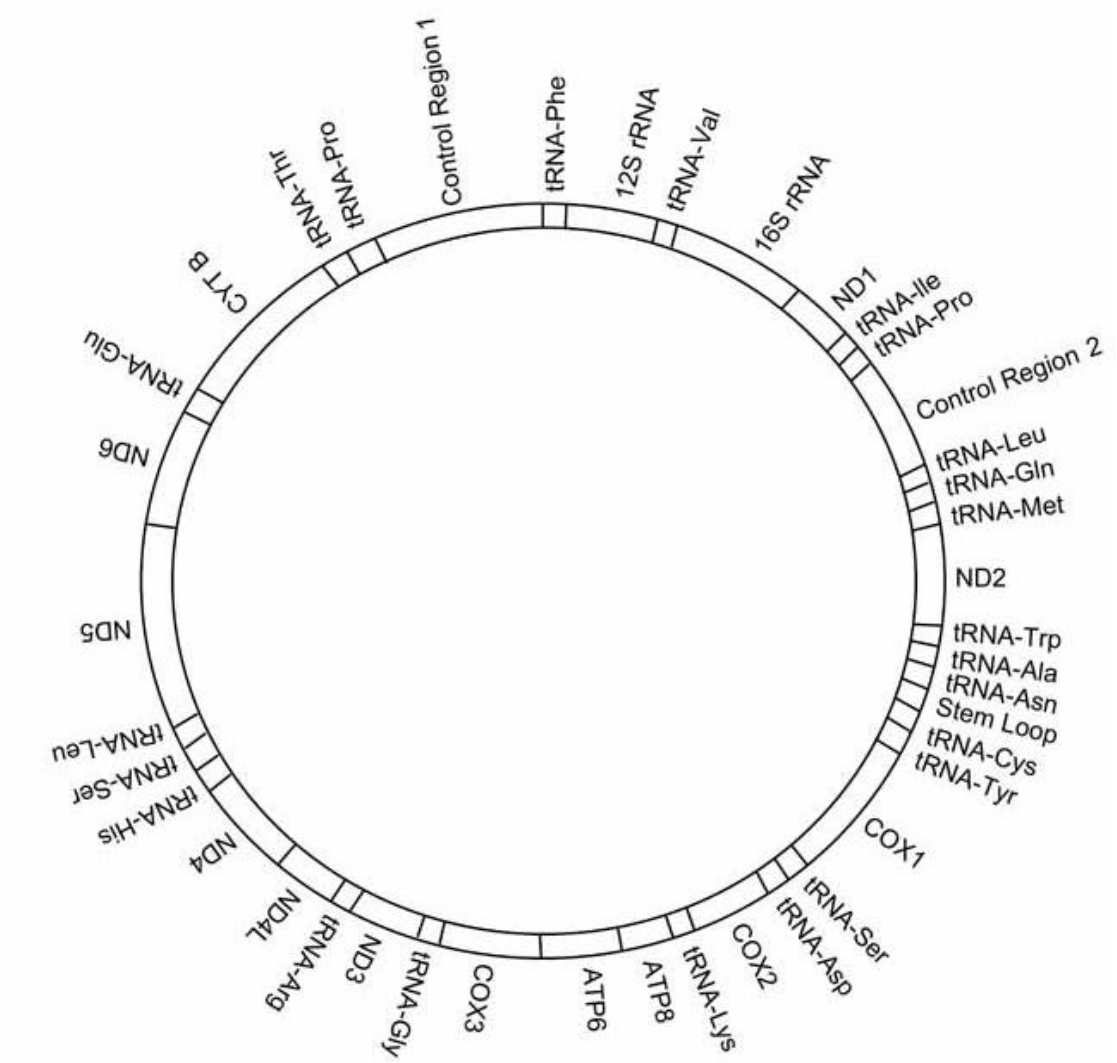

Fig. 5-1. Gene order of snake mitochondrion depicted from *Dinodon semicarinatus* (Kumazawa et al., 1996). Note that there is a duplicated control region nested between tRNA-Pro and tRNA-Leu.

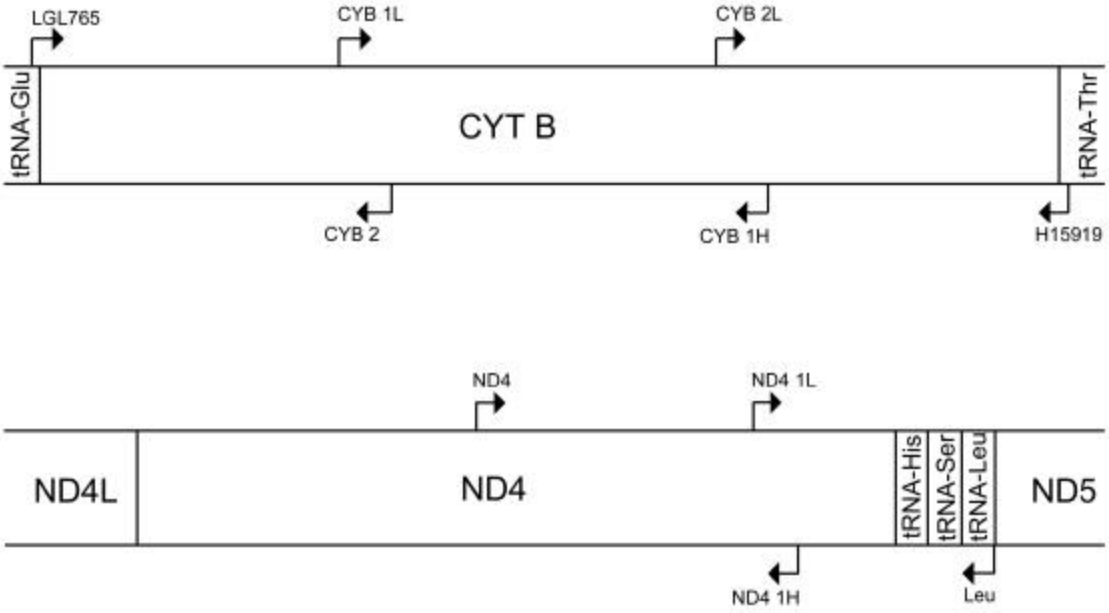

Fig. 5-2. Cytochrome *b* and ND4 regions of mtDNA sequenced for kingsnakes, *Lampropeltis getula* complex, illustrating approximate annealing positions of oligonucleotide primers. Arrows indicate the 5’ to 3’ direction, and their sequences are listed in Table 2.

