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Abstract

Geographic variation is assessed among the Central and South American snakes *Liophis lineatus lineatus, L. l. dilepis, L. l. meridionalis, L. flavifrenatus,* and *L. paucidens. Liophis lineatus dilepis* and *L. l. meridionalis* are elevated to full species based on distribution, pattern, and morphological characters; the latter are analyzed by univariate and multivariate statistics.

Introduction

The colubrid snake genus *Liophis* is currently composed of 34 species (Dixon and Thomas, 1985). The *Liophis lineatus* Complex contains three species *(L. l. lineatus, L. l. dilepis, L. l. meridionalis, L. flavifrenatus,* and *L. paucidens)* that form a natural assemblage and inhabit savannas of Central and South America. The systematic status of the genus *Liophis* has long been in a state of disarray. Until Dixon's (1980) redefinition of the genus, the species of *Liophis* were attributed to a multitude of different genera due to the vast amount of geographic variation within and among species. Dixon (1980) used morphological characters to synonymize *Dromicus, Leimadophis, Liophis,* and *Lygophis* under the oldest available name, *Liophis* Wagler, 1830.

The classification of these taxa has remained confused because of the variation within and among taxa. In many species of *Liophis* there is an ontogenetic change in color and pattern; in others, there is sexual dimorphism of color and pattern. The taxa of *Liophis* under investigation are not affected by these changes, but all show clinal variation of certain morphological characters throughout their geographic distribution.

The nomenclatural history of these snakes has also created considerable taxonomic confusion. Some species of the genus *Liophis* are steeped in over 250 years of nomenclature, predating Linnaeus' tenth edition of *Systema Naturae* (1758) by 24 years (Seba, 1734); although nothing before 1758 is relevant.

The objective of this paper is to present a logical explanation of the nomenclatural history and to assess the variation among three currently recognized species of *Liophis* based on distribution, morphological characters, and pattern types.

Materials and methods: Morphometric data were obtained by the examination of 423 museum specimens. The morphological characters used include: number of scale rows around the body (counts made at the tenth ventral, midbody, and the tenth from the last ventral); number of ventrals (counted according to Dowling's (1951) method); number of subcaudals, supralabials, infralabials, preoculars, postoculars, temporals, supralabials entering the orbit, loreals, maxillary teeth; condition of anal plate (single or divided); length of the *in situ* hemipenis (expressed in number of subcaudals); primary scale row reduction site (ventral number corresponding to the anteriormost point of reduction of dorsal scale rows); secondary reduction site; total length; tail/total ratio (the tail length as a percentage of the total length); and the presence or absence of scale pits. The mean ($\bar{x}$) is given in the text where appropriate, and for characters that show little variation (preoculars, postoculars, loreals, for example), the range is followed by the mode, in parenthesis. Sexually dimorphic characters are listed for males and females separately.

The specimens examined were borrowed from the following museums or investigators: AMNH — American Museum of Natural History, New York; ANSP —

Academy of Natural Sciences of Philadelphia; BM — British Museum (Natural History), London; CM — Carnegie Museum of Natural History, Pittsburgh; FMNH — Field Museum of Natural History, Chicago; IB — Instituto Butantan, São Paulo, Brazil; FML — Fundacion, Instituto Miguel Lillo, Tucuman, Argentina; KU — University of Kansas Museum of Natural History, Lawrence; LACM — Los Angeles County Museum of Natural History; MCZ — Museum of Comparative Zoology, Harvard University, Cambridge; MHNG — Museum D'Histoire Naturelle, Geneve, Switzerland; MHNLS — Museo de Historia Natural La Salle, Caracas, Venezuela; MHNP — Museum D'Histoire Naturelle, Paris; MZUSP — Museu de Zoologia Universidade de São Paulo; NS — Norman J. Scott, Jr., University of New Mexico, Albuquerque; TCWC — Texas Cooperative Wildlife Collection, College Station; UMMZ — University of Michigan Museum of Zoology, Ann Arbor; USNM — National Museum of Natural History, Washington, D.C.; UTA — University of Texas at Arlington; UZM — Universitetets Zoologisk Museum, Copenhagen, Denmark; WWL — William W. Lamar (uncatalogued UTA), University of Texas at Arlington; ZMH — Zoologisches Institut und Zoologisches Museum, Hamburg, Germany.

After all specimens were examined and data obtained, several methods of univariate and multivariate statistical analyses were employed; these are the TTEST Procedure of the Statistical Analysis System (SAS; Goodnight, 1979), Duncan's Multiple Range Test in conjunction with the General Linear Models Procedure of the SAS (Goodnight, 1979), principle components analysis (PCA) and cluster analysis using the unweighted pair-group method based on arithmetic averages (UPGMA) of the Numerical Taxonomy System (NT-SYS; Rohlf and Kishpaugh, 1972), and a canonical analysis used in conjunction with the Multivariate Analysis of Variance (MANOVA) from the SAS library.

In addition, the vegetation zones that are inhabited by each species are discussed. All references to habitat types and vegetation are from Hueck and Seibert (1972).

Species Accounts: The following accounts present a brief synonymy for each species, followed by a comment section to clarify synonym usage, if necessary. Each species synonymy is followed by the distribution and habitat of the species, and a summarized statement of the species essential attributes. This information is followed by a description of the sexual dimorphism of morphometric variables. Finally, interspecific variation is presented.

Liophis lineatus (Linnaeus, 1758)

Coluber lineatus Linnaeus 1758:221.
Type-locality: "Asia" (in error)
Coluber jaculatrix Linnaeus 1766:381.
Type-locality: Surinam
Natrix lineatus Merrem 1820:112.
Coluber terlineatus Lacépède 1826:106.
Type-locality: none given
Herpetodryas lineatus Schlegel 1837:191.
Lygophis lineatus Fitzinger 1843:26.
Dromicus lineatus Duméril 1853:477.
Lygophis lineatus Cope 1862a:76.

Aporophis lineatus Cope 1878:34.
Lygophis lineatus Amaral 1929a:19.
Lygophis lineatus lineatus Hoge 1953b:249.
Liophis lineatus lineatus Dixon 1980:10.

Comment. Coluber minervae, described by Linnaeus (1754), has been listed as a synonym of *Liophis lineatus*. Linnaeus lists *C. minervae* in the tenth edition of *Systema Naturae* (1758) and refers to his 1754 publication for its description. Although originally described in 1754, the appearance of *C. minervae* in the tenth edition of *Systema Naturae* (1758) established its nomenclatural status. In these two publications, Linnaeus often attributed species to earlier authors. This is not the case for *C. minervae* and it can be assumed that this species belongs solely to Linnaeus. He stated that *C. minervae* has 238 ventrals and 90 subcaudals, and gave a color description. Two specimens from the Museum Drottningholm are preserved in the Royal Museum in Stockholm and labeled as *C. minervae*. Linnaeus described *C. minervae* from only one specimen. Also, these individuals have ventral/subcaudal counts of 167/83 and 163/76. Andersson (1899) doubted that Linnaeus could make such a gross error and attributed this to a mistake in transcription. Andersson (1899) believed *C. minervae* may be a synonym of *C. lineatus* and subsequent authors followed this. Hoge (1953b) received notes and photographs of the two specimens of *C. minervae* from the Royal Museum and determined that *C. minervae* is synonymous with *C. lineatus*. However, we do not believe these individuals are what Linnaeus described as *C. minervae*. It was not an uncommon practice in collections for changes to be introduced by the substitution of better specimens for poorer ones or by the replacement of lost specimens. The color description given for *C. minervae* by Linnaeus is very close to that of *L. lineatus*. We believe that specimens of *L. lineatus* were substituted for the specimen of *C. minervae* based on color, without the ventrals or subcaudals having been counted. Therefore, we remove *C. minervae* from the synonymy of *L. lineatus* and suggest that it be considered *incertae sedis*.

Distribution and Habitat. Liophis lineatus ranges from central Panama, eastward through Colombia, Venezuela, Guyana, Surinam, and French Guiana, to the mouth of the Amazon River in Brazil (Figure 1).

There are three specimens of *Liophis lineatus* that require locality clarification. One specimen (AMNH 5304) is recorded from Limon, Costa Rica. We believe this to be in error. The characteristics of this individual are unlike those of specimens from Central America and from west of the Andes in South America. We believe this specimen came from somewhere east of the Andes.

The other two specimens are from Ecuador. These are MHNG 1367.83 from Maicito, and AMNH 20410 from Esmeraldas (Figure 1). Peters (1957) examined AMNH 20410 but was in error when he indicated that the specimen did not fit well within the typical subspecies *(lineatus)* as defined by Hoge (1953b), and that its pattern is much more similar to that of *Lygophis lineatus dilepis* Cope. Peters' analysis appears to be based on a reproduced photograph (Hoge, 1953b). Peters was correct in assigning this specimen to *L. l. lineatus* (although he did this based on zoogeography, and *L. lineatus* does not occur in Ecuador), rather than agreeing with Hoge (1953b) the Reinhardt and Lütkin's (1862) Guayaquil reference is to *Lygophis dilepis*. Both of these specimens are definitely *Liophis lineatus*. These individuals are very similar to the Panamanian specimens and probably originated there. Both Guayaquil (located near Maicito) and Esmeraldas are port cities and these specimens may have reached Ecuador via cargo ships from Panama.

