

often be ingested at night. A subsequent study on the acceptance of dead prey by snakes was undertaken by curator Edward George Boulenger in 1915 (Proc. Zool. Soc. London 1915:583–587). The situation at the London Zoo becomes clear when one refers to a quote by Mitchell in 1929: “My rule about no living prey being given except with special and direct authority is faithfully kept, and permission has to be given in only the rarest cases, these generally of very delicate or new-born snakes which are given new-born mice, creatures still blind and entirely unconscious of their surroundings.”

<sup>7</sup> Edward Horatio Girling, head keeper of the snake room in 1852 at the London Zoo, may have been the first zoo snakebite victim. After consuming alcohol in prodigious quantities in the early morning with fellow workers at the Albert Public House on 29 October, he staggered back to the Zoo and announced that he was inspired to grab an Indian cobra a foot behind its head. It bit him on the nose. Girling was taken to a nearby hospital where current remedies available at the time were tried: artificial respiration and galvanism; he died an hour later. Many respondents to *The Times* newspaper articles suggested liberal quantities of gin and rum for treatment of snakebite but this had already been accomplished in Girling’s case. Other recommendations were a bit unnerving: 1) being buried in manure to the neck; 2) application of a white-hot iron or other fiery instrument for at least an hour; 3) solicit a bite from a second snake to neutralize the effects of the first one; and 4) since sleep was always fatal, taking desperate measures to keep the injured party awake. For example, two Indians in the British army had dragged a screaming victim around a verandah for 3½ hrs; death was prevented.

<sup>8</sup> Two of the three most popular exhibits were the aquarium and reptile house at the London Zoo (Balmford 2000).

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## POINTS OF VIEW

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### The Destabilization of North American Colubroid Snake Taxonomy

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The classification of taxa has always been an area of debate among systematists—empirically, methodologically, and philosophically. Arguably, the single most important change over the past forty years is the widespread recognition that a classification system is only useful when it functions as a storage and retrieval system of phylogenetic information. Although the type of information to be stored has largely been agreed upon (i.e., propinquity of descent and monophyly), debate continues on the method of this system (e.g., PhyloCode: Cantino and de Queiroz 2003; contra Keller et al. 2003; Nixon et al. 2003). Regardless, the role of classification as a subdiscipline of the science of systematics is clear, and it is separate from that of nomenclature, although both are subdisciplines of taxonomy (de Queiroz 2006). Taxonomy is informed by phylogenetics, and this information is used in the naming of biodiversity (nomenclature) and in the organization of the named groups (classification). All systems of classification and nomenclature that are based on evolutionary hypotheses (phylogeny) provide ranks and names for only monophyletic groups. It is from this framework that we address recently proposed changes to the taxonomy of the Colubroidea in North America (NA; Table 1).

One of the largest groups of squamates, the Colubroidea, was recently found to contain a number of families and subfamilies that were determined to be para- or polyphyletic (Kelly et al. 2003; Lawson et al. 2005). The ‘traditional’ classification, with four families and 15 subfamilies, has remained in this state at least since Dowling and Duellman (1978; although five of the aforementioned subfamilies were used as tribes in that work). Virtually all of these subfamily names (except Pseudoxyrhopiinae), even those used as tribes in Dowling and Duellman (1978), long predate that publication (Table 2). To rectify this disconnection between phylogeny and taxonomy, establish consistency with phylogenetic hypotheses generated from a large number of morphological and molecular studies (see references in Lawson et al. 2005), and make

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TABLE 1. A comparison of recent classifications of North American colubroid snake genera.