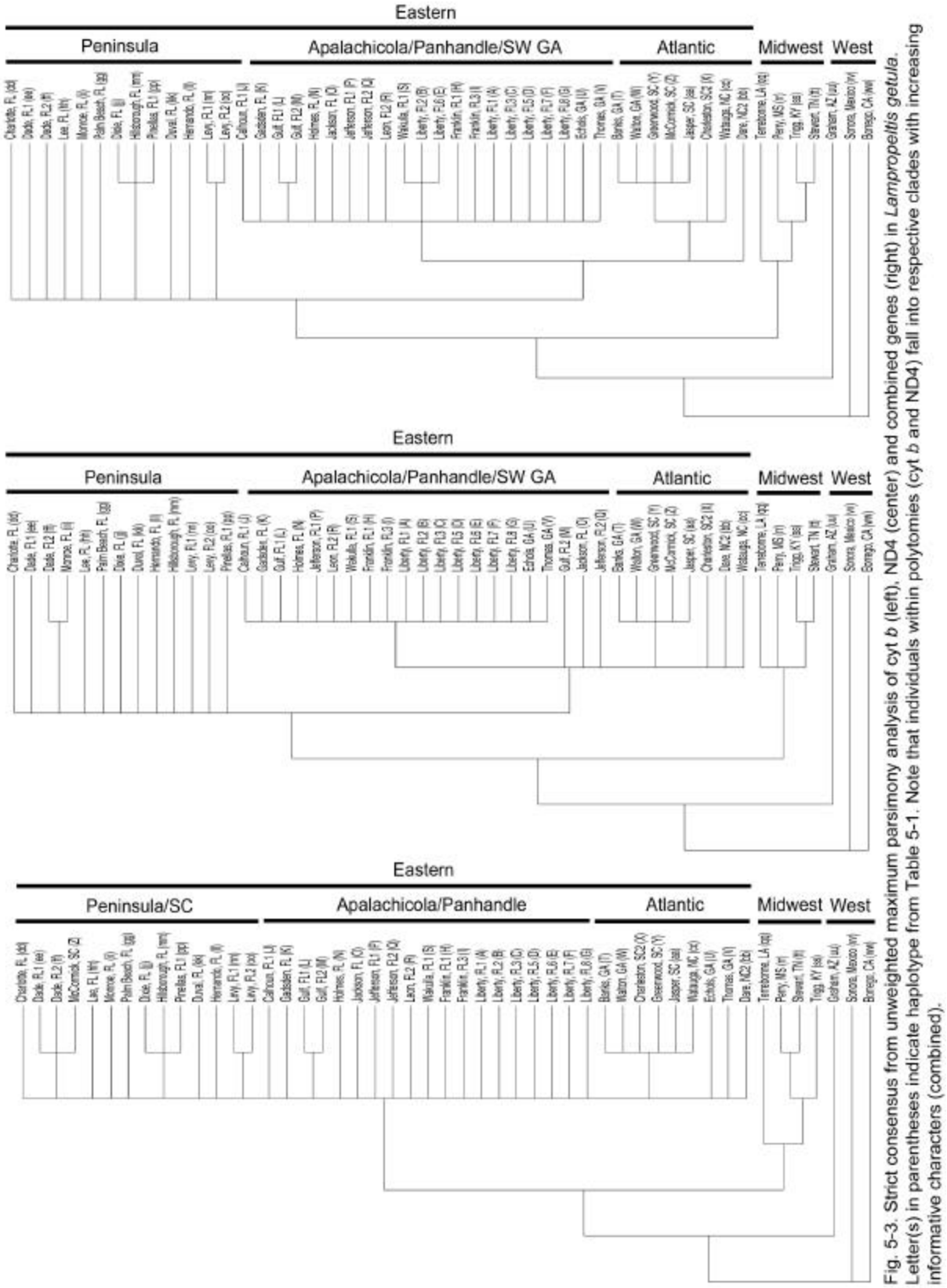

Fig. 5-3. Strict consensus from unweighted maximum parsimony analysis of cyt *b* (left), ND4 (center) and combined genes (right) in *Lampropeltis getula*. Letter(s) in parentheses indicate haplotype from Table 5-1. Note that individuals within polytomies (cyt *b* and ND4) fall into respective clades with increasing informative characters (combined).

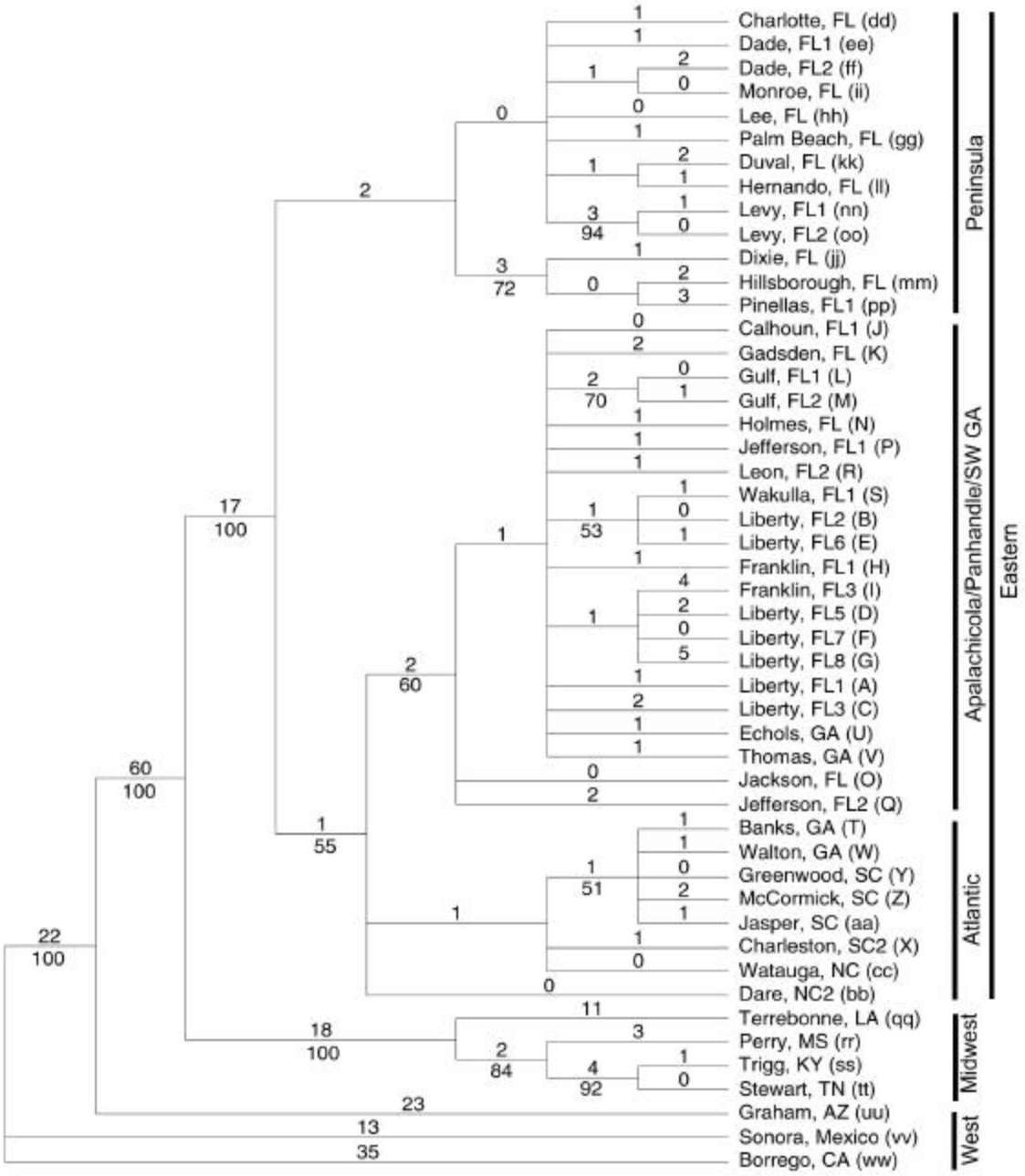

Fig. 5-4. Random single representative of 2474 trees with number of base differences (above) and bootstrap values (> 50%, below) from unweighted maximum parsimony analysis with combined cyt *b* and ND4 genes in *Lampropeltis getula*. Letter(s) in parentheses indicate haplotype from Table 5-1.