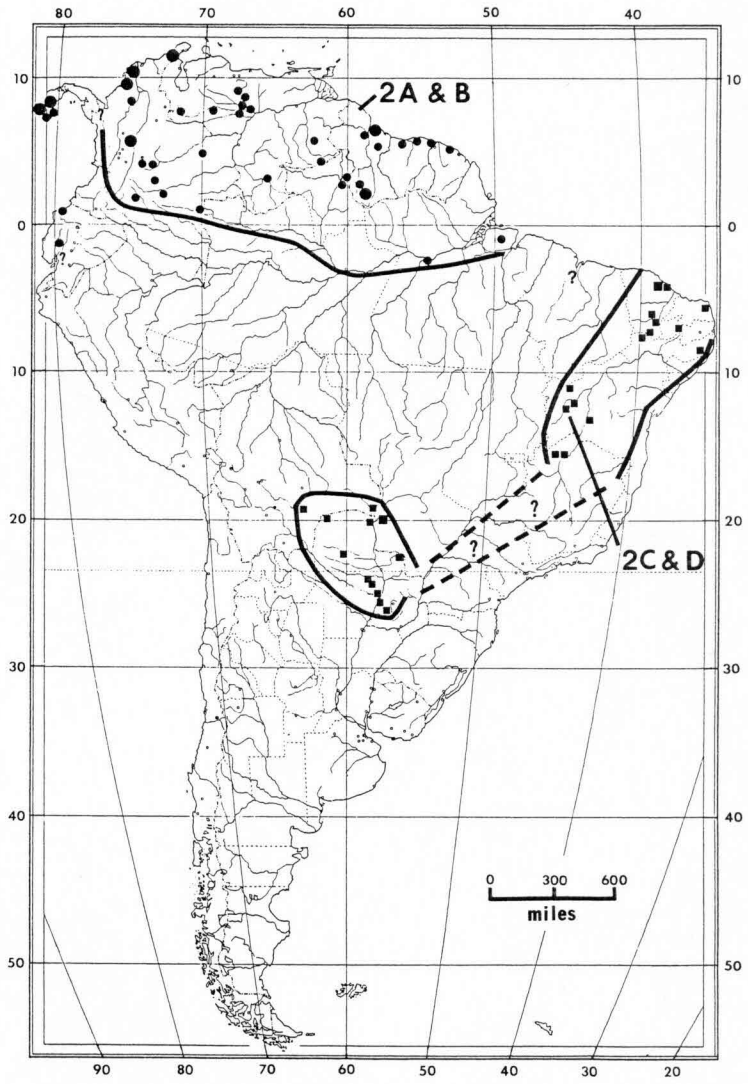

Figure 1. Distribution of *Liophis lineatus* (circles), and *Liophis dilepis* (squares). Small circles and squares represent a single locality. Larger circles and squares represent more than one locality within that area. The numbers represent the localities of the specimens whose patterns are depicted in the corresponding numbered Figure. The question mark near the Gulf of Guayaquil, Ecuador indicates that these specimens are out of their normal range and may have come from Panama. The question mark between Panama and Colombia notes the absence of *L. lineatus* in the tropical forest of southern Panama and western Colombia. The question mark between the ranges of *L. lineatus* and *L. dilepis* pertains to *L. dilepis*. The literature suggests that *L. dilepis* occurs in the western Caatinga of Brazil, and may occur throughout the Caatinga. The dashed lines represent the absence of *L. dilepis* specimens between two disjunct populations. (Map #103 of the Goode Base Map Series).

Liophis lineatus is a widely distributed species that occurs in three major vegetation types: grass and bush steppes, dry forest, and coastal savanna. In southern Panama, *L. lineatus* occurs in arid deciduous forest and savanna. The Panamanian population is isolated from other populations by the tropical evergreen rainforest of the Pacific and Caribbean regions. The arid deciduous forest and savanna exists in an Arid Lower Tropical Zone extending in a belt of varying width along the Pacific slope from the southeastern border of Costa Rica, eastward through Panama to the valley of the Tuira River (Shelford, 1926). This area corresponds closely to Savage's (1966) distribution of the Recent Panamanian herpetofauna. However, in Panama, *L. lineatus* is known only from the provinces of Coclé, Herrera, Los Santos, and Veraguas. In Transandean Colombia, *L. lineatus* occurs in Caribbean dry forest that is dominated by thorny trees, shrubs, and cacti. The snake also occurs in dry forest in the Andean valleys of west-central Colombia. *Liophis lineatus* occurs in the grasslands (Llanos) of Venezuela and Colombia east of the Andes. The species occurs in coastal savanna and farther inland in the grass steppes of the Campos Limpos in Guyana, Surinam, and French Guiana. *Liophis lineatus* also inhabits grass steppes of extreme northern Brazil, and on the Island of Marajó. This species may also occur in the coastal grass steppe of northwestern Maranhão, Brazil (western edge of the Bay of São Marcos), but we have no records suggesting its presence there.

Definition. Liophis lineatus is a slender snake with three dark, longitudinal stripes on a light background and an immaculate venter. Two narrow, pale stripes border the dark middorsal stripe (Figure 2). The pattern depicted in Figure 2 is typical for individuals that inhabit the eastern portion of the species distribution. Transandean specimens have a pattern that more closely resembles *L. dilepis,* namely the lateral stripes are wider (Michaud and Dixon, in prep.). Scale rows are 18-19 anteriorly, 19 at midbody, and 15-17 posteriorly, (19-19-17; $n = 153$). Ventrals are 159-179, $\bar{x} = 168$. Subcaudals are 77-97, $\bar{x} = 88$ for males; 70-98, $\bar{x} = 84$ for females. Supralabials are 7-9, (8). Infralabials are 8-12, (10). Preoculars are 1-2, (1). Postoculars are 1-2, (2). Temporal arrangements are varied, (1 + 2). Supralabials entering the orbit vary from 3rd to 6th, (4 + 5). Loreals are 1-2, (1). Maxillary teeth are 19-24, $\bar{x} = 22$. The anal plate is divided. Hemipenes are 13-22, $\bar{x} = 17$ subcaudals in length. Primary scale row reduction sites are 85-122, $\bar{x} = 102$. Maximum total length is 635 mm for males, 737 mm for females. Tail/total length ratios are 24.2-30.8, $\bar{x} = 28.0$ for males; 22.9-29.2, $\bar{x} = 26.4$ for females. The scales are smooth with a single apical pit.

Sexual Dimorphism. The TTEST Procedure was used to determine whether or not any morphometric variables differ significantly ($\alpha = 0.05$) between males and females. The males and females of *Liophis lineatus* differ significantly in subcaudal number and tail/total length ratio (Table 1), the males having higher mean values in both characters.

Table 1

Range, Mean, Standard Deviation (SD), Standard Error (SE), and Sample Size (N), of subcaudals and tail/total length (%) for males and females of *Liophis lineatus*. Significant differences ($\propto = 0.05$) between males and females were observed for these variables when analyzed with the TTEST Procedure.

		Liophis lineatus				
VARIABLE	SEX	RANGE	MEAN	SD	SE	N
Subcaudals	Males:	77-97	87.9	4.56	0.75	37
	Females:	70-98	84.0	4.82	0.59	66
Tail/Total (%)	Males:	24.2-30.8	28.0	1.40	0.23	37
	Females:	22.9-29.2	26.4	1.43	0.18	65

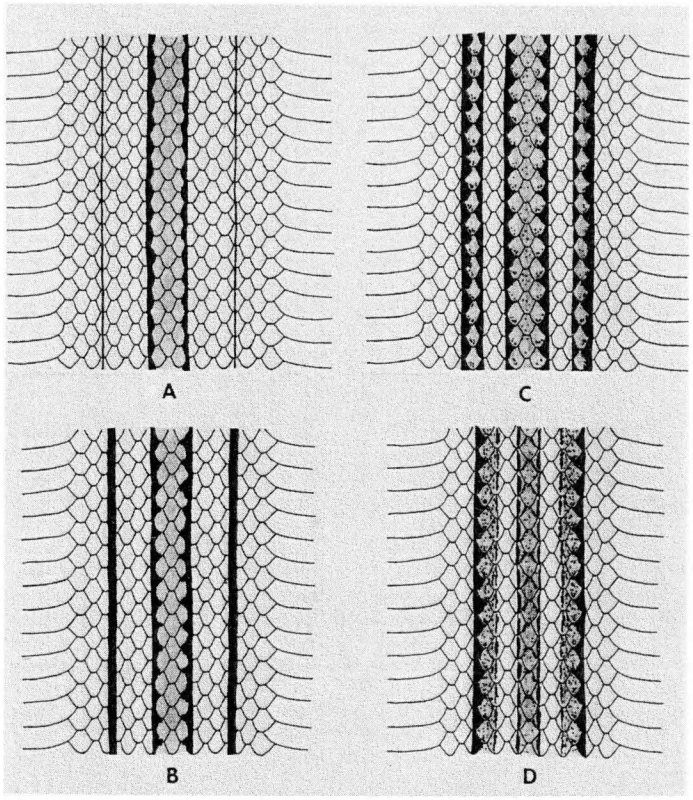

Figure 2. A. *Liophis lineatus* (AMNH 36121; Guyana). Pattern illustration of the anterior (ventrals 60-73) portion of the specimen (19 scale rows). **B.** The posterior (ventrals 125-137) pattern of AMNH 36121 (17 scale rows). **C.** *Liophis dilepis* (UMMZ 108756; Bahia, Brazil). Pattern illustration of the anterior (ventrals 60-73) portion of the specimen (19 scale rows). **D.** The posterior (ventrals 125-137) pattern of UMMZ 108756 (15 scale rows).