Zaher (1999) and Zug et al. (2001)		Lawson et al. (2005)		Collins (2006)	
Family	Subfamily	Genus	Family	Subfamily	Genus
Colubridae	Colubrinae	<i>Arizona</i>	Colubridae	Colubrinae	Colubridae
		<i>Bogertophis</i>			N/A
		<i>Cemophora</i>			
		<i>Chilomeniscus</i>			
		<i>Chionactis</i>			
		<i>Coluber</i>			
		<i>Drymarchon</i>			
		<i>Drymobius</i>			
		<i>Ficimia</i>			
		<i>Gyalopion</i>			
		<i>Lampropeltis</i>			
		<i>Masticophis</i>			
		<i>Ophedrys</i>			
		<i>Oxybelis</i>			
		<i>Pantherophis [Elaphe]</i>			
		<i>Phyllorhynchus</i>			
		<i>Pituophis</i>			
		<i>Rhinocellus</i>			
		<i>Salvadora</i>			
		<i>Senticolis</i>			
		<i>Sonora</i>			
		<i>Stilosoma</i>			
		<i>Tamilla</i>			
		<i>Trimorphodon</i>			
	Natricinae	<i>Clonophis</i>		Natricinae	Natricidae
		<i>Nerodia</i>			
		<i>Regina</i>			
		<i>Seminatrix</i>			
		<i>Storeria</i>			
		<i>Thamnophis</i>			
		<i>Tropidoclonion</i>			
		<i>Virginia</i>			
		<i>Arizona</i>			
		<i>Bogertophis</i>			
		<i>Cemophora</i>			
		<i>Chilomeniscus</i>			
		<i>Chionactis</i>			
		<i>Coluber</i>			
		<i>Drymarchon</i>			
		<i>Drymobius</i>			
		<i>Ficimia</i>			
		<i>Gyalopion</i>			
		<i>Lampropeltis</i>			
		<i>Masticophis</i>			
		<i>Ophedrys</i>			
		<i>Oxybelis</i>			
		<i>Pantherophis</i>			
		<i>Phyllorhynchus</i>			
		<i>Pituophis</i>			
		<i>Rhinocellus</i>			
		<i>Salvadora</i>			
		<i>Senticolis</i>			
		<i>Sonora</i>			
		<i>Stilosoma</i>			
		<i>Tamilla</i>			
		<i>Trimorphodon</i>			
		<i>Clonophis</i>			
		<i>Nerodia</i>			
		<i>Regina</i>			
		<i>Seminatrix</i>			
		<i>Storeria</i>			
		<i>Thamnophis</i>			
		<i>Tropidoclonion</i>			
		<i>Virginia</i>			

TABLE 1. Continued.

Zaher (1999) and Zug et al. (2001)		Lawson et al. (2005)		Collins (2006)	
Family	Subfamily	Genus	Family	Subfamily	Genus
Colubridae	Dipsadinae (Xenodontinae)	<i>Carphophis (incertae sedis)</i>	Colubridae	Xenodontinae	<i>Carphophis</i>
		<i>Contia (incertae sedis)</i>			<i>Contia</i>
		<i>Coniophanes</i>			<i>Coniophanes</i>
		<i>Diadophis (incertae sedis)</i>			<i>Diadophis</i>
		<i>Hypsiglena</i>			<i>Farancia</i>
		<i>Leptodeira</i>			<i>Heterodon</i>
		<i>Rhadinea</i>			<i>Hypsiglena</i>
					<i>Leptodeira</i>
					<i>Rhadinea</i>
					Xenodontinae (Xenodontinae)
Elapidae	Elapinae	<i>Farancia</i>	Elapidae	Elapinae	<i>Farancia</i>
		<i>Heterodon</i>			<i>Heterodon</i>
					<i>Micrurus</i>
					<i>Micruroides</i>
					<i>Pelamis</i>
Viperidae	Crotalinae	<i>Agkistrodon</i>	Viperidae	Crotalinae	<i>Agkistrodon</i>
		<i>Crotalus</i>			<i>Crotalus</i>
		<i>Sistrurus</i>			<i>Sistrurus</i>
Elapidae	Elapinae	<i>Micrurus</i>	Elapidae	Elapinae	<i>Micrurus</i>
		<i>Micruroides</i>			<i>Micruroides</i>
Viperidae	Crotalinae	<i>Pelamis</i>	Viperidae	Crotalinae	<i>Pelamis</i>
Viperidae	Hydrophiinae	<i>Pelamis</i>	Hydrophiidae	Hydrophiinae	<i>Pelamis</i>
Viperidae	Crotalinae	<i>Agkistrodon</i>	Crotalinae	Crotalinae	<i>Agkistrodon</i>
		<i>Crotalus</i>			<i>Crotalus</i>
		<i>Sistrurus</i>			<i>Sistrurus</i>
Viperidae	Hydrophiinae	<i>Pelamis</i>	Hydrophiidae	Hydrophiinae	<i>Pelamis</i>
Viperidae	Crotalinae	<i>Agkistrodon</i>	Crotalinae	Crotalinae	<i>Agkistrodon</i>
		<i>Crotalus</i>			<i>Crotalus</i>
		<i>Sistrurus</i>			<i>Sistrurus</i>
Viperidae	Hydrophiinae	<i>Pelamis</i>	Hydrophiidae	Hydrophiinae	<i>Pelamis</i>
Viperidae	Crotalinae	<i>Agkistrodon</i>	Crotalinae	Crotalinae	<i>Agkistrodon</i>
		<i>Crotalus</i>			<i>Crotalus</i>
		<i>Sistrurus</i>			<i>Sistrurus</i>