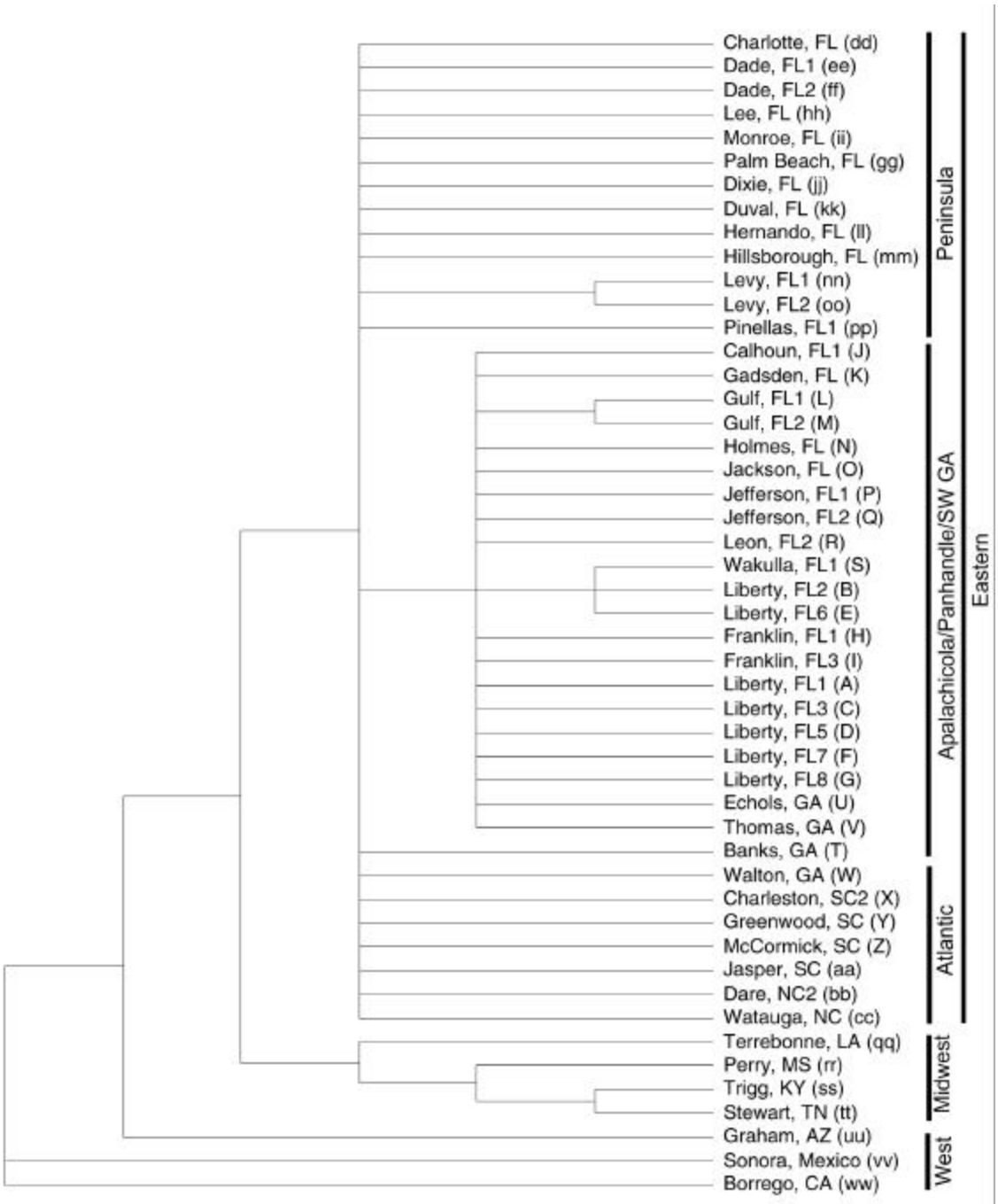

Fig. 5-5. Strict consensus of 5143 most parsimonious trees (CI=0.831, RI=0.893) from weighted maximum parsimony analysis of combined cyt *b* and ND4 genes in *Lampropeltis getula*. Letter(s) in parentheses indicate haplotype from Table 5-1.

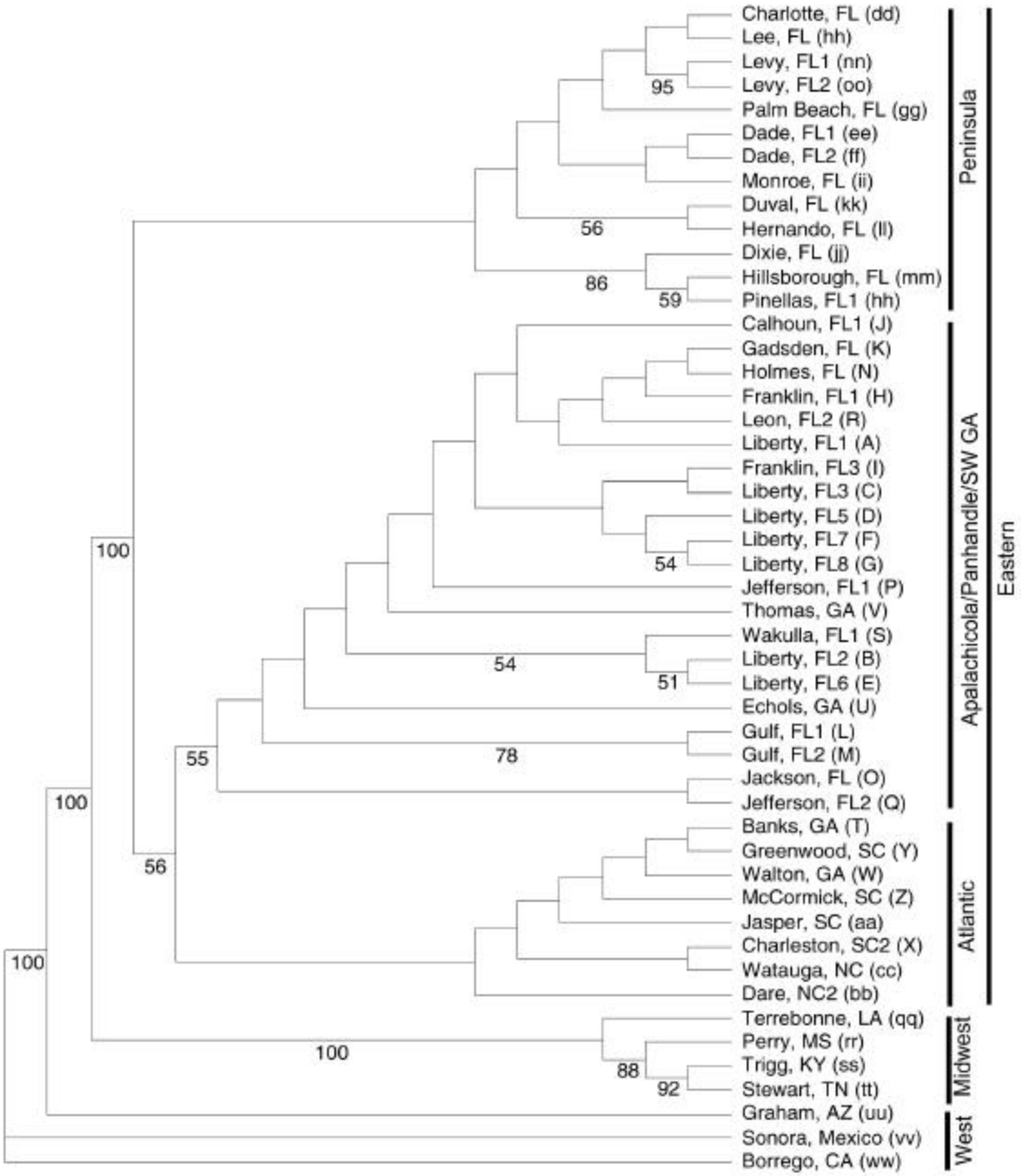

Fig. 5-6. Neighbor-joining tree with bootstrap values (> 50%) of combined cyt *b* and ND4 genes in *Lampropeltis getula*. Letter(s) in parentheses indicate haplotype from Table 5-1.

CHAPTER 6
CONCLUSIONS

Phylogeography

All morphological and molecular analyses performed in this study support a western origin of *L. getula* in the eastern U.S. The evolutionary history of eastern *L. getula* appears to be linked to the geological history of the Coastal Plains derived from ancient coastlines. Fossil remains indicate that ancestral western *L. getula* utilized a Gulf Coast corridor to disperse east into Florida during low sea levels in the Pliocene between 2-5 million years ago (Mya) (Auffenburg, 1963). Estimates of mtDNA sequence divergence for reptile species range from 0.47 to 1.32% per million years (Zamudio and Greene, 1997). The smallest percentage sequence divergence between the eastern and western clades of *L. getula* is 5.56%, which translates into 4.2-11.8 Mya, a time frame that overlaps the sequence of events hypothesized by Auffenburg (1963). Although some midwestern samples were much closer geographically to eastern samples, they are much less closely related relative to the range of divergences within the eastern clade. A rapid range expansion from southern refugia into northern areas as glaciers retreated could account for the high haplotype diversity and low genetic distances (maximum $d = 0.91\%$) in the east in comparison with other geographic areas. Interestingly, additional snake taxa with similar distributions in the midwestern and eastern U.S. have been reported to exhibit similar phylogeographical patterns (Rodriguez-Robles and Jesus-Escobar, 1999b, 1999a; Burbrink et al., 2000; Burbrink, 2001). Thus, the evolution of the three identified

subclades within the eastern clade is probably related to more recent glacial events during the Pleistocene (10,000-2 Mya).