Liophis dilepis (Cope, 1862)

Lygophis dilepis Cope 1862b:348.
Type-locality: Paraguay
Aporophis dilepis Cope 1885:191.
Aporophis lineatus Boulenger 1894:158.
Aporophis dilepis Peracca 1895:15.
Aporophis dilepis Boulenger 1896:634.
Lygophis lineatus Amaral 1929b:87.
Lygophis lineatus dilepis Hoge 1953b:251.
Liophis lineatus dilepis Dixon 1980:7.

Comment. The taxonomic confusion between *Liophis dilepis* and *L. lineatus* began with Boulenger (1894) when he placed *Aporophis dilepis* in the synonymy of *A. lineatus*. Peracca (1895) disagreed with Boulenger and believed that *dilepis* was a valid taxon. Boulenger (1896) realized that he was in error and in the addendum to his Catalogue of the Snakes in the British Museum (Natural History), removed *dilepis* from the synonymy of *lineatus* and recognized it as a full species. Even though Boulenger straightened out the problem and Berg (1898) concurred with the decision, taxonomic confusion continued between these two species. In two different publications, Koslowsky (1898a and b) referred to specimens of *Aporophis dilepis* but called them *A. lineatus*. Bertoni (1913) did not know what to do with *dilepis* and listed it as a questionable synonym of *Aporophis lineatus*. Gomes (1918) mistakenly referred to *Aporophis dilepis* as *A. lineatus*. Serié (1921) also referred specimens to *Aporophis lineatus* that were actually *A. dilepis*. Amaral (1929a) removed *lineatus* from *Aporophis* and returned it to *Lygophis*. Amaral (1929b) also returned *dilepis* to the synonymy of *lineatus,* and continued to follow this classification in a subsequent paper (1929c). Consequently, many future workers either referred to *Lygophis dilepis* as *Lygophis lineatus,* or when speaking of *lineatus* gave ranges for *lineatus, dilepis,* and/or *meridionalis* (Amaral, 1934, 1935, 1937, 1948a and b; Serié, 1936; Bertoni, 1939; Niceforo, 1942; Beebe, 1946; Marcuzzi, 1950; Schmidt and Inger, 1951; and Aleman, 1953). The latter confusion makes it extremely difficult to ascertain which taxon of snake was being discussed unless there was an accompanying description. Hoge (1953b) resurrected *dilepis* as a subspecies of *Lygophis lineatus*. However, the distinction between *Lygophis l. dilepis* and *L. l. lineatus* was still not clear. Later, Hoge et al. (1978) referred to two specimens of *Lygophis lineatus dilepis* simply as *L. lineatus*, while in 1980 Hoge et al. referred to a specimen of *L. l. dilepis* as *L. dilepis*.

Distribution and Habitat. Liophis dilepis ranges from northeastern Brazil, southward to southern Brazil and Paraguay, then northwestward through Paraguay to southern Bolivia (Figure 1).

Liophis dilepis is narrowly distributed in dry forests. It is restricted to the Caatinga in northeastern Brazil, and then its distribution shows a curious hiatus in the Cerrado of central Brazil, appearing again in the Chaco Boreal of southern Bolivia, northern and central Paraguay, and northeastern Argentina (Figure 1). These two major areas of occurrence for *L. dilepis* are separated by well over 1000 km of Campos Cerrados and, to a lesser extent, deciduous mesophytic subtropical forest. We are unable to suggest why this hiatus exists.

Definition. Liophis dilepis is a slender snake with three broad, dark, longitudinal stripes on a light background and an immaculate venter. Two narrow, pale stripes border the dark middorsal stripe (Figure 2). Scale rows are 19 anteriorly, 19 at

midbody, and 15 posteriorly (n = 130). Ventrals are 160-189, $\bar{x} = 175$. Subcaudals are 66-83, $\bar{x} = 75$ for males; 58-88, $\bar{x} = 70$ for females. Supralabials are 6-10, (8). Infralabials are 9-12, (10). Preoculars are single. Postoculars are 1-3, (2). Temporal arrangements are varied, (1 + 2). Supralabials entering the orbit vary from 3rd to 6th, (4 + 5). Loreals are single. Maxillary teeth number 17-25, $\bar{x} = 20$. The anal plate is usually divided (95.3% of the time), but may be entire. Hemipenes are 9-17, $\bar{x} = 13$ subcaudals in length. Primary scale row reduction sites are 88-117, $\bar{x} = 101$. Secondary scale row reduction sites are 92-125, $\bar{x} = 104$. Maximum total length is 585 mm for males, 808 mm for females. The tail/total length ratios are 21.9-27.1, $\bar{x} = 24.8$ for males; 19.0-27.4, $\bar{x} = 22.5$ for females. The scales are smooth and lack an apical pit.

Sexual Dimorphism. The males and females of *Liophis dilepis* differ significantly in subcaudal number and tail/total length ratio (Table 2), males having higher mean values in both characters.

Table 2

Range, Mean, Standard Deviation (SD), Standard Error (SE), and Sample Size (N), of subcaudals and tail/total length (%) for males and females of *Liophis dilepis*. Significant differences ($\alpha = 0.05$) between males and females were observed for these variables when analyzed with the TTEST Procedure.

		Liophis dilepis				
VARIABLE	SEX	RANGE	MEAN	SD	SE	N
Subcaudals	Males:	66-83	75.2	3.91	0.63	39
	Females:	58-88	69.6	5.34	0.70	58
Tail/Total (%)	Males:	21.9-27.1	24.8	1.10	0.18	39
	Females:	19.0-27.4	22.5	1.67	0.22	57

***Liophis meridionalis* (Schenkel, 1901)**

Aporophis lineatus var. *meridionalis* Schenkel 1901:160.
Type-locality: "Mte. Sociedad", Bemalcue, Paraguay
Aporophis lineatus lativittatus Müller 1928:74.
Type-locality: San Fermin (Chiquitos), Bolivia
Lygophis lineatus Amaral 1929b:19.
Lygophis lineatus meridionalis Hoge 1953b:252.
Liophis lineatus meridionalis Dixon 1980:11.

Distribution and Habitat. *Liophis meridionalis* ranges from central Brazil and northern Bolivia southward to southern Paraguay, the northeastern tip of Argentina, and southeastern Brazil (Figure 3).

Liophis meridionalis is a wide-ranging species that is found in a wide variety of habitats. It occurs in the palm savanna of Bolivia, dry forests of the Chaco in Bolivia and Paraguay, and in the Pantanals, Campos Limpos, Campos Cerrados, and the deciduous mesophytic subtropical forest of central and southern Brazil.

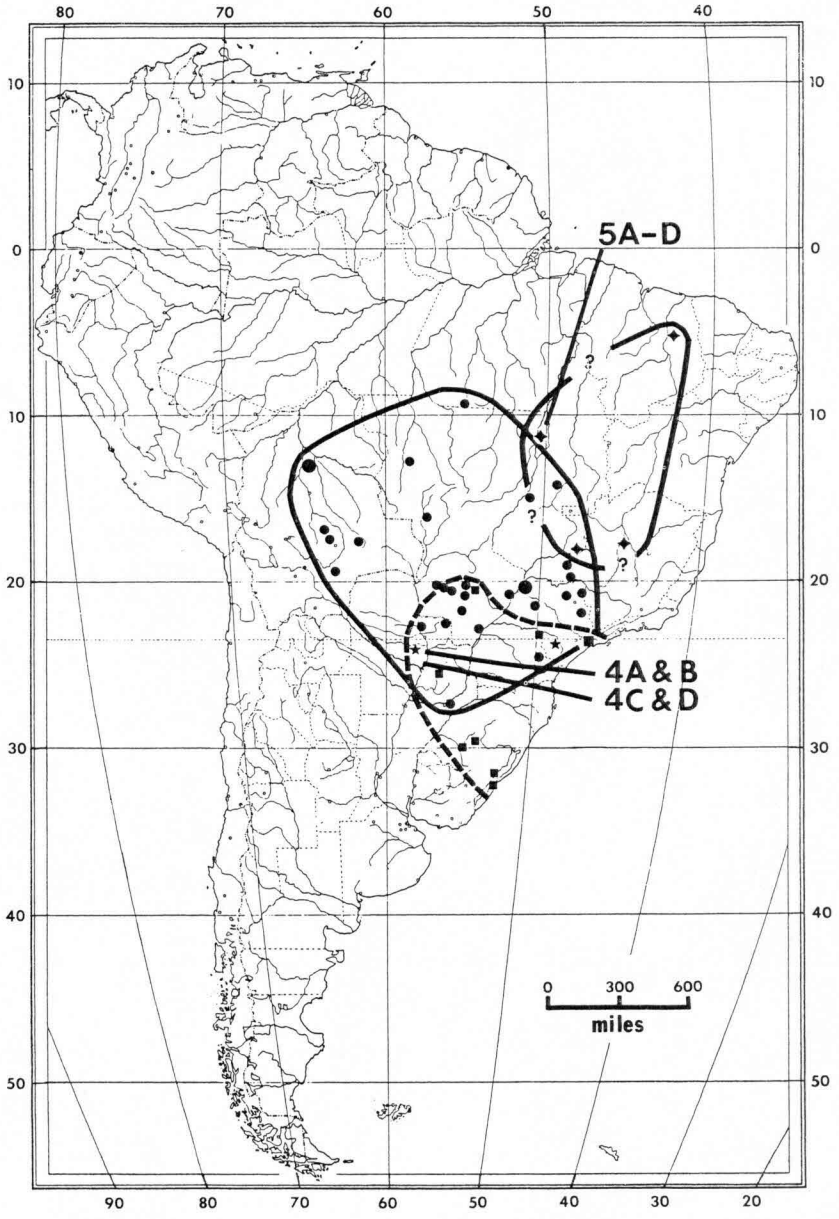

Figure 3. Distribution of *Liophis meridionalis* (circles), *Liophis flavifrenatus* (squares), and *Liophis paucidens* (diamonds). Small circles, squares, and diamonds represent a single locality. Larger circles and squares represent more than one locality within that area. The stars represent sympatric localities of *L. meridionalis* and *L. flavifrenatus*. The numbers represent the localities of the specimens whose patterns are depicted in the corresponding numbered Figure. (Map #103 of the Goode Base Map Series).