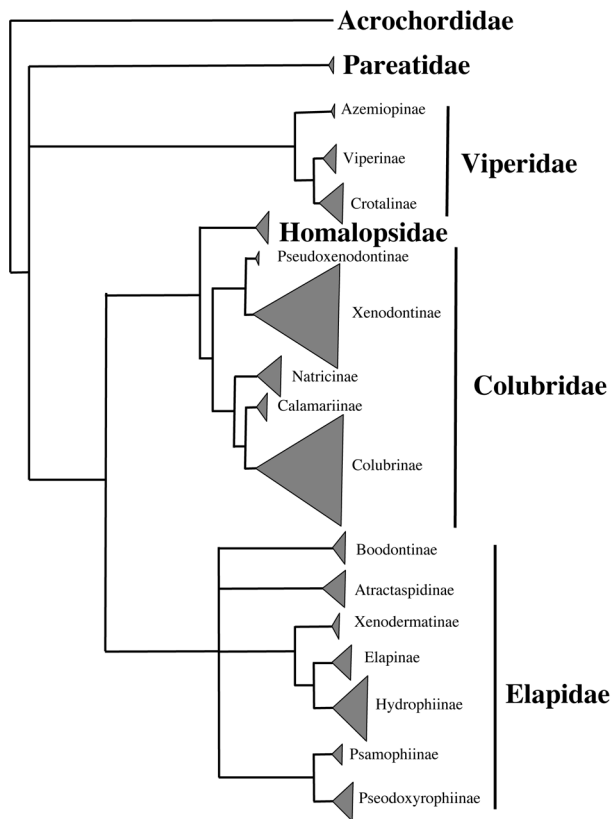


FIG. 1. Phylogenetic relationships of the Colubroidea (including the outgroup Acrochordidae) based on Lawson et al. (2005). The widths of the triangles for families and subfamilies indicate relative numbers of genera.

only modest corrections to the currently used taxonomy, while providing enough information to reflect taxonomic changes, Lawson et al. (2005) proposed a new classification (Table 1; Fig. 1). This classification included the following five families and 15 subfamilies (in parentheses): Colubridae (Calamariinae, Colubrinae, Natricinae, Pseudoxenodontinae, and Xenodontinae), Elapidae (Atractaspidinae, Boodontinae, Elapinae, Hydrophiinae, Psammophiinae, Pseudoxyphiinae, and Xenodermatinae), Homalopsidae, Pareatidae, and Viperidae (Azemiopinae, Crotalinae, and Viperinae). The only radical change here concerned the inclusion of “nonvenomous” snakes (in the traditional sense) in the Elapidae; however, both venomous subfamilies of the former Elapidae, Elapinae and Hydrophiinae, were retained. This taxonomic decision was based on strong evidence and an application of the oldest family name, Elapidae, to the most recent common ancestor of the node including all aforementioned taxa (Fig. 1).

Collins (2006) suggested that placing the NA colubroid snake genera into the seven basic Linnean categories (Kingdom, Phylum, Class, Order, Family, Genus, and Species) would be more useful because the “layperson” would have difficulty memorizing one extra category, the subfamily. Aside from an unqualified assessment concerning the intelligence of the public on taxonomic matters, the system unilaterally proposed by Collins (2006) destabilizes colubroid classification to an extent possibly worse than the para- or polyphyletic classification in existence prior to Lawson et al. (2005). Here we address several major concerns that the pro-

posal of Collins (2006) would have on colubroid classification. We also present a classification of the NA colubroid snakes that reflects Lawson et al. (2005), which provides the maximum phylogenetic information in this nomenclatural system (Table 1). Finally, we discuss three main areas where the classification of Collins (2006) is detrimental to information storage, communication, and phylogenetic representation.

#### THE LOSS OF PHYLOGENETIC INFORMATION

By eliminating the subfamily classification, Collins (2006) has effectively reduced the phylogenetic information inherent in the taxonomy proposed by Lawson et al. (2005). The arrangement of the NA Colubroidea in Collins (2006) simply elevates seven subfamilies to familial level while discarding interfamilial relationship. Retaining these as subfamilies nested within families, as suggested by Lawson et al. (2005), reveals information concerning relationships among these subfamilies (Table 1; Fig. 1). For example, it is not clear in Collins (2006) that the Elapidae and Hydrophiidae share a more recent common ancestor with each other than any of the other NA families of the Colubroidea (i.e., Colubridae, Natricidae, etc.).

