Karyotypic Studies of Thirty-Eight Species of North American Snakes

ROBERT J. BAKER, GREG A. MENGDEN AND JAMES J. BULL

Chromosomal data are presented for 110 specimens representing 38 species of North American snakes. Karyotypes are divided into three categories. Category I contains species from the Colubridae (subfamilies Colubrinae and Xenodontinae) and the Crotalidae. Category II contains only Elaphe subocularis of the subfamily Colubrinae, and category III contains species from the colubrid subfamily Natricinae. The category III karyotype is believed to be derived, and it may help delimit the Natricinae line of evolution. Of the 30 species where females were studied, 21 exhibited heteromorphism. Only 13 of 22 species of the Colubridae revealed obvious heteromorphism, whereas all eight crotalid species were heteromorphic.

Introduction

The problems of determining phylogenetic affinities of snake taxa based on more classical studies are a poor fossil record and a low number of useful morphological characters. In such cases, it is important to have karyological and biochemical data as an adjunct to the morphological approach. From a genetic standpoint the gross anatomical, karyological, and biochemical aspects are related and interdependent in varying degrees, and it is likely that data from each of these will reveal valuable insights into the evolution of snakes. In the final analysis it will be a synthesis of data from all levels that will result in the most probable estimate of the phylogeny of Serpentes.

We present new karyological data from 110 specimens representing thirty-eight species and comment on patterns of chromosomal evolution found in North American snakes. Karyotypic data for snakes were reviewed by Becak and Becak (1969). A summary of the chromosomes of North American colubrids was presented by Bury et al. (1970). Previously, the chromosomes of 19 species of North American colubrids and 5 species of North American crotalids have been reported. Of these, females have been studied for sex chromosome heteromorphism in only six species.

Methods and Materials

Specimens were collected from natural populations and karyotyped from in vivo cultures of blood utilizing injections of Phytohemagglutinin and Velban (Baker et al., 1971) or from bone marrow cultures
Table I. Chromosomal Data for 38 Species of North American Snakes. Het. = indicates if heteromorphism is found in females. Pr. = indicates size of pair that is heteromorphic in females. M = metacentric, Sm = submetacentric, St = subtelenicentric, A = acrocentric, ? = doubtful, N.A. = number of arms.

<table>
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Utilizing only Velban. Chromosomes were obtained from larger snakes by using rib bone marrow after a nine-hour incubation with Velban (injection rate as described by Baker et al., 1971). The bone marrow was flushed from the ribs and treated as for mammalian bone marrow (Baker, 1970). A minimum of five clearly definable chromo-
some spreads were analyzed for each specimen (in all but six specimens, ten or more spreads were studied). Sex chromosomes were determined by comparing idiograms prepared from enlarged photomicrographs of chromosomes from males and females. These results from photographs were compared with other spreads. Number of arms (NA) was calculated by giving a value of two to each metacentric, submetacentric, or subtelocentric chromosome and a value of one to each acrocentric or microchromosome of the male complement. The W chromosome is the most variable element, and utilizing the male karyotype eliminates this variation. The terms metacentric, submetacentric, subtelocentric, and acrocentric are used as defined by Patton (1967).

**RESULTS AND DISCUSSION**

Chromosomal data for 38 species of North American snakes that were studied are summarized in Table 1. Females were examined in 30 species. Specific locality, sex, and museum number of snakes are given under "specimens examined." We present our data by photomicrographs (Figs. 1–38). This makes a separate description for most species unnecessary; however, where clarification is needed, it is presented in the following discussion.

At least partial karyotypes are shown for all species studied except Lampropeltis getulus, L. mexicana, Phyllorhynchus decurtatus, Salvadora grahamiae, and Crotalus molossus. Karyotypes of Lampropeltis getulus and Phyllorhynchus decurtatus are given by Bury et al. (1970) and Crotalus molossus by Baker et al. (1971). The chromosomes of Lampropeltis mexicana and L. getulus are indistinguishable from those shown for L. calligaster (Fig. 6), and the chromosomes of Salvadora grahamiae are indistinguishable from those shown for S. lineata (Fig. 10). Our data agree with prior descriptions of karyotypes for: Arizona elegans, Lampropeltis getulus, Pituophis melanoleucus, Phyllorhynchus decurtatus, Coluber constrictor (from Bury et al., 1970), and Natrix rhombifera (from van Brink, 1959).

No indication of chromosomal variation
within individuals was noted. In individuals having microchromosomes, the number appeared to be constant with minor variations being best explained as a technical problem.

Since a small sample size was available from each locality, and since in only a few cases were specimens of the same species examined from widely separated localities (see specimens examined), the possible amount of populational and geographic variation revealed by our samples is minimal.