Definition. Liophis meridionalis is a slender snake with three dark, longitudinal stripes on a light background. Two narrow, yellow stripes border the dark middorsal stripe and scattered blotches of dark pigment occur on the background color between the longitudinal stripes, and between the stripes and the ventrals. Each ventral has two black spots, one in contact with each of the outermost scale rows (Figure 4).

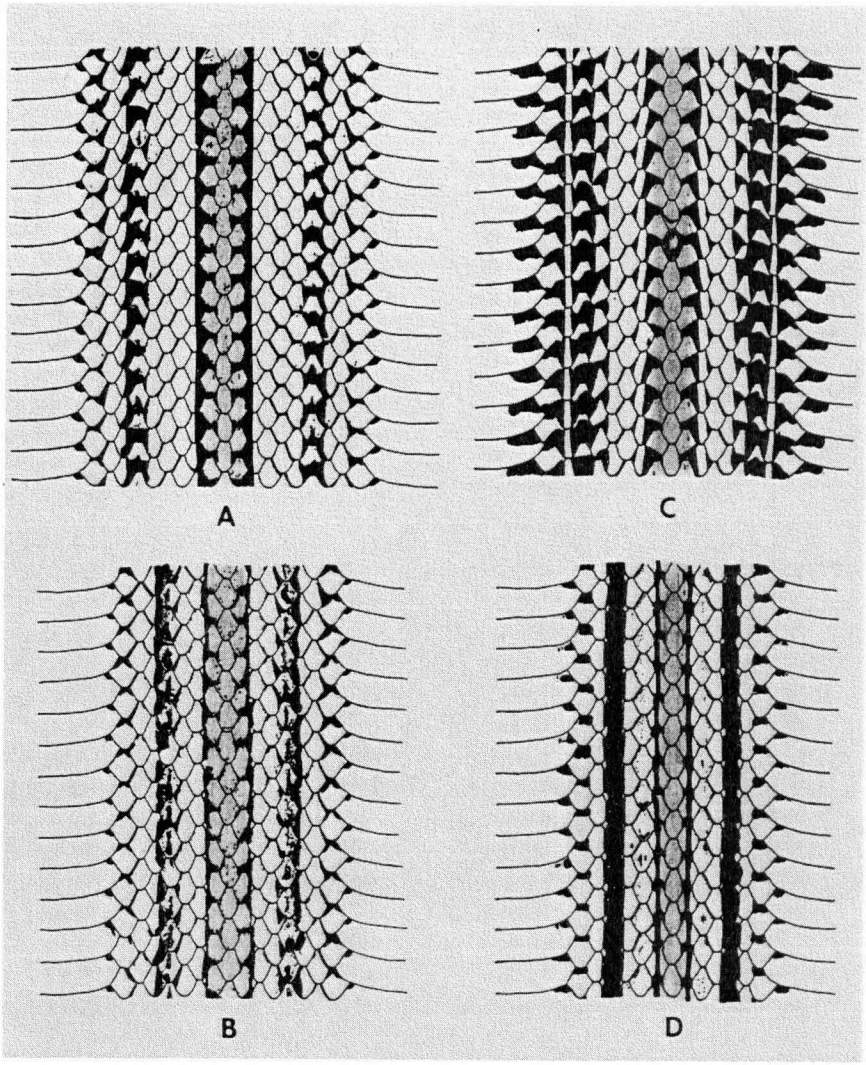

Figure 4. A. *Liophis meridionalis* (BM 1958.1.2.22; Presidente Hayes, Paraguay). Pattern illustration of the anterior (ventrals 60-73) portion of the specimen (19 scale rows). **B.** The posterior (ventrals 125-137) pattern of BM 1958.1.2.22 (15 scale rows). **C.** *Liophis flavifrenatus* (ANSP 4604, co-type; Presidente Hayes, Paraguay). Pattern illustration of the anterior (ventrals 60-73) portion of the specimen (17 scale rows). **D.** The posterior (ventrals 125-137) pattern of ANSP 4604 (13 scale rows).

Scale rows are 18-21 anteriorly, 19 at midbody, and 15-17 posteriorly, (19-19-15; n = 96). Ventrals are 160-174, $\bar{x} = 166$ for males; 158-183, $\bar{x} = 172$ for females. Subcaudals are 80-96, $\bar{x} = 86$ for males; 75-91, $\bar{x} = 83$ for females. Supralabials are 7-9, (8). Infralabials are 8-11, (10). Preoculars are single. Postoculars are 2-3, (2). Temporal arrangements are varied, (1 + 2). Supralabials entering the orbit vary from 4th to 6th, (4 + 5). Loreals are single. Maxillary teeth number 22-29, $\bar{x} = 25$. The anal plate is usually divided, but is entire in one specimen. Hemipenes are 7-18, $\bar{x} = 14$ subcaudals in length. Primary scale row reduction sites are 82-107, $\bar{x} = 98$ for males; 90-112, $\bar{x} = 100$ for females. Secondary scale row reduction sites are 82-143, $\bar{x} = 105$ for males; 78-119, $\bar{x} = 102$ for females. Maximum total length is 595 mm for males, 843 mm for females. Tail/total length ratios are 24.5-29.8, $\bar{x} = 27.5$ for males; 23.4-28.9, $\bar{x} = 26.4$ for females. The scales are smooth and lack an apical pit.

Sexual Dimorphism. The males and females of *Liophis meridionalis* differ significantly in ventral and subcaudal numbers, and in tail/total length ratio (Table 3). The females have more ventrals, while the males have more subcaudals and a longer tail.

Table 3

Range, Mean, Standard Deviation (SD), Standard Error (SE), and Sample Size (N), of ventrals, subcaudals, and tail/total length (%) for males and females of *Liophis meridionalis*. Significant differences ($\alpha = 0.05$) between males and females were observed for these variables when analyzed with the TTEST Procedure.

	Liophis meridionalis					
VARIABLE	SEX	RANGE	MEAN	SD	SE	N
Ventrals	Males:	160-174	165.6	3.52	0.60	34
	Females:	158-183	171.6	4.35	0.56	61
Subcaudals	Males:	80-96	86.4	4.17	0.80	27
	Females:	75-91	83.3	4.12	0.60	47
Tail/Total (%)	Males:	24.5-29.8	27.5	1.21	0.23	27
	Females:	23.4-28.9	26.4	1.04	0.15	47

Liophis flavifrenatus (Cope, 1862)

Lygophis flavifrenatus Cope 1862a:80.
Type-locality: Rio Vermejo (Bermejo) region, Paraguay
Dromicus amabilis Jan 1867: Livr. 24.
Type-locality: Brazil
Aporophis flavifrenatus Cope 1885:191.
Lygophis flavifrenatus Amaral 1929a:87.
Liophis flavifrenatus Dixon 1980:8.

Distribution and Habitat. Liophis flavifrenatus ranges from southern Brazil southward through central and southern Paraguay, northeastern Argentina, and extreme southeastern Brazil (Figure 3).

Liophis flavifrenatus has a rather restricted distribution compared to the other four species under investigation. From the limited number of specimens available to us of this species, it appears to be closely tied to the Araucarian forest *(Araucaria*

angustifolia) of southeastern Brazil, while not actually occurring in this vegetative zone. *Liophis flavifrenatus* occurs mainly in the deciduous mesophytic subtropical forest that surrounds the *Araucaria* forest. The snake also inhabits dry to slightly moist forest of the eastern Chaco in Paraguay, and grass and shrub cover of the hilly Pampas in southwesternmost Brazil.

Definition. Liophis flavifrenatus is a slender snake with three dark, longitudinal stripes on a light background. Two narrow, yellow stripes border the dark middorsal stripe and scattered blotches of dark pigment occur on the background color between the longitudinal stripes, and between the stripes and the ventrals. This scattered dark pigment is more prominent than in *L. meridionalis*. Each ventral has two black spots, one in contact with each of the outermost scale rows (Figure 4). Scale rows are 17 anteriorly, 17 at midbody, and 13-15 posteriorly, (17-17-13; n = 37). Ventrals are 152-166, $\bar{x} = 157$ for males; 155-168, $\bar{x} = 162$ for females. Subcaudals are 82-98, $\bar{x} = 89$ for males; 77-95, $\bar{x} = 83$ for females. Supralabials are 7-8, (8). Infralabials are 9-11, (10). Preoculars are single. Postoculars are 2-3, (2). Temporal arrangements are varied, (1 + 2). Supralabials entering the orbit vary from 3rd to 5th, (4 + 5). Loreals are single. Maxillary teeth number 22-29, $\bar{x} = 26$. The anal plate is divided. Hemipenes are 8-16, $\bar{x} = 13$ subcaudals in length. Primary scale row reduction sites are 76-103, $\bar{x} = 91$ for males; 79-98, $\bar{x} = 90$ for females. Secondary scale row reduction sites are 86-141, $\bar{x} = 102$ for males; 90-135, $\bar{x} = 107$ for females. Maximum total length is 568 mm for males, 755 mm for females. Tail/total length ratios are 27.0-30.8, $\bar{x} = 28.9$ for males; 24.9-29.1, $\bar{x} = 26.9$ for females. The scales are smooth and lack an apical pit.