The lowest sequence divergence between the eastern and midwestern clades is 2.18%, which translates into 1.65-4.6 Mya (early Pleistocene to early Pliocene). There were four major glacial events during the Pleistocene, with the first being the greatest followed by less intense episodes (Webb, 1990; Brown and Lomolino, 1998). During these glacial events sea level was >100 meters (m) lower than present-day (Lidz and Shinn, 1991), Florida was nearly twice its present size and land was continuous from the present Florida mainland to the Dry Tortugas (MacNeil, 1950; Hoffmeister and Multer, 1968). In order to escape from cooler climates and ice masses, extreme northeastern *L. getula* populations must have been extirpated or pushed southward, whereas peninsular and panhandle populations experienced an expansion following suitable habitat. These conditions of displacement and expansion would have promoted mixing among SE U.S. populations. This is evident because of their close genetic relationships as well as certain shared morphological characters such as ontogenetic interband lightening found in Florida and as far north as the Outer Banks of North Carolina (Barbour and Engles, 1942; Lazell and Musick, 1973; Blaney, 1977). However, a less likely but alternative hypothesis is that the character of ontogenetic interband lightening evolved multiple times along the Coastal Plains. During major interglacial events much of present-day Florida was inundated except for higher elevations in the peninsula and panhandle. These areas of higher elevations have been identified as ancient shorelines in the peninsula (Jackson, 1973; Webb, 1990; Clark et al., 1999), as well as ancient barrier islands in the eastern Apalachicola Lowlands (Brenneman, 1957; Brenneman and Tanner,

1958). During these times, Atlantic populations were capable of expanding their range northward following warmer climate, but peninsular and panhandle populations were geographically isolated. Peninsular populations were probably found in mesic habitats extending into the southern peninsula (Watts and Hansen, 1988). Panhandle populations were probably isolated on barrier islands in the eastern Apalachicola Lowlands (Brenneman, 1957), which correlate well with a large number of endemic and relict plants and animals there (Table 3-10; James, 1961; Clewell, 1977; Yerger, 1977; Ward, 1979; Judd, 1982; Gilbert, 1987; Coile, 1996; Chafin, 2000; Chaplin et al., 2000). Thus, the distributions of the Apalachicola Lowlands endemic plants and animals possibly were a result of the same geological event. Since the last glacial maximum around 18,000 years before present (BP), North American glaciers have melted and retreated northward, sea level has risen steadily (Randazzo and Halley, 1997). Again, populations of eastern *L. getula* will eventually become isolated in the peninsula and panhandle, while others expand their range northward.

Taxonomy

Under the Apomorphic Species Concept (ASC), species are considered to be well-supported minimal monophyletic groups. In all morphological and molecular analyses in this study, the eastern populations of *L. getula* represent the smallest well-supported monophyletic group, which suggests recognition as a separate species. Recently, users of the various Phylogenetic and Evolutionary Species Concepts (PSC and ESC respectively) have objected to the subspecies concept because they claim it is not operational within their definitions of reciprocal monophyly (Mayr and Ashlock, 1991; Baum, 1992; Burbrink et al., 2000). Additionally, beginning with Wilson and Brown (1953) the

subspecies concept has been criticized because subspecies were commonly identified on too few and arbitrary delimited characters. And in many cases where several characters were used, each character varied independently because of differing locally adaptive pressures, which resulted in different subspecies distributions and arbitrary cline slices (Frost and Hillis, 1990). Nonetheless, under the ASC one may recognize subspecies as subclades within species, where subclades have weaker support because of occasional gene flow or recent evolutionary divergence (Mishler and Theriot, 2000). Mayr (1969) and Smith et al. (1997) also recognize subspecies as geographic races with relatively homogenous phenotypic patterns, which have the ability to exchange genes with adjacent races. Areas where subspecies come into genetic contact are identified as intergradation zones (Mayr, 1969; Smith et al., 1997). Because gene flow will obscure boundaries of subspecies and prevent them from attaining reciprocal monophyly at the mtDNA level, this criterion should not invalidate subspecies recognition (Patton and Smith, 1994; Rodriguez-Robles et al., 1999c).

The traditional subspecies recognized in *L. getula* in the eastern U.S. correspond closely to the phylogenetic patterns that I have uncovered. After examination of hundreds more specimens than any previous researcher for a study of geographic variation using morphology (Chapter 3), I identified three subspecies in Florida: 1) *L. g. floridana* from central and southern peninsular Florida, 2) *L. g. getula* from NW peninsular Florida north to southern New Jersey, and 3) unnamed populations in the eastern Apalachicola Lowlands. In the morphological and molecular analyses, the three consistently identified subclades correspond exceptionally well to the three identified geographic races (Chapter 3). Because each of these subspecies can be diagnosed by at

least one synapomorphy, this evidence suggests that they represent evolutionary processes rather than ecotypic variants.

Individuals from the western Apalachicola Lowlands were once believed to represent a distinct subspecies, *L. g. goini* (Neill and Allen, 1949). However, Blaney (1977) invalidated *L. g. goini* by speculating that it represented a Pleistocene intergrade between panhandle *L. g. getula* and now disjunct peninsular *L. g. floridana*. Additionally, Means (1977) believed that *L. g. goini* indeed represented an intergrade population, but *L. g. goini* was intermediate between unnamed populations in the eastern Apalachicola Lowlands and *L. g. getula* that surrounds the region. The most consistent subclade with statistical support in morphological and molecular analyses consisted primarily of eastern Apalachicola Lowlands and panhandle individuals. Additionally, there are five synapomorphies supporting the monophyly of the eastern Apalachicola Lowlands populations. Morphological data examined on a much finer geographic scale (Chapter 3) revealed that the eastern Apalachicola Lowlands populations possess relatively homogeneous color patterns that grade into populations in surrounding areas (i.e., gene flow) consisting of *L. g. getula*. Because *L. g. goini* possesses intermediate characters between eastern Apalachicola Lowlands snakes and *L. g. getula*, I relegate *L. g. goini* to intergrade status. Therefore, because *L. g. getula* and *L. g. floridana* are already recognized subspecies, the eastern Apalachicola Lowlands populations deserve equivalent taxonomic recognition as well. As systematists it is our responsibility to document biological diversity, and it is essential to recognize both species and subspecies otherwise everyone worldwide will fail to notice biological diversity without names

(Dobzhansky, 1970; Smith et al., 1997). A taxonomic amendment regarding the eastern Apalachicola Lowlands populations is in progress and will be treated in a separate paper.

I was unable to find evidence supporting the recognition of both *L. g. brooksi* and *L. g. sticticeps* using morphology and mtDNA. Individuals from the extreme southern Florida peninsula were once believed to represent a distinct subspecies, *L. g. brooksi* (Barbour, 1919), yet its validity quickly came into question (Blanchard, 1920, 1921; Wright, 1935). Becasue only 15 individuals from the Florida peninsula were sequenced for mtDNA, this small sample size might have been insuffiecient to find genetic partitioning within the peninsula. Nonetheless, Duellman and Schwartz (1958), Blaney (1977), Krysko (1995), and Krysko (this study) could not find morphological characters for diagnosing *L. g. brooksi*, and the mtDNA data indicate that the Florida peninsula is a panmictic population (Tables 5-4, 5-5). Barbour and Engles (1942) described *L. g. sticticeps* from the Outer Banks of North Carolina based on head morphology and ontogenetic interband lightening of the dorsal pattern (Lazell and Musick, 1973). However, Hillestad et al. (1975), Blaney (1977), Gibbons and Coker (1978) and Palmer and Braswell (1995) did not accept that a distinct geographic race existed on the Outer Banks. My morphological and molecular data further corroborate these authors, as I found snakes from the Outer Banks with mtDNA haplotypes identical to adjacent mainland snakes as well as those as far away as SW Georgia.

This study represents an important contribution to our understanding of the systematics of the *L. getula* complex, as well as species concepts and mtDNA interpretation. My data suggests that not all subspecies are human constructs or arbitrary subdivisions of clines. Like species, they may represent discrete biological entities, albeit

often more recently evolved and characters less differentiated morphologically and genetically. With close examination, using both molecular and morphological data, I believe that an accurate representation of the evolutionary history can be revealed in many species complexes. My phylogenetic hypothesis of the eastern *L. getula* populations should represent the basis for further studies into the midwestern and western complexes. Based on the data I have gathered, I believe that the midwestern and western populations may reveal additional taxa as well.