The only indication of populational variation found in our studies was a consistent heteromorphism in pair five in one of two male *Pituophis melanoleucus* from the same locality in California (Figs. 5c and 9). Based on the experience of one of us (Baker) such problems in recognizing homologous pairs from photographs of somatic chromosomes are not rare. Therefore, no significance is attached to this case except that if the same degree of variation had been found in a female it probably would have been attributed to ZW heteromorphism.

There are four cases where our data reveal possible geographic variation. In *Thamnophis marcianus*, from Texas a female from Lorenzo, Crosby Co., a female from Plainview, Hale Co., and a female from Denver City, Yoakum Co., had an acrocentric W (Fig. 19). Two females collected near Fort Davis, Jeff Davis Co., had a submetacentric W. A female *Storeria dekayi* from Ouachita Parish, Louisiana, had a distinctly heteromorphic fourth or fifth chromosome pair, whereas a female of this species from Robert Lee, Coke Co., Texas, had a homomorphic karyotype. The third possible case of geographic variation is based on a comparison of our data with that from an abstract of a report of the chromosomes of *Elaphe obsoleta* (Fischman et al., 1968). All five of our *E. obsoleta* had the sixth pair acrocentric with the remainder of the macrochromosomes being biarmed (Fig. 3). Fischman et al. (1968) reported a similar karyotype for *E. carinata*; however, they found pair eight to be acrocentric in *E. o. obsoleta* and pair six to be metacentric. Our specimens are from the subspecies *E. o. lindheimeri* (four individuals) and *E. o. bairdi* (one individual). The fourth possible example involves *Crotalus viridis*. All macroelements were biarmed in our samples (Fig. 31), as was the case in all crotalids studied by us. However, the three smallest pairs of macrochromosomes were reported by Mon-


roe (1962) to be acrocentric in two subspecies from the northwestern U.S. The technique used by Monroe was the older, more difficult, squashed type, and this may account for this variation. On the other hand, his description of the other aspects of the karyotype of C. viridis was accurate, and this variation may be real. In two of the four cases described above, the variation involved only the W chromosome. The mammalian Y (analogous to the reptilian W) is also the most variable chromosome for that class.

For convenience of discussion the karyotypes of North American snakes studied by us are arranged into three categories. As each category is presently defined, to change the karyotype of one category into that of any other would require a minimum of five rearrangements. From the review by Becak and Becak (1969) it is obvious that there are other categories of snake karyotypes and that in some cases the limits of categories will overlap because of intermediate karyotypes. It is also evident that the evolutionary significance of a "category" varies and we do not imply any fixed taxonomic value to this classification.

In category I (See Figs. 1–11 and 24–33) the diploid number is 36, and the karyotype is readily divisible into 16 macrochromosomes and 20 microchromosomes. The NA value is 50 or 52. Where they can be determined, the sex elements are clearly the fourth largest pair. The Z chromosome is never longer than 50% of the length of the longest autosome. The second category has a diploid number of 40 with 18–20 macroelements and 20–22 microchromosomes. The NA value is 44. The sex chromosomes are the third largest pair, and the general size of the sex elements relative to the largest autosome is like that described for category I. The third karyotypic group has a diploid number of 36, but the karyotype is not readily divisible into macro- and microchromosomes, although the smallest pair is no larger than the microchromosomes of species from categories one and two. The NA value is 68 to 72. The sex chromosomes generally appear to be the fifth largest pair, but in some cases may be the fourth pair as the size of these two pairs is almost identical. The length of the Z element is always greater than 70% of the length of one of the largest pair of autosomes. At least eight of the ten smallest pairs are distinctly biarmed, and in

...some cases (as Storeria, Fig. 15, and Thamnophis radix, Fig. 21) all are biaimed.

Karyotypic category I is characteristic of taxa examined from the colubrid subfamilies Colubrinae and Xenodontinae as well as all species of the Crotalidae. The category II karyotype is known from only one species, Elaphe subocularis, (Fig. 4) which is a member of the subfamily Colubrinae. The category III karyotype is presently known only for genera from the colubrid subfamily Natricinae (Underwood, 1967, considers this a separate family, Natricidae).

North American colubrid species known to have category I karyotype are Arizona elegans (Fig. 1; see also Bury et al., 1970), Coluber constrictor (Fig. 2 and Bury et al., 1970), Elaphe obsoleta (Fig. 3), E. guttata (Fig. 5b), Lampropeltis getulus (Bury et al., 1970), L. calligaster (Fig. 6), L. mexicana, Masticophis flagellum (Fig. 7 and Bury et al., 1970), M. taeniatus (Fig. 8), Phyllorhynchus decurtatus (Bury et al., 1970), Pituophis melanoleucus (Fig. 9 and 5c, and Bury et al., 1970), Salvadora lineata (Fig. 10), S. graminiae, and Heterodon nasicus (Fig. 11).