In classification B of Collins (2006), he misrepresents Lawson et al. (2005) by suggesting this system contains less taxonomic information than his preferred system (classification A; Table 1) because it only reveals two taxonomic groupings for the Colubroidea of NA: Colubridae and Elapidae. If he were to use the classification system in Table 5 of Lawson et al. (2005) for NA snakes, then it should have been clear that various monophyletic groups within NA are represented by subfamilies nested within families. This not only yields more taxonomic information than Collins (2006), but also is more consistent with the historical use of these names and modern phylogenetic hypotheses.

The claim that Collins (2006) represents a standard classification because it refers only to the seven primary Linnean groupings is also misleading. For example, Collins (2006) only includes two of the Linnean ranks (family and genus)—a practice that is not commonplace in herpetology. In fact, the oldest use of subfamilies for the Colubroidea dates back to 1768 (Viperinae; Laurenti) and the majority of the others date to the 1800s (Table 2). All the names applied in Lawson et al. (2005) were used in Dowling and Duellman (1978) and are still used by two of the standard college texts on Herpetology (Pough et al. 2004; Zug et al. 2001).

#### DISRUPTION OF INTERNATIONAL SCIENTIFIC COMMUNICATION

The primary goal of the Linnean hierarchy is to facilitate accurate scientific communication among researchers living throughout the world and speaking different languages. Elevating the subfamily names for colubroid snakes only occurring north of the Mexican border ignores the higher-level taxonomy of snakes living outside of the U.S. and Canada. It does not facilitate scientific communication between researchers speaking different languages when the same taxa found in two different countries are represented by two different classification systems. For instance, 92% of the snake genera in the U.S. and Canada are also found in Mexico (Conant and Collins 1991; Stebbins 2003), but the proposal of

TABLE 2. Earliest usage of colubroid subfamily and tribe names adopted by Lawson et al. (2005).

Taxon Name	Author(s)	Dowling & Duellman (1978)
Atractaspidinae	Guenther (1858)	Subfamily
Azemiopinae	Liem et al. (1971)	Subfamily
Boodontinae	Cope (1893)	Tribe
Calamariinae	Bonaparte (1838)	Tribe
Colubrinae	Oppel (1811)	Subfamily
Crotalinae	Oppel (1811)	Subfamily
Elapinae	Boie (1827)	Subfamily
Homalopsinae	Jan (1863)	Tribe
Hydrophiinae	Boie (1827)	Subfamily
Natricinae	Bonaparte (1838)	Subfamily
Pareatinae	Romer (1956)	Tribe
Psammophiinae	Bonaparte (1845)	Tribe
Pseudoxenodontinae	McDowell (1987)	Not used
Pseudoxyrhophiinae	Dowling (1978)	Tribe
Xenodermatinae	Smith (1939)	Tribe
Xenodontinae	Bonaparte (1845)	Subfamily
Viperinae	Laurenti (1768)	Subfamily

Collins (2006) only grants the same hierarchical classification for species in the two countries north of Mexico. Moreover, this taxonomic change also does not consider how to place the nearly 90% of other snake genera not found within the U.S. and Canada. For instance, the family Colubridae of Lawson et al. (2005) contains 244 genera in five subfamilies and occurs on all continents except Antarctica. In comparison, the family Colubridae of Collins (2006) addresses only 25 genera, no subfamilies, and only applies to the U.S. and Canada. It is not a grand revelation to understand that species distributions do not coincide with political boundaries. Likewise, classification systems should not be bounded by political borders.

#### PHYLOGENETIC INACCURACIES

In two cases, the elevation of subfamily to family by Collins (2006) requires a taxonomic decision not in keeping with the phylogenetic hypothesis presented by Lawson et al. (2005). The Xenodontinae have typically been divided into two groups: the Xenodontinae representing South American genera and the Dipsadinae representing Central American genera (Cadle 1984; 1985; Crother 1999). For the nine genera of NA xenodontines, Zaher (1999) tentatively placed *Farancia* and *Heterodon* in the Xenodontinae and the remaining genera in the Dipsadinae. Lawson et al. (2005) found a sister relationship between *Farancia* (Xenodontinae) and *Carphophis* (Dipsadinae), which suggests that either the taxonomic contents of the subfamilies are incorrect, or that these groups are artificial. Lawson et al. (2005) contended that their sampling was not adequate to address this issue, so they placed both the Xenodontinae and Dipsadinae under the heading of Xenodontinae in their taxonomic list in Table 5. This classification placed all of the monophyletic Xenodontinae and Dipsadinae

under one subfamily, but still made note of the traditional groupings of Xenodontinae and Dipsadinae of Zaher (1999). Collins (2006), without conducting any original phylogenetic research or reanalysis of available data, indicated that the uncertainty in the classification of the Xenodontinae had been solved when he placed *Farancia* and *Heterodon* in the family Xenodontidae and the other NA xenodontines in Dipsadidae. To aid with the description of this putatively paraphyletic classification, he also invented new common names for these subfamilies that do not accurately define either group: slender rear-fanged snakes (Dipsadidae) and robust rear-fanged snakes (Xenodontidae). Again, this classification does not reflect the phylogeny presented in Lawson et al. (2005), creates two paraphyletic groups, and should not be supported.