Sexual Dimorphism. The males and females of *Liophis flavifrenatus* differ significantly in ventral and subcaudal numbers, and in tail/total length ratio (Table 4). The females of *L. flavifrenatus* have more ventrals, while the males have more subcaudals and a longer tail.

Table 4

Range, Mean, Standard Deviation (SD), Standard Error (SE), and Sample Size (N), of ventrals, subcaudals, and tail/total length (%) for males and females of *Liophis flavifrenatus*. Significant differences ($\alpha = 0.05$) between males and females were observed for these variables when analyzed with the TTEST Procedure.

	Liophis flavifrenatus					
VARIABLE	SEX	RANGE	MEAN	SD	SE	N
Ventrals	Males:	152-166	156.7	4.10	1.06	15
	Females:	155-168	161.6	4.02	0.86	22
Subcaudals	Males:	82-98	88.5	4.29	1.11	15
	Females:	77-95	82.6	4.80	1.16	17
Tail/Total (%)	Males:	27.0-30.8	28.9	0.99	0.27	14
	Females:	24.9-29.1	26.9	1.16	0.28	17

Comment. One specimen (UMMZ 79661) from São Paulo, Brazil, has an unusual pattern that appears to be the result of hybridization between *L. meridionalis* and *L. flavifrenatus*.

This female specimen has 17-19-14 scale rows, 175 ventrals, 74+ subcaudals, 8/8

supralabials, 9/9 infralabials, 1/1 preoculars, 2/2 postoculars, 1+2/1+2 temporals, 4-5/4-5 supralabials entering the orbits, loreals are absent, 22/22 maxillary teeth, divided anal plate, 96/93 ventrals at the primary reduction site, 726+ mm total length, 176+ mm tail length, and smooth scales lacking an apical pit.

This individual shares characteristics of both *L. meridionalis* and *L. flavifrenatus*. The scutellation and morphological characters are concordant with those of *L. meridionalis*. The pattern of this snake is most like *L. flavifrenatus* but it is more melanistic than either of these two species. The head shape and scutellation of this individual are aberrant. Perhaps these aberrancies were manifested in an irregular development of the fertilized hybrid egg. The snout is blunt, with fewer maxillary teeth than is usually observed for either species. The preoculars are much wider than usual and the loreals are absent. These conditions were never observed for either *L. meridionalis* or *L. flavifrenatus*.

An alternative is that this snake may represent a different species. This possibility is highly unlikely. The aberrancies of the head shape and scutellation of this individual are not normally observed for any species of *Liophis*.

Liophis paucidens (Hoge, 1953)

Lygophis paucidens Hoge 1953a:253.
Type-locality: Mato Verde, Mato Grosso, Brazil
Liophis paucidens Dixon 1980:13.

Comment. Liophis paucidens is known from only 8 specimens that we are aware of and all are females. We have examined 6 of these.

Distribution and Habitat. Liophis paucidens occurs in east-central Brazil (Figure 3).

Liophis paucidens inhabits the Campos Cerrados of east-central Brazil and groundwater grass cover of the Babacu *(Orbignya martiana)* region in northeastern Brazil.

Definition. Liophis paucidens is a slender snake with three dark, longitudinal stripes on a light background and an immaculate venter (Figure 5). Four pattern illustrations are presented for the holotype of *Liophis paucidens* to demonstrate the changing appearance of the middorsal and lateral stripes. As with the other four species, *L. paucidens* has a wide middorsal stripe and two narrower lateral stripes on the extreme anterior (Figure 5A) and posterior (Figure 5D) portions of the body. This general pattern is continuous on the entire body for the other four species under investigation. However, the pattern of *L. paucidens* over the majority of the body appears as two black, dorsolateral stripes with a lighter stripe between them (Figure 5B and C). This is due to the disappearance of the inside border of the lateral stripe, with the area from the outside border of the lateral stripe to the border of the middorsal stripe becoming more melanistic. The most posterior portion of the body (Figure 5D) shows the reappearance of the inside border of the lateral stripe and the differentiation between middorsal and lateral stripes. The snake has a pattern that looks as if it goes from three stripes, to two stripes, then back to three again. This pattern is typical of all the *L. paucidens* we have examined. Scale rows are 17-17-15. Ventrals are 167-172, $\bar{x}=169$. Subcaudals are 64-70, $\bar{x}=67$. Supralabials are 8. Infralabials are 10. Preoculars are single. Postoculars are 2. Temporal arrangements are varied, (1+2). Supralabials 4 and 5 enter the orbit. Loreals are single. Maxillary teeth number 13-15, $\bar{x}=14$. The anal plate is divided. Primary scale row reduction sites are 82-120, $\bar{x}=103$. Tail/total length ratios are 22.1-24.8, $\bar{x}=23.2$. The scales are smooth and lack an apical pit.

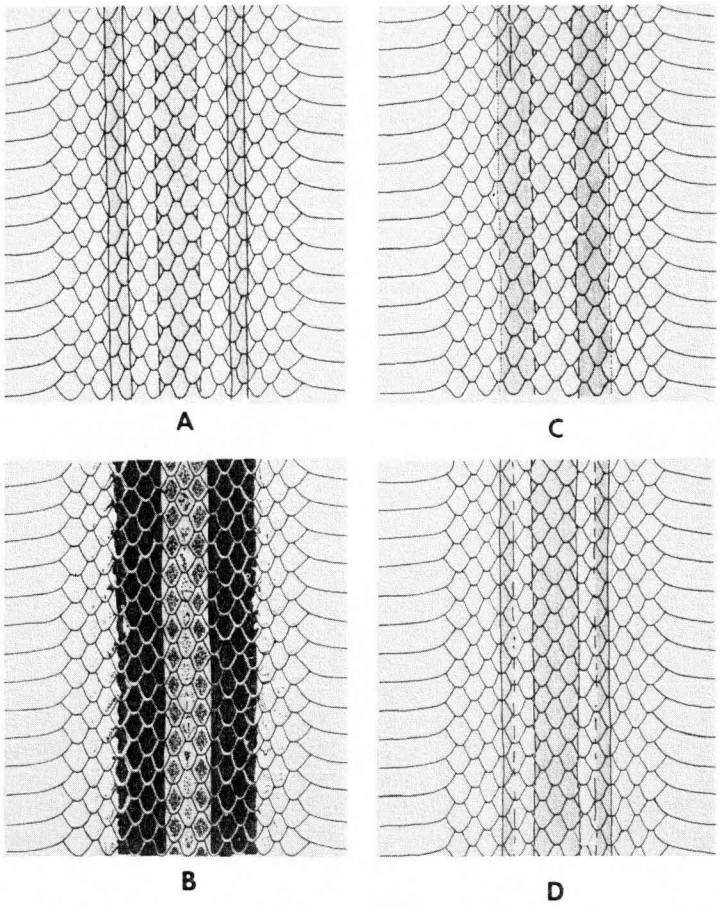

Figure 5. *Liophis paucidens* (IB 12016, holotype; Mato Grosso, Brazil). Pattern illustrations of the: **A.** neck; **B.** anterior body (ventrals 60-73); **C.** posterior body (ventrals 125-137); and **D.** pre-vent. *Liophis paucidens* has 17 scale rows anteriorly and 15 posteriorly.

Interspecific variation: Males and females were examined separately for interspecific variation.

The General Linear Models Procedure (GLM) with Duncan's Multiple Range Test was used to determine if there is any significant difference ($\propto = 0.05$) among each of the five groups of snakes for each individual variable. Supralabials, infralabials, preoculars, postoculars, temporals, supralabials entering the orbit, loreals, and anal plate do not differ significantly among any of the five taxa. Ventrals, subcaudals, maxillary teeth, hemipenis, reduction sites, tail/total length ratio, and presence or absence of a scale pit differ significantly among at least two of the five taxa (Tables 5 and 6).

Table 5

Mean ($\bar{x}$), Sample Size (N), and Significant Difference ($\propto = 0.05$) of seven characters among males of *L. lineatus* (1), *L. dilepis* (2), *L. meridionalis* (3), and *L. flavifrenatus* (4), resulting from the General Linear Models Procedure and Duncan's Multiple Range Test. Species underscored by the same line do not differ significantly.