All crotalids thus far studied (Monroe, 1962; Ohno, 1967 and Becak and Becak 1969) have a category I karyotype, with possibly the greatest variation found in some subspecies of Crotalus viridis (Monroe, 1962, see geographic variation above). Published data for other North American crotalids are Crotalus cerastes (Ohno, 1967) and C. molossus (Baker et al., 1971). Other species reported here are Agkistrodon contortrix (Fig. 24), A. bilineatus (Fig. 25), A. piscivorus (Fig. 26), Crotalus atrox (Fig. 27), C. basiliscus (Fig. 28), C. horridus (Fig. 29), C. lepidus (Fig. 30), C. viridis (Figs. 5d and 31), C. scutulatus (Fig. 32), and Sistrurus catenatus (Fig. 33), and all have remarkably similar karyotypes.

One karyological difference is evident between the two colubrid subfamilies of category I. All members of the Colubrinae have an acrocentric sixth pair, whereas Heterodon nasicus, the only member of the subfamily Xenodontinae examined, has the sixth pair biarmed and subtelocentric (Fig. 11). The chromosomes of Heterodon platyrhinos were reported by Edgren (1968) as having a diploid number of 40+. We examined a single specimen of H. platyrhinos, and found it to have a karyotype like H. nasicus. Unfortunately, the voucher specimen was misplaced, and, therefore, this taxon is not included here. All of the crotalids examined are similar to Heterodon in that the sixth pair is biarmed and subtelocentric.

Presence of the category I karyotype in two subfamilies of colubrids as well as the crotalids is best explained by their common ancestor having this karyotype (however, the pair six may or may not have been acrocentric) with subsequent morphological divergence between the two families not being accompanied by any major observable chromosomal rearrangements.

The similar karyotypes of Heterodon and the crotalids suggest a possibility of a close relationship between the subfamily Xenodontinae of the Colubridae to the pit vipers. Care must be taken not to place too much emphasis on the similarity, as it is not known if the acrocentric or subtelocentric condition of pair six is primitive, and because only one chromosomal rearrangement is required to derive the Heterodon karyotype from the common North American colubrine karyotype.

The only species found in category II is Elaphe subocularis. The potential origins of this karyotype are discussed by Baker et al. (1971), and it is believed to be derived from a karyotype like that characteristic of category I. As such, it would represent a side branch and not the karyotype primitive for the Elaphe group.

The category III karyotype is characteristic of taxa from the subfamily Natricinae (Malnate, 1960). It was found in Natr... (truncated)
considerable discussion concerning the status and taxa of the Natricinae (Malnate, 1960 and Underwood, 1967) and it is possible that karyotypic data may be useful in delimiting this subfamily. It has been hypothesized that the karyotype characteristic of the snake ancestor that gave rise to the Colubridae, as well as other snakes, was composed of 20 micro- and 16 macrochromosomes with a probable diploid number of 36 (Werner, 1959; Singh et al., 1968; Becak and Becak, 1969; Gorman and Gress, 1970; and Baker et al., 1971; see also above discussion of the category I karyotype). If this is true, then the category III karyotype represents a derived condition. To evolve such a karyotype would involve changes in at least eight of the ten pairs of microchromosomes. Other obvious differences between our category I and III is the size of the Z element relative to the longest pair of autosomes. As indicated above, in all species of category I the length of the Z is less than 50% of that of the longest pair of autosomes. If the size of the Z has remained constant in relationship to the total genome (see support for this idea in Ohno, 1967, and Becak et al., 1964), then there has clearly been a reduction in the relative size of the larger autosomes in category III as compared to category I. Therefore, we hypothesize that the category III karyotype was derived from the category I karyotype by a series of unequal translocations between the macrochromosomes and microchromosomes which has resulted in some of the macrochromosomes being reduced in size, but with at least eight pairs of microchromosomes increasing in size.

The two most important points are (1) the category III karyotype is derived (not primitive) and (2) the number and type of changes required to produce such a karyotype suggest that it is highly improbable that it evolved on more than one occasion. Therefore, forms having the category III karyotype may be presumed to have descended from a common ancestral stock that diverged from the main line of snake phylogeny. At present we do not feel that these karyotypic data either support or refute the idea that the Natricinae may deserve familial status. However, if additional data reveal the origin of this karyotype, then some light may be shed on the problem.