Future Projections

Although kingsnakes appear to still be widespread because they are occasionally encountered at scattered localities throughout the state, they appear to have declined drastically or completely disappeared from most areas where they were once common and presently exist in only a few disjunct populations. Unfortunately, the projection for the continued existence of kingsnakes in Florida appears bleak based on the alarming decline in encounter rates over the last few decades. Possible causes for the population declines include habitat loss and fragmentation, road mortality, pollution, toxin buildup in tissues, red imported fire ants, and over-collecting by commercial collectors for the pet trade, but a combination of all these factors may be the best explanation.

Although D. Jouvenaz (pers. comm.) believed that red imported fire ants were the sole cause for extirpation of kingsnakes on Paynes Prairie, I believe other factors have contributed to this loss. If fire ants alone are causing population declines, it is not yet apparent, because the largest kingsnake populations in Florida presently exist around Lake Okeechobee, where the density of fire ant mounds is extremely high along canal banks. However, Mount (1981) suggested that there might be a lag time of more than

one decade before the effects of these ants are observed on reptile populations. Nonetheless, the widespread decline of kingsnakes in Florida is a serious conservation problem that requires further documentation and attention, and the causes are in need of prompt resolution.

Habitat Protection

The history of land development regulations in Florida began with wetlands protection in the 1970s (Mitsch and Gosselink, 1993). This directed urban development toward upland communities including sandhill and scrub communities. More recently, policies and regulations for protection of these upland communities have been targeted for conservation easements due to the increasing rarity of these habitats (Florida Department of Environmental Protection and the Florida Greenways Coordinating Council, 1998; Board of Trustees of the Internal Improvement Trust Fund, 1999; Hoctor et al., 2000). This has placed developmental pressures on crucial mesic habitats including longleaf pine forests, which are an important habitat for kingsnakes (Enge, 1997).

Principal reasons for the extensive loss of mesic longleaf pine forests include large-scale industrial logging, interruption of natural fire cycles, industrial agriculture, urbanization, and silviculture (Means, 1996; Platt, 1999). Slash Pine plantations probably have been as responsible for replacing native longleaf pine forests as agriculture (Means, unpubl. data). McWilliams et al. (1993) estimated that pine plantations now make up 36% of all pine stands in the South and projected that within 20 years they will account for 70%. Slash pine plantations are very different habitats from native longleaf pine savanna, especially when management practices are considered. When the surface is

disturbed by fire management or clear cutting practices, many animals normally retreat under ground. However, following tree harvesting, mechanical site preparation (MSP) takes place before replanting. The most commonly used forms of MSP include drum chopping, disking, scalping, and shearing or bulldozing with a KG blade. Unfortunately, any animal remaining directly under the surface during these practices is unlikely to survive. Furthermore, MSP destroys subterranean cavities and other refugia that are vital for vertbrate survival (Means, unpubl. data).

Habitat loss because of poor management practices and development dictates the need for protection of remaining mesic communities. I suggest developing less destructive and improved management practices for silviculture, which result in plantations that more closely simulate the natural community. Additionally, restoration of areas to their native vegetation and physiognomy must take place. The State of Florida currently has the fourth largest human population in the U.S. (U.S. Census Bureau, 2001), and it is expected to become the third most populated state by 2025. Therefore, large tracts of land must be set aside now and protected from development to insure the continued existence of *L. getula* as well as other native plants and animals.

Species Protection

Most *L. getula* populations in Florida have declined severely or been extirpated over the last few decades (Wilson and Porras, 1983; Krysko, 1995; Means, 2000), leaving few remaining isolated populations scattered around the state. My genetic data suggest that the three subclade regions are demographically isolated from each other and, at least, should be considered as distinct management units (Avise, 1994; Bowen, 1998). Management units are populations that have significant divergence of allele frequencies

at the nuclear or mitochondrial level (Moritz, 1994). Populations that are not strongly connected by gene flow at the present time, as for the three identified subclade regions, are not likely to recover from additional factors such as fragmentation by natural recruitment from other populational sources (Avise, 1994). Therefore, I believe that the protection status of all Florida *L. getula* populations must be re-evaluated promptly in order to preserve biodiversity.

Populations of *L. getula* in Florida are protected only in national and state parks, and no other populations outside of these areas receive protection by state agencies. In order to help prioritize vertebrate conservation efforts in Florida, biological scores were developed to rank taxa according to their biological vulnerability, extent of current knowledge of population status, and management needs (Millsap et al., 1990). The protection status of taxa (with biological scores) include endangered (> 32), threatened (29 - 32), and species of special concern (24 - 28)(Millsap et al., 1990). More than ten years ago, biological scores of 18 and 13 were assigned to the Florida kingsnake (*L. g. floridana*) and eastern kingsnake (*L. g. getula*), respectively (Millsap et al., 1990). Yet, there is no mention of the Apalachicola populations of *L. getula*. Other species that are encountered much more often in the wild than kingsnakes, and presently receive protection by the State of Florida (endangered, threatened, or species of special concern) include the gopher frog (*Rana areolata*), striped newt (*Notophthalmus perstriatus*), green turtle (*Chelonia mydas*), loggerhead turtle (*Caretta caretta*), gopher tortoise (*Gopherus polyphemus*), Florida scrub lizard (*Sceloporus woodi*), and lower keys corn snake (*Elaphe guttata*). Because most populations of *L. getula* have been reduced to

fragmented populations throughout the state over the last few decades, I believe that each of the three subspecies of *L. getula* in Florida need to be reevaluated immediately.

Protection by the State of Florida include those organisms that are designated as endangered, threatened or species of special concern. Within these categories, species are defined as a (1) species, (2) subspecies, or (3) isolated population (Florida Fish and Wildlife Conservation Commision, 2001). Below are the guidelines for "species of special concern", as listed by the Florida Fish and Wildlife Conservation Commision (2001).

> (73) Species of special concern — As designated by the Commission, a species subspecies, or isolated population of a subspecies which is facing a moderate risk of extinction in the future, as determined by (a), (b), (c), (d) or (e) below:
>
> (a) Population reduction in the form of either:
>
> 1. An observed, estimated, inferred or suspected reduction of at least 20% over the last ten years or three generations, whichever is longer, based on, and specifying, any of the following:
>
> a. Direct observation
>
> b. An index of abundance appropriate for the species
>
> c. A decline in area of occupancy, extent of occurrence and/or quality of habitat
>
> d. Actual or potential levels of exploitation
>
> e. The effects of introduced species, hybridization, pathogens, pollutants, competitors or parasites.
>
> 2. A reduction of at least 20%, projected or suspected to be met within the next ten years or three generations, whichever is longer, based on, and specifying, any of 1.b, 1.c, 1.d or 1.e above.
>
> (b) Extent of occurrence estimated to be less than 7,700 square miles or area of occupancy estimated to be less than 770 square miles, and estimates indicating any two of the following:
>
> 1. Severly fragmented or known to exist at only a single location.

2. Continuing decline, observed, inferred or projected, in any of the following:

a. Extent of occurrence

b. Area of occupancy

c. Area, extent and/or quality of habitat

d. Number of locations or subpopulations

e. Number of mature individuals.

3. Extreme fluctuations in any of the following:

a. Extent of occurrence

b. Area of occupancy

c. Number of locations or subpopulations

d. Number of mature individuals.

(c) Population estimated to number fewer than 10,000 mature individuals and either:

1. An estimated continuing decline of at least 10% within ten years or three generations, whichever is longer or

2. A continuing decline, observed, projected, or inferred, in numbers of mature individuals and populations structure in the form of either:

a. Severely fragmented (i.e., no subpopulation estimated to contain more than 1,000 individuals)

b. All individuals are in a single subpopulation

(d) Population very small or restricted in the form of either of the following:

1. Population estimated to number fewer than 1,000 mature individuals

2. Population is characterized by an acute restriction in its area of occupancy (less than 40 square miles) or in the number of locations (fewer than 5).