CHARACTERS		MALES			
Ventrals	$\bar{x}$:	175	168	166	157
	Species:	2	1	3	4
	N:	52	49	34	15
Subcaudals	$\bar{x}$:	89	88	86	75
	Species:	4	1	3	2
	N:	15	37	27	39
Maxillary teeth	$\bar{x}$:	26	24	22	20
	Species:	4	3	1	2
	N:	13	27	49	49
Hemipenis length	$\bar{x}$:	18	14	13	13
	Species:	1	3	2	4
	N:	42	30	32	14
Prim. scale row reduction site	$\bar{x}$:	102	101	98	91
	Species:	1	2	3	4
	N:	47	31	18	7
Sec. scale row reduction site	$\bar{x}$:	106	105	102	
	Species:	2	3	4	
	N:	31	18	6	
Tail/Total (%)	$\bar{x}$:	28.9	28.0	27.5	24.8
	Species:	4	1	3	2
	N:	14	37	27	39

Table 6

Mean ($\bar{x}$), Sample Size (N), and Significant Difference ($\alpha = 0.05$) of six characters among females of *L. lineatus* (1), *L. dilepis* (2), *L. meridionalis* (3), *L. flavifrenatus* (4), and *L. paucidens* (5), resulting from the General Linear Models Procedure and Duncan's Multiple Range Test. Species underscored by the same line do not differ significantly.

CHARACTERS		FEMALES				
Ventrals	$\bar{x}$:	174	172	169	168	162
	Species:	2	3	5	1	4
	N:	78	61	5	101	22
Subcaudals	$\bar{x}$:	84	83	83	70	67
	Species:	1	3	4	2	5
	N:	66	47	17	58	5
Maxillary teeth	$\bar{x}$:	25	25	22	20	14
	Species:	4	3	1	2	5
	N:	18	55	100	76	3
Prim. scale row reduction site	$\bar{x}$:	103	103	100	100	90
	Species:	5	1	2	3	4
	N:	4	95	42	38	11
Sec. scale row reduction site	$\bar{x}$:	107	103	102		
	Species:	4	2	3		
	N:	9	41	37		
Tail/Total (%)	$\bar{x}$:	26.9	26.4	26.4	23.2	22.5
	Species:	4	1	3	5	2
	N:	17	65	47	4	57

The results of the GLM Procedure and Duncan's Multiple Range Test suggests that *Liophis lineatus* is a distinct species from those once thought to be its subspecies: *L. l. dilepis* and *L. l. meridionalis*. *Liophis flavifrenatus* and *Liophis paucidens* are currently recognized as distinct species, and this test substantiates that fact. *Liophis lineatus* differs significantly from *L. dilepis* in: numbers of scale rows, ventrals, subcaudals, and maxillary teeth; hemipenis length and relative tail length; presence or absence of scale pits; secondary scale row reduction site; and pattern. *Liophis lineatus* differs significantly from *L. meridionalis* in: numbers of scale rows and maxillary teeth; hemipenis length; presence or absence of scale pits; secondary scale row reduction site; and pattern. *Liophis dilepis* differs significantly from *L. meridionalis* in: numbers of subcaudals and maxillary teeth; relative tail length; and pattern. *Liophis flavifrenatus* differs significantly from all four of the other species in: numbers of scale rows and ventrals; primary scale row reduction site; and pattern. *Liophis paucidens* differs significantly from all four of the other species in: numbers of scale rows and maxillary teeth; and pattern. The scale row reduction site is unique. There is only one reduction, but it results from the fusion of scale

rows six and seven, rather than three and four. Scale rows six and seven are the ones that would normally fuse for the secondary reduction site (Dixon, 1981).

A Canonical Analysis in conjunction with the Multivariate Analysis of Variance (MANOVA) from the SAS library were used to determine if there are any significant differences ($\propto = 0.05$) among each of the five groups of snakes for a group of variables. These combined tests provide a multiple discriminant function that shows maximum intersample differences versus intrasample differences (Gould and Johnston, 1972). MANOVA was performed using several different groups of variables. Initially, all variable characters for the five groups of snakes were used. After this, only those variables that were shown to be significantly different between at least two of the five taxa by the GLM Procedure were used. Finally, this group of variables was used, minus two variables that are dependant upon others in the group. This data set includes: the anterior and posterior number of scale rows around the body; numbers of ventrals, subcaudals, and maxillary teeth; and presence or absence of scale pits (Figures 6 and 7). All three sets of variables used gave results similar to those in Figures 6 and 7. Each ellipse represents one taxon as compared to the others, for these variables, with a 95% level of confidence. The results of MANOVA, as with the GLM Procedure, depict significant differences among all five taxa. *Liophis dilepis* and *L. meridionalis* are shown to be distinct clusters, significantly different from *Liophis lineatus* and from one another. Based on all the information at hand, *Liophis lineatus dilepis* and *Liophis lineatus meridionalis* are elevated to species status; *Liophis dilepis* and *Liophis meridionalis*. The relationship among these five species is the remaining question to be addressed.

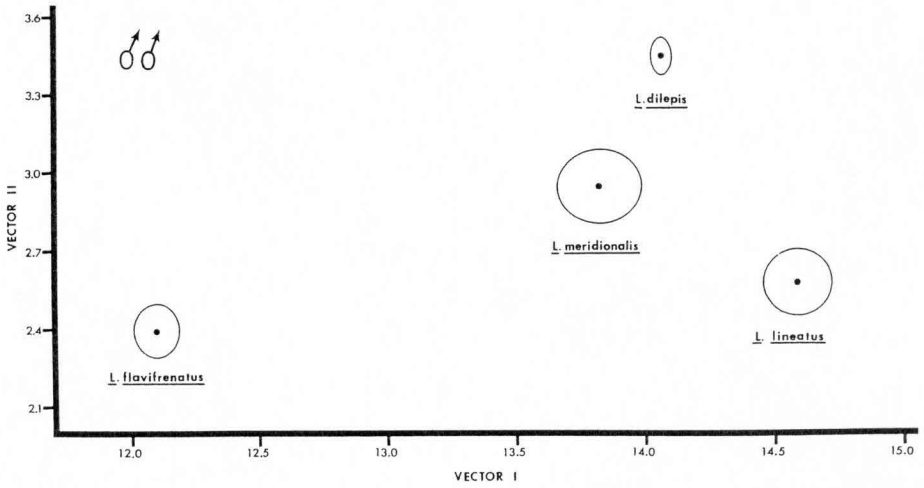

Figure 6. Elliptical projections of the first two canonical vectors for males. Each ellipse represents one taxon with a 95% level of confidence.

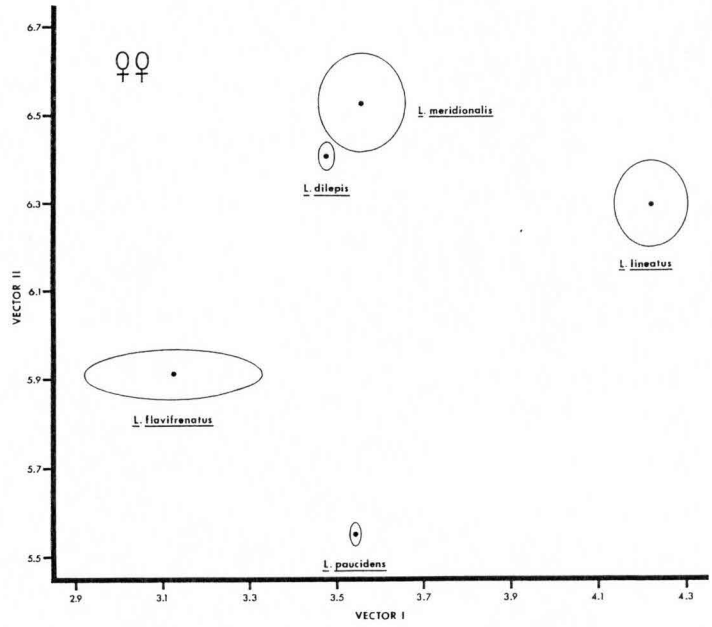

Figure 7. Elliptical projections of the first two canonical vectors for females. Each ellipse represents one taxon with a 95% level of confidence.

The following two tests are multivariate programs of the Numerical Taxonomy System (NT-SYS; Rohlf and Kishpaugh, 1972). These are cluster analysis, using the unweighted pair-group method based on arithmetic averages (UPGMA), and principle components analysis (PCA). Both tests were used to assess the phenotypic affinities of individual operational taxonomic units (OTU's). These were chosen because UPGMA is probably the most frequently used clustering strategy and PCA is a commonly employed ordination technique (Sneath and Sokal, 1973). Correlation and distance matrices among OTU's were generated from standardized character values. Each matrix was clustered using UPGMA. Phenograms were generated from the correlation and distance matrices. Principle components analysis (PCA) was performed on the correlation matrix to obtain vectors, indicating major trends of variation among OTU's.

Making a choice between the correlation and distance matrix implies an assumption about the variance in the original data. Relative amounts of variation are at least partly a function of scaling; if a variety of units were employed (such as meristic counts and ratios in our data set), the correlation matrix is generally preferable (Neff and Marcus, 1980). A phenogram generated from the correlation matrix depicting phenotypic affinities among males used the following variables: numbers of ventrals, subcaudals, and maxillary teeth; hemipenis length; primary scale row reduction site; and relative tail length (Figure 8). All these variables demonstrated significant differences ($\propto = 0.05$) among groups when analyzed using GLM with Dun-

can's Multiple Range Test. A phenogram generated from the correlation matrix depicting phenotypic affinities among females used the following variables: numbers of ventrals, subcaudals, and maxillary teeth; primary scale row reduction site; and relative tail length (Figure 9).