Of the 30 species where females were studied, consistent heteromorphism was detected in 21 species. With the exception of Salvadora and Lampropeltis, heteromorphic sex chromosomes are clearly present in all category I colubrids (total of seven species) where females were studied. Elaphe subocularis of the category II karyotype also was heteromorphic (Baker et al., 1971). In category III, consistent heteromorphism was found in females but not in males in one of three species of Natrix, in one of two female Storeria dekayi, and three of seven species of Thamnophis (a total of five species. Table 1 and Figs. 12–23). In all eight species of crotalids in which we studied females, as well as in all species reported in the literature (Becak and Becak, 1969), there was clear heteromorphism in the fourth pair. Ohno (1967) hypothesized that the crotalids evolved from an ancestor having established heteromorphism. Our data would support this idea. On the other hand, only 13 of 23 species of North American colubrids have females which exhibit heteromorphism. The frequency of this derived condition (heteromorphic sex elements) further documents the advanced position of the crotalids with respect to the colubrids. Our sample indicates that of the three categories, category III taxa may have the lowest frequency of heteromorphism.

It seems significant that there is considerable variation in the W and that the length of the W is always 50% or more of that of the Z. The smallest Ws in our samples were found in Thamnophis marcellus and Agkistrodon piscivorus. In closely related species as well as populations from the same species, the morphology of the W varies (for instance, compare the W of Agkistrodon contortrix, Fig. 24, and A. piscivorus, Fig. 26, and see the above discussion of the variation of the Ws of Thamnophis marcellus and Storeria dekayi). In fact, the only consistent karyotypic difference evident between the various crotalid species examined by us involved the morphology of the W. Our data suggest that the W is the most actively changing chromosome in snake karyotypes. Intensive studies will probably reveal several species where the W is polymorphic or geographically variable.

**APPENDIX**

Specimens examined. All voucher specimens are deposited in the Texas Tech University Museum of Her-
petology. Museum numbers follow sex. Species are listed alphabetically by family.

*Arizona elegans* Texas: Winkler Co., 8 km NE of Kermit on Hwy. 115 (1 male 5136); Lubbock Co., 5 km NW Lubbock (1 female 5510).

*Coluber constrictor* California: Santa Cruz Co., Santa Cruz, University of California campus (1 female 4925).

*Elaphe obsoleta* Texas: Lubbock Co., Lubbock (1 male 5183); Wichita Co., Wichita Falls (2 males 5176, 5186, 1 female 5121); Jeff Davis Co., Davis Mountain State Park (1 female 5207).

*Elaphe dansi* Texas: Jeff Davis Co., Davy Crockett Park (1 female 5208); Davis Mountain State Park, Indian Lodge (1 female 5212). Wichita Co., 2.5 km S of Wichita Falls (2 females 5158, 5168); Gonzales Co., Gonzales (1 male 5169); Wichita Co., 14 km S of Holliday (1 male 5182).


*Heterodon nasicus* Texas: Crockett Co., 14 km NE of Slaton (1 female 5181); Lubbock Co., 24 km NW Lubbock (1 male 5226).

*Lampropeltis calligaster* Texas: Delta Co., 3 km S of Cooper (1 female 5242).

*Lampropeltis getulus* Texas: Hockley Co., Yellow House Canyon (1 female 5174); 3 km S of Oklahoma Flats on FM 1490 (1 male 5116). California: San Luis Obispo Co., San Luis Obispo (1 female 5140).

*Lampropeltis mexicana* (alterna morph) Texas: Jeff Davis Co., 14 km N of Jct. of Hwy. 17 & 118 on Hwy. 17 (1 male 4791).

*Masticophis flagellum* Texas: Bexar Co., 5 km W of Elmendorf (1 male 5168, 1 female 5167); Mitchell Co., 32 km S of Colorado River at Rendellbrook-Spade Ranch (2 males 5169, 5171; 1 female 5170); Dickens Co., 5 km W of Spur (1 male 5200; 1 female 5173); Lubbock Co., Lubbock (1 male 5165). New Mexico: Eddy Co., E boundary of Lincoln National Park (1 male 5164).

*Masticophis taeniatus* Texas: Cameron Co., 8 km E Brownsville (1 female 5331).

*Natrix erythrogaster* Texas: Garza Co., Double Mountain Fork of the Brazos River (1 male 5124); Mason Co., 1 km S of the jct. of the Llano and James Rivers (1 male 5152); Coke Co., 2 km S Robert Lee (1 female 5322).