(e) Quantitative analysis showing the probability of extinction in the wild is at least 10% within 100 years.

Based on the state's definitions, I believe that *L. g. floridana* and *L. g. getula* most appropriately fall under the "species of special concern" category at the present time. These taxa almost certainly face a moderate risk of extinction in the future, as determined by (a), (b), and (c) listed above. However, because of the drastically declined populations and extremely small range of *L. getula* in the eastern Apalachicola Lowlands, these populations might be most appropriately listed under a higher category of protection status, threatened or endangered as determined by (a), (b), (c), and (d) and listed above.

The docile disposition and numerous color variations of kingsnakes from Florida have created a lucrative market in the pet trade. Almost 10 years ago, Means (1992) reported adult Apalachicola kingsnakes selling for $200-$300 each. However, excellent captive husbandry practices by many herpetological enthusiasts have dramatically reduced pet trade prices as well as the number of individuals taken from the wild. Captive born hatchlings presently sell for $15-$35. My intention is to insure protection of remaining wild kingsnake populations, not to adversely affect captive propagation by hobbyists. If the present trend of habitat loss and decreasing kingsnake populations in the wild continue, in the future kingsnakes might be only found alive in captivity.

Future Research

It is crucial to initiate kingsnake research before remaining Florida and SE U.S. populations become extirpated. Intense kingsnake ecological studies have been limited to only the southern peninsular populations (Krysko, unpubl. data), mainly because sufficient sample sizes have been unattainable elsewhere (i.e., where populations have drastically declined or been extirpated). Unfortunately, other populations in Florida representing two additional distinct taxa, can only be assumed to exhibit similar life

history patterns as those in the southern peninsula (Means, 1978). Radiotelemetry studies can inform us on daily and seasonal movements. Direct population monitoring with appropriate survey techniques can inform us on the ecological status of certain populations (i.e., population density, and if a population continues to decline). Because kingsnakes are ophiophagous, the effects of pollutants and toxin buildup in tissues should be examined. Additional appropriate molecular analyses should be conducted to reveal both valid and invalid taxa, taxonomic boundries, and gene flow between populations. Finally, kingsnakes presently kept as pets (with locality data), voucher specimens consisting of photographs from surveys, and all DORs should be salvaged for preservation in natural history museums.

APPENDIX A
SPECIMENS REFERENCED FOR FLORIDA LOCALITIES

Source acronyms follow Leviton et al. (1985), with the addition of ANSP–Academy of Natural Sciences of Philidelphia; DBM– D. Bruce Means, Coastal Plains Institute, and Florida State University, Tallahassee, FL; ENP– Everglades National Park Museum, Homestead, FL; GHD– George H. Dalrymple, Everglades Research Group, Florida City, FL; JZG– Jacksonville Zoological Gardens, Jacksonville, FL; KLK– Kenneth L. Krysko, Florida Museum of Natural History; KME– Kevin M. Enge, Florida Fish and Wildlife Conservation Commission, Quincy, FL; UCF– University of Central Florida, Orlando, FL.

Lampropeltis getula listed by Florida county: ALACHUA: AMNH 3745, 22996, 36715, 63432, 63974; ANSP 18961; AUM 1967, 2584; FMNH 95183-84; UF 1667, 1667–2, 1691–1, 1691–2, 1724, 1724–1, 1724–2, 1818, 1818–2, 1825, 1859, 2499, 3041-45, 5975, 7398, 7887–2, 9552, 14065-67, 14288, 14438-39, 18133, 33768, 33771-78, 33781-82, 33786, 33789-92, 33794, 38869, 73272, 95466-67, 95474-76, 95482-84; USNM 64203-04, 310970. BAKER: LSUMZ 19011; UF 2103. BAY: KLK xx227; UF 74479. BREVARD: UF 46062-65, 48196, 49716-17, 50825; USNM 310971. BROWARD: AMNH 97657; KU 68920, 176765; UF 11929; UMMZ 104607-08, 106221. CALHOUN: DBM 49, 2361; KLK 255, xx031, xx032, xx219; UF 34696, 55368, 84007, 87155, 95471. CHARLOTTE: CAS SU-10147; UF 2455(DBUF). CITRUS: UF 33769, 33780, 80788, 95472. COLLIER: ANSP 32133; CM 22752; KLK

95019, xx270, xx272; NCSM 27947; UF 14210, 19170, 19389, 19390, 19676, 21648, 33767, 43939-40, 73244-45, 87569, 117401-07. COLUMBIA: UF 39973, 78086, 95486. DADE: CAS 62998-99; CM 7758, 9843, 24914-16; ENP 4520; FMNH 95187; GHD 2015, 2196, 2307, 2308, (1) no catalog #; KLK 91006, 93009-10, 93019-21, 93024-27, 93032-40, 94002, 94021-25, 94040, 94044-45, 94084, 95011-12, xx161, xx274, xx321-22; LSUMZ 8942-43, 38721, 38744, 38757; UF 7612, 19675, 33784, 86888, 88537, 102087-89, 102091, 102156-59, 105382, 117408-10; USNM 36564. DESOTO: USNM 22368. DIXIE: KLK xx316; UF 33783, 70564, 95477, 95487-89. DUVAL: KME 2, 3, 5, 10-12, 16, 23; UF 3494(DBUF), 34698, 95478; USNM 14140-2. FRANKLIN: DBM 32, 37, 44; JZG 485046; KLK 244, 245, 264, 287, 288, 305, xx220, xx221, xx231; LSUMZ 27708; UF 15977, 32987, 34699, 55369, 55375-76, 55383, 55391-93, 55419, 55430, 57740, 73432, 73639, 95485, 115937. GADSDEN: KLK xx222-24; UF 73438. GLADES: ANSP 32980; CAS 207273; KLK 91007, 91009-10, 93001-07, 93011-15, 94031-32, 94139-45, 95013, 95020-26; UF 9272, 9273, 95532. GULF: AUM 21639; KLK 197-213, 217-18, 258, 272-78, 288-90, 295-97, xx562; KME m25, m26; UF 9466, 16263, 32986, 33779, 34700-01, 55372-74, 55390, 71962. HAMILTON: UF 95481. HARDEE: UF 47156. HENDRY: KLK 93016-17, 94033-38; NCSM 9124; UF 50287, 55363. HERNANDO: KLK xx274-76; UF 95479. HIGHLANDS: AMNH 65635; USNM 307583. HILLSBOROUGH: AMNH 139395; CAS 190537; KLK xx139-40, xx143-45, xx301, xx312; KME m1, f1; UF 1459, 18130, 102088-89; USNM 212239. HOLMES: KLK xx257; LSUMZ 6505, UF 95473. INDIAN RIVER: USNM 2375. JACKSON: KLK 27, 224-27, xx319; LSUMZ 19340, UF 115938. JEFFERSON: KLK 124-25, 293, xx225; UF 16124, 55367, 55377, 64341,