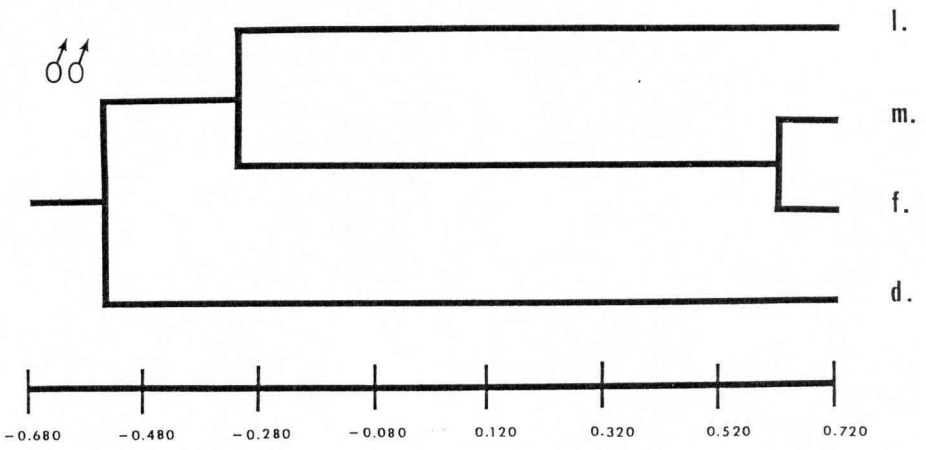

Figure 8. Phenogram of the males of *L. lineatus* (l.), *L. meridionalis* (m.), *L. flavifrenatus* (f.), and *L. dilepis* (d.) based on UPGMA cluster analysis of correlation coefficients on six variables. The cophenetic correlation coefficient is 0.958.

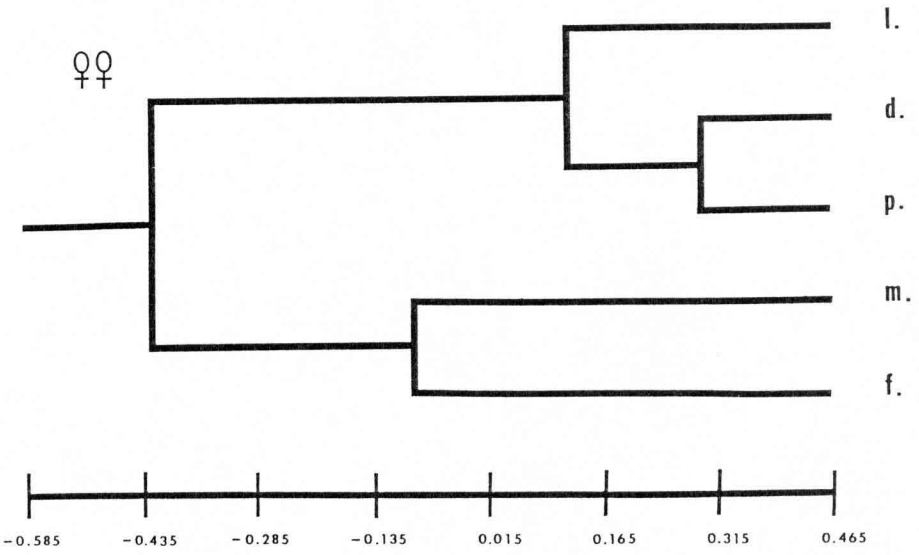

Figure 9. Phenogram of the females of *L. lineatus* (l.), *L. dilepis* (d.), *L. paucidens* (p.), *L. meridionalis* (m.), and *L. flavifrenatus* (f.) based on UPGMA cluster analysis of correlation coefficients on five variables. The cophenetic correlation coefficient is 0.819.

In determining the relationship among the five species in this study, the phenograms presented depict the phenetic relationship among these species, but may or may not represent their true phylogenetic relationship. The phenogram of the males of *L. lineatus, L. meridionalis, L. flavifrenatus,* and *L. dilepis* based on UPGMA cluster analysis is shown in Figure 8. *Liophis meridionalis* and *L. flavifrenatus* are closely related sister species, with *L. lineatus* more closely related to these than is *L. dilepis*. The phenogram of the females includes the species *L. paucidens* (Figure 9). *Liophis meridionalis* and *L. flavifrenatus* are still shown to be closely related. *Liophis paucidens* pairs with *L. dilepis,* and in this instance *L. lineatus* is more closely related to *L. dilepis* and *L. paucidens* than to *L. meridionalis* and *L. flavifrenatus*. Obviously, the manner in which these species relate to *L. lineatus* varies according to sex. It was not possible to resolve this relationship by generating a correlation matrix that would depict phenotypic affinities of combined samples of males and females. Such a matrix would violate the basic assumption of PCA; that the data are multivariately normally distributed (Neff and Marcus, 1980). Also, all the specimens of *Liophis paucidens* are females.

The elliptical projections (Figures 6 and 7) show *L. dilepis* and *L. meridionalis* being more similar to one another than to any other taxon. This has resulted primarily because these two species have identical scale row counts (19-19-15). The phenograms (Figures 8 and 9) resulted in the paring of *L. dilepis* with *L. paucidens,* and *L. meridionalis* with *L. flavifrenatus*. Compared to *L. meridionalis* and *L. flavifrenatus, L. dilepis* and *L. paucidens* have greater numbers of ventrals, shorter tails, and fewer maxillary teeth. *Liophis lineatus* is shown to be more closely related to *L. dilepis* and *L. paucidens* than it is to the other two taxa (Figure 9), but this is due simply to a similarity in numbers of ventrals and corresponding primary scale row reduction site. We concur with the pairing of *L. dilepis* with *L. paucidens* and *L. meridionalis* with *L. flavifrenatus,* but believe that *L. lineatus* shows closer affinities to *L. meridionalis* and *L. flavifrenatus*.

When the results of all the statistical analyses are considered in light of each species distribution and pattern, the following hypothetical relationship is proposed.

Liophis meridionalis and *L. flavifrenatus* are closely related phenetically and phylogenetically. This is substantiated by both phenograms and by the discovery of a possible hybrid between these two species. *Liophis dilepis* and *L. paucidens* are related primarily on the basis of similar numbers of subcaudals and tail/total length ratios; they are both short-tailed snakes compared to the other taxa. We do not believe that these two species are as closely related as suggested in Figure 9. We believe that *L. dilepis* is closely related to *L. lineatus,* while *L. paucidens* is the most distantly related. Figure 10 represents what we believe to be the most parsimonious phenogram showing the relationships among the five species.

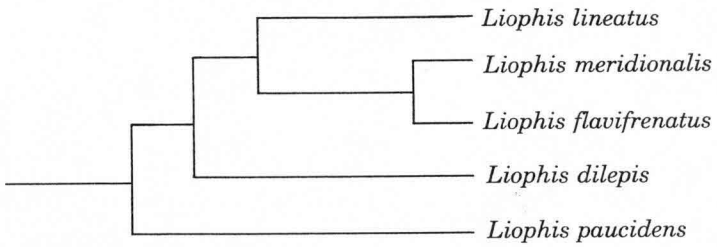

Figure 10. Phenogram depicting a hypothetical relationship among five species of *Liophis*.

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Specimens Examined

Liophis lineatus. No known locality: AMNH 2191, USNM 61965. "Brasilieu": UZM 601265. South America: MHNP 1104, 1104A, USNM 423. Surinam; Guiana: AMNH 3589, 3590. Venezuela and Surinam: AMNH 4416-4420. BRAZIL MHNP 7459. (PARÁ) Igrapé Jaramacaru, Campos do Ariramba: MZUSP 4818; Ilha de Marajó: MCZ 22449; Santarem: IB 16832, MCZ 2803, 3006, MHNP 5350. (RORAIMA) São Marcos: IB 24026; Surumu: MZUSP 4663. BRITISH WEST INDIES (in error) Little Tobago Island: AMNH 84230. COLOMBIA (ANTIOQUIA) Nechí: FMNH 54889. (ATLANTICO) Cienaga de Amajahuevo, CVM Fishery Station: FMNH 165221, 165523; Canal de Dique, CVM Fishery Station: FMNH 165520. (BOLIVAR) CVM Fishery Station, in front of San Cristobal: FMNH 165527, 166027; Gambote, Canal de Dique: FMNH 165852, 165853; 22 km N San Onofre: FMNH 165633; Santa Rosa: MZUSP 6183-6186; region of Santa Rosa: FMNH 165231-165235; Sincelejo: FMNH 165487; road between Sincerin and Malagena: FMNH 165337; Sucre, Tolu: LACM 114647. (CAQUETA) Rio Tuna, tributary of upper Rio Yari, close to S. slope of Cordillera Oriental: FMNH 165560. (CUNDINAMARCA) Casanare, Llanos Orientales: MZUSP 6126; Palauquero Base Area, on Rio Magdelena: LACM 103624, 103625. Kotsipa(?), bassin de l'Orénoque: MHNP 1973/457. (LA GUAJIRA) Merochon, about 5 km SE Uriba: AMNH 110016; 0.5 miles S Pajaro: USNM 151642. (MAGDALENA) Magdalene-Flodue: UZM 601269. (META) Lomalinda: UTAR 3554, 3658, 3712, 3846, 3863, 5169, 5170, 5197; Peralanzo (Peralonso): MZUSP 6102. (TOLIMA) Honda: USNM 156902. (VAUPES) Caño Aqua Bonita, near San Jose del Guaviare: FMNH 75686, 75687; Valle, Río Vaupes, Mitu: USNM 153841. (VICHADA) WWL 587. COSTA RICA (in error) Limon: AMNH 5304. ECUADOR (ESMERALDAS) Esmeraldas: AMNH 20410. (MANATI (MANABÍ)) Maicito: MHNG