*Natrix hirtieri* Texas: Coke Co., 2 km S of Robert Lee on the Colorado River (2 males 5157, 5230; 3 females 5234, 5235, 5236).

*Natrix rhombifera* Texas: Mason Co., 2 km S jct. Llano and James Rivers (1 male 5153); Webb Co., 13 km E of Encinal (1 male 5185); Uvalde Co., Uvalde (1 female 5227).

*Phylorhynchus decurtatus* California: San Bernardino Co., Palm Springs Depot Rd. (1 male 4923).

*Pituophis melanoleucus* California: San Bernardino Co., 5 km S Adelanto (2 males 4920, 5202). *P. m. sayi* Texas: Wichita Co., Wichita Falls (1 male 5130); Hale Co., 16 km SW Plainview (1 male 5229).

*Slandovita grahaniae* Texas: Jeff Davis Co., 8 km NE Ft. Davis (1 female 5144).

*Slandovita linda* Texas: Bexar Co., San Antonio (2 males 5137, 5146).


*Thamnophis couchi* California: Santa Cruz Co., University of California campus (1 male 4926; 1 female 4927).

*Thamnophis cyanopis* Texas: Presidio Co., 16 km NW of Valentine, Clay Miller Ranch (1 female 5156).

*Thamnophis elegans* California: Santa Cruz Co., University of California campus (1 female 4925). New Mexico: Quay Co., 5 km N of Bagland Hwy 18 (1 male 5187).

*Thamnophis maricatus* Texas: Bexar Co., San Antonio, Stinson Field (1 male 5142); Crockett Co., 8 km E of Lometa (1 female 5141); Jeff Davis Co., 5 km N Fort Davis (4 males 5204, 5206, 5245, 5247; 2 females 5205, 5246); Mitchell Co., 32 km S of Colorado City, Rendellbrook-Spade Ranch (1 male 5192); McCullough Co., 2 km N of Rochelle (1 male 5177); Yoakum Co., St. Lawrence, 24 km S of Denver City (1 female 5191); Hale Co., 20 km N Plainview (1 female 5238).

*Thamnophis proximus* Texas: Mason Co., 1 km S jct. of James and Llano Rivers (4 females 5147, 5148, 5149, 5150); Comal Co., 10 km N Hwy 46 on Bear Creek Rd. (1 female 5203); Kleberg Co., 21 km S Kingsville (1 female 5233). *Thamnophis radix* Kansas: Sherman Co., 16 km S Goodland (1 female 5228).

*Thamnophis ruffipectus* Arizona: Coconino Co. Oak Creek Canyon. (1 female 4924). *Thamnophis sirtalis* New Mexico: Dona Ana Co., 2 km W of Las Cruces on Rio Grande (1 female 5151).

*Agkistrodon bilineatus* Mexico: State of Colima, Colima (1 male 5118).

*Agkistrodon piscivorus* Oklahoma: Love Co., 11 km NE of Lake Texoma Biological Station (1 female 5110). Texas: Harris Co., Houston (1 male 5163); Bexar Co., 5 km W Elmendorf (1 female 5239; 1 male 5209).

*Crotalus atrox* Mexico: State of Nuevo Leon, 16 km N of Monterrey (1 male 5125). Texas: Mill Co., Goldthwaite (2 females 5115, 5117); Howard Co., 23 km S of Big Spring (1 male 5162, 1 female 5130); Dickens Co., 5 km S of Spur (1 female 5190).

*Crotalus basiliscus* Mexico: State of Colima, Colima (1 female 5126).

*Crotalus horridus* Captive born (1 female 5135).

*Crotalus lepidus* Texas: Jeff Davis Co., 3 km N of jct. of Hwy. 118 and 17 (1 male 5129, 1 female 5128), 23 km NW of jct. of Hwy. 118 and 17 on Hwy. 118 (1 male 5779).

*Crotalus molossus* Texas: Jeff Davis Co., Davis Mountain State Park (1 male 4921); Val Verde Co., 2 km W of Comstock on U.S. 90 (1 male 5198). Mexico: State of Sonora, near Guaymas (1 female 5197).

*Crotalus viridis* California: San Bernardino Co., Helen Dale Boy Scout Ranch (1 male 4919). Texas: Winkler Co., 4 km W of Kermit (1 female 5173); Glasscock Co., 11 km S of Garden City on FM 33 (1 female 5145); Howard Co., 23 km S of Big Spring (1 male 5122).

*Crotalus scutulatus* Texas: Jeff Davis Co., 29 km N of jct. 17 and 118 on Hwy. 17 (1 male 5168).

*Sistrurus catenatus* Texas: McLennan Co., China Springs (1 male 5144).

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LITERATURE CITED