115939-40. LAFAYETTE: UF 20634. LAKE: CAS SU-10475; UMMZ 44550, 77477, 77479, 96787; USNM 69667. LEON: AMNH 58601; KLK 145, 270, 291-92, xx226, xx321-322, xx324-25; UF 55382, 55384, 73427-28, 73431, 74469-76, 87154, 115941-115943, 115947. LEVY: FMNH 95185; UF 2575, 3040, 9831, 14106, 19406, 29200, 43153, 95544-46, 95556-58; UMMZ 221422; USNM 2369, 313368. LIBERTY: AUM 26495; DBM 5, 8, 9, 22, 25, 29-31, 33-36, 38-39, 41-43; KLK 98-99, 146, 162, 186-87, 247-48, 251-53, 256-57, 279, 281-82, 285-86, xx213, xx247; LSUMZ 40422; UF 55362, 55364-66, 55370-71, 55378, 55385-89, 55416, 55420-21, 55426-29, 55447-49, 55455, 73433-35, 73638, 91600, 105383, 115948-49, 115951-96, 115957, 123329, 123331; UMMZ 183055. MADISON: LSUMZ 35341; UF 74480. MARION: ANSP 16641; CM 2096-97, 6417, 12148, R-2105; FMNH 7474, 48267; KU 55397; UF 19391-93, 36602; UMMZ 57037. MONROE: AMNH R-95952, 97747; ENP 4524; NCSM 4455; UF 115958; USNM 85325-26. NASSAU: USNM 16698. OKALOOSA: AUM 29740, 29742, 30434, 30463, 32396, 32524; UF 74477, 103289, 117411; USNM 116461. OKEECHOBEE: KLK 95005-08, 95010; UF 528. ORANGE: AMNH 6935, CAS SU-10476; CM S-7154; KLK xx302; UCF (1) no catalog #; USNM 84886, 124141-42. OSCEOLA: AMNH 5936-40, 5998; ANSP 17237; USNM 28892, 28894, 29103-04, 29106, 29108. PALM BEACH: KLK 93050, 94003, 94004, 94006-08, 94010-11, 94013-20, 95001-04, 95014-18, xx326; UF 2389, 99065, 99739. PINELLAS: AMNH 7573-74; CAS 175024, 202551; CM 91765; KLK 93022, 94177, xx193-94, xx309-10, xx333; UF 2531(DBUF), 95530, 98411, 102091. POLK: AMNH 25522; CM 14020, 91554; KLK xx303-304; UF 95549-53; UMMZ 111184-85. PUTNAM: UMMZ 106218. SANTA ROSA: AUM 29747, 30277; UF 3923–1, 3923–2, 95547-48.

SEMINOLE: UF 95554; USNM 307584. ST. JOHNS: UF 66935; USNM 64205, 130144. SUMTER: UF 95525. TAYLOR: FMNH 21564; LSUMZ 24796; UF 4318, 32988, 74481, 95533-34, 95541-42. VOLUSIA: UF 95526-29. WAKULLA: AUM 1178; DBM 27, 28; KLK 163, 246, 250, 254, 263, xx243-244, xx307; KME f3, m13; UF 10172, 18144, 19366, 33770, 33785, 33793, 55380-81, 55417-18, 55422-25, 55450, 68897, 95535, 115959-61, 117413-17. WALTON: UF 74863. WASHINGTON: UF 34702, 64715, 77354.

APPENDIX B
SPECIMENS EXAMINED FOR SEXUAL AND GEOGRAPHIC VARIATION

Source acronyms follow Leviton et al. (1985), with the addition of DBM– D. Bruce Means, Coastal Plains Institute, and Florida State University, Tallahassee, FL; ENP– Everglades National Park Museum, Homestead, FL; GHD– George H. Dalrymple, Everglades Research Group, Florida City, FL; JZG– Jacksonville Zoological Gardens, Jacksonville, FL; KLK– Kenneth L. Krysko, Florida Museum of Natural History; KME– Kevin M. Enge, Florida Game and Fresh Water Fish Commission, Quincy, FL; UCF– University of Central Florida, Orlando, FL.

Lampropeltis getula floridana listed by Florida county: ALACHUA: UF 1724, 95482. BREVARD: UF 46062-65, 48196, 49716, 49717, 50825, 95468-70. BROWARD: AMNH 97657; KU 68920, 176765; UMMZ 104607, 104608, 106221. CHARLOTTE: CAS SU-10147; UF 2455(DBUF). CITRUS: UF 33780. COLLIER: KLK 95019, xx270, xx272; LSUMZ 38731; NCSM 4455; UF 14210, 19170, 19389, 19390, 19676, 33767, 34697, 43939, 43940, 73244, 73245, 87569, 117401-07. DADE: ENP 4520, 4524; GHD 2015, 2196, 2307, 2308, f281, (2) no catalog #; KLK 91006, 93009-10, 93019-21, 93024-27, 93032-40, 93050-51, 94002, 94021-25, 94040, 94044-45, 94066-84, 94100-06, 94130-37, 95011-12, 95180, xx161, xx273-274, xx308, xx320-22; LSUMZ 8942-43, 38721, 38744, 38757; UF 7612, 19675, 21648, 33784, 86888, 88537, 99740, 99741, 102087-89, 102091, 102156-59, 105382, 117408-10. DESOTO: USNM 22368. GLADES: KLK 91007, 91009-10, 93001-07, 93011-15, 94031-32,

94139, 94143-45, 95013, 95020-26; UF 9272, 9273, 95532. HENDRY: KLK 93016, 93017, 94033-38; LSUMZ 38753; UF 50287, 50288, 55363. HERNANDO: KLK xx275. HIGHLANDS: AMNH 65635. HILLSBOROUGH: CAS 190537; KLK xx139-140, xx143-45, xx280, xx282-84, xx293-94, xx286-91, xx295-300, xx312; KME m1, f1; UF 1459, 18130, 102088-89; USNM 212239. INDIAN RIVER: USNM 2375. LAKE: UMMZ 77477. LEE: LACM 59086. MONROE: AMNH R-95952, 97747; UF 115958; USNM 85325-26. OKEECHOBEE: KLK 94056-64, 95005-08, 95010; UF 528(DBUF). OSCEOLA: AMNH 5938-40; USNM 28892, 28894, 29103-04, 29106, 29108. PALM BEACH: KLK 94003, 94004, 94006-08, 94010, 94011, 94013-20, 95001-04, 95014-18, xx326; UF 2389, 99739. PINELLAS: CM 91765; KLK 94053. POLK: CM 14020, 91554; KLK xx303-304; UF 95549-53; UMMZ 111184-85. VOLUSIA: UF 95526-29. LAKE: UMMZ 77479, 69667. PASCO: UF 95543. SEMINOLE: CM R-382. ST. JOHNS: USNM 64205. SUMTER: UF 95525. ST. JOHNS: CM R-1950-51. SEMINOLE: CM R-383; UF 95554; USNM 307584. ORANGE: AMNH 6935, CAS SU-10476; KLK xx302; UCF (1) no catalog #; USNM 84886. PINELLAS: KLK xx050; UF 2531(DBUF), 95530, 95531.

Lampropeltis getula getula listed by Florida county: ALACHUA: UF 1859, 3041-45, 5975, 7887–2, 9552, 33768, 33772-73, 33775-76, 33778, 33790-91, 73272, 95466-67, 95482. BAY: KLK xx227; LSUMZ 38719, 38725, 38732, 38733, 38758, 38759, 38773; UF 74479. CALHOUN: DBM 2361; KLK 95030-32, 95185-86, 96001, xx032, xx219; UF 34696, 55368, 84007, 87155, 95471. CITRUS: UF 33769. COLUMBIA: UF 39971, 95486. DIXIE: KLK xx316; UF 33783, 70564, 95477, 95487, 95489. DUVAL: KME 16; LSUMZ 38747; UF 95478. GADSDEN: KLK xx222-24.

GILCHRIST: UF 95480. HAMILTON: UF 95481. FRANKLIN: KLK 264; UF 55391. WALTON: UF 74863. HOLMES: KLK xx257; LSUMZ 6505, 38735; UF 95473. JACKSON: KLK 27, 224-27, xx319; LSUMZ 19340, UF 115938. LAFAYETTE: UF 20634. GULF: LSUMZ 38711; UF 32986, 33779, 55390. JEFFERSON: KLK 293, xx225; LSUMZ 38718, 38729, 38741, 38774; UF 16124, 64341, 115939. LEON: KLK 145, 291-92, xx226, xx321-25; LSUMZ 38707-08, 38751; UF 54166, 55382, 55384, 73428-31, 73640, 74469-76, 87154, 115943-47. LEVY: UF 2575, 3040, 9831, 19406, 29200, 95544-46, 95555-58. MADISON: LSUMZ 35341; UF 74480. NASSAU: USNM 16698. OKALOOSA: AUM 29740, 29742, 30434, 30463, 32396, 32524; KLK xx334; UF 74477, 103289, 117411. WASHINGTON: UF 34702, 64715. SANTA ROSA: AUM 29747, 30277; KLK xx327; UF 3923-1, 3923-2, 95547, 95548. TAYLOR: LSUMZ 24796; UF 4318, 32988, 74481, 95533-34, 95541. MARION: UF 19391-93, 36602. WAKULLA: KLK 163, 254; LSUMZ 38715; UF 18144, 33785, 33793, 55381, 55418, 55422-23, 68897, 95539-40, 117413-16. LIBERTY: KLK 260-61, 267; UMMZ 183055.