1367.83. FRENCH GUIANA (CAYENNE) Sinnamary: IB 13752, 13756. GUYANA AMNH 36121-36125. (EAST DEMERARA — WEST COAST BERBICE) Berbice: BM 53.4.6.65; Demerara: AMNH 36091, BM 55.8.28.24, 55.8.28.39, 55.8.28.40, 55.8.28.40A-D, 55.8.28.63, FMNH 3302, 26669-26671, 26736-26738, UMMZ 85283, USNM 12736, UZM 601259, 601263; Georgetown: AMNH 2664, FMNH 170766, UMMZ 80424, 80425, 83641. (MAZARUNI — POTARO) Kartabo: AMNH 14265, 98206. (RUPUNUNI) Isheartun (Isherton): AMNH 60837, 60838; Parabam (Parabara): AMNH 60789; between Wichabai and Isheartun (Isherton): AMNH 60836. PANAMA USNM 53627. (COCLÉ) El Valle de Anton: AMNH 71670; 5.3 km N Nata: KU 110726. (HERERA) 5 km E Santa Maria: KU 110727. (LOS SANTOS) 6 km NE Macaracas: KU 107777. (VERAGUAS) Santiago: AMNH 71671; 21 km SW Santiago: KU 107778. PARAGUAY (in error) USNM 6088. SURINAM AMNH 97712, ANSP 5535-5538, MHNP 1100, 1100A, UZM 601256-601258, 601260. (MAROWIJNE) Langamankondre: MZUSP 4563. (SARAMACCA) somewhere up the Coppename River: AMNH 73842. (SURINAME) Paramaribo: AMNH 4426, 8662-8664, TCWC 60542; Botanical Gardens: AMNH 104625; Pl. Maretrait: AMNH 97711. VENEZUELA MHNP 1902/222, UZM 601261, 601262, 601264. St. Helena(?): UMMZ 124217. (AMAZONAS) Esmeralda: AMNH 36603, 36623. (APURE) FMNH 204487; 5 km SW Bruzval: TCWC 46265; San Fernando: MHNP 1976/378. (BOLIVAR) Auyantepui: AMNH 61021, 61023, 61026-61029, 61039. (GUARICO) 8 km N Calabozo: UMMZ 82863; 35 km S Calabozo: USNM 198545; Mangas Cobera: MHNP 1976/377; 15.5 km N San Fernando de Apure: TCWC 47928. (TACHIRA) 7.5 km SW Punta de Piedra: KU 167605.

Liophis dilepis. BOLIVIA (SANTA CRUZ) Puerto Suárez: BM 1907.10.31.31; Sara: BM 1907.10.31.30. BRAZIL IB 21967, ZMH R01823. (BAHIA) Barreiras: UMMZ 108745-108759; Bom Jesus da Lapa: UMMZ 108742, 108743; Jupagua, on Río Grande: UMMZ 108744; Santa Rita de Cassia: MZUSP 3620. (CEARÁ) Arajara: MZUSP 7211-7213; Fortaleza: UMMZ 80767; Jua, near Iguatu: FMNH 5702; Justiniano Serpa (Coluna): MZUSP 5313-5316; Lima Campos: USNM 146612; Maranguape: UMMZ 84267; Maranguape (Acude Amanari): MZUSP 3363, 3364; Morro Branco: MZUSP 5326-5328; Pacajus (Guarani): MZUSP 5301. (MATO GROSSO) Bodoquena: IB 14561; Carandazal: IB 13533, 14372; Pôrto Esperança: IB 15746. (MINAS GERAIS) Januaria: UMMZ 108723-108741; Rio Pandeiras: IB 9156, 9157. (PARAÍBA) São Jose de Espinharas: MZUSP 5963. (PERNAMBUCO) MHNP 1967/144-1967/147; Exu: MZUSP 6744-6764, 7114-7133; 5 km E Exu: MZUSP 7134, 7135; 13 km E Exu: MZUSP 6949; 5 km N Exu: MZUSP 6918; Fazenda Batente: UMMZ 149015. (RIO GRANDE DO NORTE) Ceara Mirim: FMNH 64405. PARAGUAY NS 127186. "Chaco": USNM 69872. (AMAMBAY) Pedro Juan Caballero: MCZ 46999, 47031. (BOQUERÓN) Agua Dulce, Parque Nacional Defensores del Chaco: NS 98664; Filadelphia: CM 94227, USNM 129455. (CENTRAL) Viletta: NS 125645. (OLIMPO) Bahia Negra, Puerto 14 de Mayo: BM 98.6.3.7, 98.6.3.8. (PARAGUARÍ) km 129, 15 km S entrance to Parque Nacional "Ybycui" on rd. to Ybycui: NS 125813. (PRESIDENTE HAYES) Chaco-í: MZUSP 2399; La Golondrina, 30 km NW Villa Hayes: NS 127185; Primavera: BM 1958.1.2.23; km 199, Trans-Chaco Highway: NS 97980.

Liophis meridionalis. Lagoa-Santa: UZM 601267, 601268; Plata-Staterne: UZM 601266. ARGENTINA (LA RIOJA, in error) Pataquía, Estancia Breyer: USNM 73432. (MISSIONES) Candelaria: BM 85.6.15.6. BOLIVIA (BENI) Inside house in Pueblo Casa de Jesus Ayala, Casa #294: FMNH 161534; San Joaquin: FMNH 161533,

161535. (SANTA CRUZ) Buena Vista: FMNH 35651-35653; Río Colorado: CM 2848; Sara: BM 1907.10.31.32, CM 5; Sara, Santa Cruz: CM 2754. BRAZIL (GOIÁS) Aruanã: MZUSP 2188; Campinas: IB 4611, 4623; Lago Itacy, Pôrto de São Felix: IB 15725. (MATO GROSSO) Agachí: IB 14525, 14559; Aquidauana: IB 16156, 16157; Bolicho: IB 16066; Cáceres: MZUSP 3360; Coronel Juvêncio: IB 18817; Maracaju: USNM 107728; Pôrto XV: MZUSP 3362; Terenos: IB 8792, 8842, 10019; Três Lagoas, Jupiá: IB 21388, 21508, 21648, 21725, MZUSP 4424; Utiariti: MZUSP 4747. (MINAS GERAIS) km 108+ on MG Rt. 2, Serra do Cipo, near Chapeu de Sol: USNM 218213; Santa Barbara: IB 2127; Uberaba: IB 10237; Uberlandia: IB 15868, 16008. (PARÁ) Ilha de Marajó (in error): BM 1926.5.5.3; Cachimbo: IB 16634, MZUSP 3359, 3365. (PARANÁ) Piraky: MCZ 39438. (SÃO PAULO) MZUSP 1167; Buri: IB 9255, 9284; Emas: IB 8854, MZUSP 2452, 2862, 2955, 2982, 2983, 3361, 4898, 4899; Franca: MZUSP 1166; near Ilha Solteira-Montante: IB 35666, 35977, 36440-36445, 36591, 36606, 36713, 37634, 37726, 37727; Ilha dos Três Estados, Río Paraná: IB 37992; Penapolis: IB 11021; Terra Roxa: IB 17180. PARAGUAY MHNP 1533, 1890/109, USNM 5810. (AMAMBAY) Pedro Juan Caballero: FMNH 42272, MCZ 46998. (CONCEPCIÓN) Puerto Pinasco: USNM 63500. (PRESIDENTE HAYES) Primavera: BM 1956.1.3.41, 1956.1.3.42, 1956.1.16.38, 1958.1.2.22, 1960.1.2.80-1960.1.2.83, 1962.73-1962.79. (SAN PEDRO) Carumbé: FML 635.

Liophis flavifrenatus. BRAZIL (MATO GROSSO) Ligação: IB 16158. (RÍO GRANDE DO SUL) Cacequy (Cacequi): CM 363; Río Grande: BM 86.10.4.9, 86.10.4.10; São Lorenzo (São Lourenço do Sul): BM 86.1.19.19, 86.1.19.20; Santa Maria: MCZ 43305, 43306. (SÃO PAULO) MCZ 20705; Barey: IB 1526; Buri: USNM 100759; Itaguerá: IB 10206-10209; Itararé: IB 45763; São Caetano do Sul: MZUSP 2820; São Paulo: IB 205, 206, 611, 815, 1043, 1330, 5962, 6547, 10289, 13554, 17126, 22271; MCZ 17912, 39439, MZUSP 1172. PARAGUAY (GUAIRÁ) Canendiyu: MZUSP 5337. (PRESIDENTE HAYES) Primavera: BM 1955.1.5.98; Río Vermejo (Bermejo) region: ANSP 4604, USNM 5397. URUGUAY (in error?) MCZ 863.

Liophis meridionalis × *Liophis flavifrenatus*. BRAZIL (SÃO PAULO) UMMZ 79661.

Liophis paucidens. BRAZIL (GOIÁS) Ipameri: IB 10448. (MATO GROSSO) Mato Verde, on Río Araguaia: IB 12016. (MINAS GERAIS) Pirapora, Lagoa da Tota: UMMZ 108763. (PIAUÍ) Teresina: IB 1225-1227.

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