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## ARTICLES

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### Notes on the Ecology of the Colubrid Snake *Leptodeira annulata* in the Pantanal, Brazil

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The ecology of many Neotropical snakes, especially Brazilian species, is poorly known (Cadle and Greene 1993; Vitt 1996). Moreover, published studies are often based on examination of preserved specimens (Marques 1996) and therefore deal mainly with diet and reproduction of particular species (e.g., Bizerra et al. 2005), whereas activity patterns, habitat use and thermal ecology are infrequently reported (e.g., Oliveira and Martins 2001).

The Brazilian Pantanal is a low-lying floodplain covering an area of some 140,000 km<sup>2</sup>, consisting of a mosaic of lakes, permanent swamps and seasonally inundated grassy fields with elevated patches bearing forest or cerrado vegetation (Ratter et al. 1988). The Pantanal is located in the Western region of Brazil and eastern Bolivia and is characterized by mean annual temperature of 25°C, and annual precipitation of 1100–1200 mm (Brasil 1997).

The Pantanal has low species richness relative to the Cerrado and Amazon, but has some locally abundant snake species, thus facilitating studies of snake ecology (Strüssmann and Sazima 1993).

In spite of being one of the most abundant species in the Pantanal, little is known about the biology of the cat-eyed snake *Leptodeira annulata* in Brazil (Brasil 1997). Moreover, available data on *L. annulata* are largely from the Amazon (Vitt 1996) and Chaco (Lavilla and Scrocchi 1996) biomes. Here we present data on the activity, thermal ecology and habitat use of *Leptodeira annulata* in the Nhecolândia region, Pantanal, collected over five months.

#### MATERIALS AND METHODS

*Study Site.*—The study was conducted from February–May and July 2005 in the vicinity of human habitation at the Nhumirim Ranch (18°98'814"S; 56°61'900"W), Corumbá municipality, Mato Grosso do Sul state, western Brazil. The region has an elevation of around 100 m and consists of a mosaic of lakes, grassland, savanna (“cerrado” vegetation) and semideciduous forest (Ratter et al. 1988).

One-hour searches were conducted on seven days each month, between 1800 h and 2400 h, with two observers searching for snakes in all accessible microhabitats. Each observed snake was considered an activity record; thus, each individual could have been observed more than once during the study. However, no snake was counted more than one time in a day.

We marked all trees (N = 32) at the 4 ha study site and recorded tree height (m) and diameter at breast height (mm). For each snake observed we recorded the microhabitat (tree, ground, building). When possible we caught the snake by hand and took the body, substrate, and air temperature with a cloacal thermometer (Miller and Weber Inc.). We considered snakes as active if they were moving or otherwise observed outside of tree holes.

In the laboratory, we measured snout–vent length (SVL) to the nearest cm using a measuring tape, tail length (TL) and head length (HL) to the nearest mm with a digital caliper (Mitutoyo Corp.), and mass to the nearest g using a Pesola scale. The snakes were sexed by probing. We then marked the individuals with ventral scale clips and released them at the site of capture.

To evaluate sexual size dimorphism we used analysis of covariance (ANCOVA) on tail length, head length, head width, and body mass with SVL as covariate and sex as a factor. Differences in SVL between sexes were tested by *t*-test. We also performed a Pearson’s correlation between body vs. air and substrate temperature.

#### RESULTS

We marked 19 (10F: 9M) *Leptodeira annulata*. Female SVL (481.60 ± 54.41 mm) was not significantly different from male SVL (528.44 ± 99 mm; *t* = 1.277, *P* = 0.218). Females also had significantly head width and were heavier than males (ANCOVA *F* = 7.097, *P* = 0.017, *r*<sup>2</sup> = 0.358; *F* = 12.434, *P* = 0.003, *r*<sup>2</sup> = 0.470; Table 1).

Observed activity of *L. annulata* (N = 81) occurred mainly between 1830 h and 2330 h, with a peak from 1930 h to 2230 h (Fig. 1). Around 1830 h snakes were observed emerging from tree holes. We found snakes in Acuri palms (*Attalea phalerata*) most often