Intergrades between *Lampropeltis getula floridana* and *L. g. getula* listed by Florida county: ALACHUA: UF 1667, 1667–2, 1691–1, 1691–2, 1724–1, 1724–2, 1818, 1818–2, 1825, 2499, 7398, 14065-67, 18133, 33771, 33774, 33777, 33781-2, 33786, 33789, 33792, 33794, 95474-76, 95483. BAKER: LSUMZ 19011; UF 2103. CITRUS: UF 80788, UF 95472. COLUMBIA: UF 39972-73, 78086. DIXIE: 95488. DUVAL: KME 2, 3, 5, 10-12, 23; LSUMZ 38720; UF 3494(DBUF), 34698; USNM 14140. HERNANDO: KLK xx274, xx276; UF 95479. HILLSBOROUGH: KLK xx277-80, xx285, xx292. LAKE: CAS SU-10475; UMMZ 44550, 96787-89. LEVY: FMNH

95185; UMMZ 221422; USNM 2369, 313368. PUTNAM: UMMZ 106218. TAYLOR: FMNH 21564; UF 95542. ORANGE: CM S-7154. MARION: CM 12148, R-2105, S-6417; KU 55397; UMMZ 57037. PINELLAS: KLK 91005, 93022, 94085-99, 94177, xx030, xx051-52, xx142, xx160, xx193-94, xx309-10, xx333; UF 98411, 102091.

Eastern Apalachicola Lowlands *Lampropeltis getula* subsp. listed by Florida county: FRANKLIN: DBM 37, 44; JZG 485046; KLK 244, 287, 288, xx221, xx231; LSUMZ 23510; UF 15977, 32987, 34699, 55369, 55375-76, 55379, 55383, 55392-93, 55419, 55430, 73432, 73639, 95485. GULF: KLK 199, 203, 204-05, 208-10, 218, 258, 277, 295. LEON: KLK 270. WAKULLA: KLK 250, KLK xx243-44, UF 55417, 55450. LIBERTY: DBM 5, 8, 9, 22, 25, 29-30, 33-36, 38, 39, 41-43; KLK 98, 99, 146, 181, 186-90, 251-52, 256-57, 280-83, 285-86, 496, xx247; UF 55362, 55365-66, 55370-71, 55378, 55385-87, 55389, 55420-21, 55426-29, 55448-49, 55455, 73433-35, 73638, 95524, 105383, 115948-49, 115957.

Intergrades between *Lampropeltis getula getula* and eastern Apalachicola Lowlands *Lampropeltis getula* subsp. listed by Florida county: CALHOUN: DBM 49, KLK 255, xx031. GADSDEN: UF 73438. FRANKLIN: DBM 32; KLK 245, xx220; LSUMZ 27708, 38724; UF 57740, 115937. GULF: AUM 21639; KLK 176,197-98, 200-02, 206-07, 211-17, 272-76, 278, 288-90, 296-97; KME m25, m26; LSUMZ 38775; UF 9466, 16263, 34700-01, 45763, 55372-74, 71962. JEFFERSON: KLK 124, 125; LSUMZ 23511; UF 55367, 55377, 115940. LEON: KLK xx320; KME m3; UF 73427, 115941-42. WAKULLA: DBM 27, 28; KLK 246; 263, 299, xx307; KME f3, m13; LSUMZ 28837, 38754; UF 10172, 19366, 33770, 55380, 55424-25, 95535, 115959-61, 117417.

LIBERTY: AUM 26495; DBM 31; KLK 162, 247-48, 253, 279, xx213; LSUMZ 40422; UF 55364, 55388, 55416, 55447, 91600, 95490.

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BIOGRAPHICAL SKETCH

Kenneth L. Krysko was raised on the Gulf Coast of Florida in Seminole, Pinellas County. As a kid, he was always playing soccer or catching fishes, reptiles, and amphibians. He would frequently make lone field-collecting trips through miles of ditches and under-road culverts to the Boca Ciega Bay, where a specimen of a salt marsh snake (*Nerodia clarkii*) would make the prize catch of the day. Because of his unusual passion for snakes most of the neighborhood girls called him "half boy, half snake." Throughout grade school he began fishing in local tournaments, especially for tarpon (*Megalops atlanticus*). He won the Suncoast Tarpon Roundup's landlubber trophy two years in a row in 1988 and 1989, with fish weighing 145 and 133 pounds, respectively. He also won the release division trophy with 32 releases. Although he had fly-fished for years for smaller tarpon and other feisty saltwater species, he began fly fishing for large tarpon with his friends off of Homasassa, FL, in the mid to late 1980s. His first large tarpon on fly was 130+ pounds.

After graduating from Seminole High School, he attended St. Petersburg Junior College. After completing his A.A. degree in 1989 he had to make an important decision. Whether to either become a fishing guide, like many of his life-long friends, or go away to school. He chose to continue his education. His experiences throughout his childhood led him to Florida State University, where he majored in Biological Sciences.

As an undergraduate at FSU (1989-1992), he received a broad background and developed a strong interest in the biological sciences. He worked as an assistant to Dr. Skip Livingston, with whom he researched invertebrates and pollution levels on the Leon Lakes Project. He received a Center for Aquatic Research and Resource Management Award for his work and dedication to the project. In addition, he began to form a particular interest in systematics and ecology of freshwater and marine fishes. As graduation approached he began searching for a graduate school in an area that would allow him to expand his interests and enhance his knowledge in systematics and ecology.

In the summer of 1992, he moved to Miami and began volunteering at the Daniel Beard Research Center in Everglades National Park, Homestead, Florida. He received the Everglades National Park VIP Award from the United States Department of Interior for his work researching sea grass die-off in Florida Bay. Simultaneously, he applied to and was accepted into the graduate program in Biological Sciences at Florida International University, Miami. In August of 1992, he moved into the dormitories on Long Pine Key in Everglades National Park. The following morning he was evacuated because of an approaching hurricane. The next day, Hurricane Andrew destroyed everything on Long Pine Key and Kenneth lost almost everything he owned. Nevertheless, he continued his volunteering and began thinking of graduate research. Although he initially thought of projects related to ichthyology, he settled on examining the taxonomy of the kingsnake, *Lampropeltis getula*, in the southern Florida peninsula under the guidance of Dr. George Dalrymple. Concurrently, Dr. Dalrymple offered him both teaching and research assistantships and he assisted his major advisor in both lectures and laboratories in the courses Herpetology and Vertebrate Zoology. Kenneth

began working for the Everglades Research Group, gained invaluable field experience, and specialized in ichthyology and herpetology of the Everglades and Big Cypress ecosystem. He learned to identify almost every amphibian, reptile, and freshwater fish species in Florida, as well as learning about their ecology and natural histories. He worked with grade school children at the Biscayne Nature Center in Miami, teaching them about the local flora and fauna and conservation of the environment.

After graduating at FIU with his M.S. degree in the summer of 1995, he moved to Gainesville to pursue his Ph.D. in Wildlife Ecology and Conservation at the University of Florida. Here, he broadened his research to examine the morphological and molecular systematics of kingsnakes in the *Lampropeltis getula* complex. He has lectured on herpetology, systematics, and zoological nomenclature at UF and herpetological societies around the state, as well as at scientific meetings as far away as La Paz, Mexico. He was funded by the Florida Fish and Wildlife Conservation Commission and Central Florida, Volusia County, and Suncoast Herpetological Societies to carry out his research.

Kenneth became involved with the Florida Museum of Natural History at UF in 1995, and became the collection manager of the Division of Herpetology in 1999. He has gained vast experience dealing with the public by participating in numerous FLMNH functions by representing the Division of Herpetology.

Kenneth does all the chores, cooks, and pays the rent for the apartment he shares with his many roommates, "Mako" his extra-large 20+ pound cat, day geckos (*Phelsuma* spp.) and leaf-nosed snakes (*Langaha madagascariensis*) from Madagascar, and wild-collected introduced cichlids. He has many goals set for himself after completing his Ph.D., including becoming a university professor, publishing scientific research,

continuing with his interests in conservation, systematics, phylogenetics, paleontology, and biogeography, and fishing regularly.