# ECOLOGY AND GEOGRAPHIC VARIATION

# OF

# THE ARIZONA MOUNTAIN KINGSNAKE

# *Lampropeltis pyromelana*

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THE ARIZONA MOUNTAIN KINGSNAKE
Lampropeltis pyromelana

(Chiricahua Mountains, Cochise County, Arizona)

## GENERAL ECOLOGY

Ecologic distribution.-- The Arizona mountain king snake, Lampropeltis pyromelana, inhabits inland southwestern United States and northwestern Mexico. It occurs today in evergreen woodland and coniferous forest habitats in a more or less north-south and disjunctive distribution from north-central Utah into southern Chihuahua, Mexico, (Fig. 3, map). It occurs in the Upper Sonoran and Transition life-zones, from approximately 4500 feet to about 9,000 feet elevation and appears to be most abundant between 6,000 and 7,500 feet (see Table 1). The Upper Sonoran woodland communities inhabited are pinyon - juniper, oak, Mexican pine - oak, and riparian. It occurs in yellow pine forest (Transition Life-zone) and may occur in fir forest (Canadian Life-zone), and is found in both of these forests in tracts of riparian woodland as well as in the forest floor microenvironments. It ranges to as low as approximately 4,500 feet elevation along major drainages in the deciduous riparian woodland habitats of the upper desert edge, as is typical of other reptilian species[1] with which it is sympatric.

Figs. 1 and 2 show coniferous forest and evergreen woodland habitats in the Santa Catalina Mountains, Pima County, Arizona. This locality is situated approximately in the center of the present geographical distribution of this snake. The Santa Catalina Mountains, a desert range, reach a maximum elevation of 9,160 feet on Mt. Lemmon. Oriented on a general east-west line, the base of the south face of

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1. For example, the Ring-necked snake Diadophis regalis, the Arizona black rattlesnake, Crotalus viridis cerberus, Alligator lizard Gerrhonotus kingi, and Sonoran skink Eumeces obsoletus.

the range is in the Sonoran Desert (paloverde - sahuaro association) at an elevation of approximately 2,900 feet, and the north base is at approximately 4,000 feet elevation in an oak woodland - desert grassland ecotone. On the south slope, desert gives way to oak woodland at approximately 4,000 feet. The biota of this southern Arizona mountain has only a very weak remaining Mexican component as compared to the Santa Rita, Huachuca, and Chiricahua mountains in southernmost Arizona.

Fig. 1 shows a yellow pine forest habitat on the south face of the Santa Catalina Mountains at approximately 7,500 feet elevation. Silverleaf oak (Quercus hypoleucoides) is the only other tree that is common here and buckbrush (Ceanothus fendleri) the only important shrub. Scattered clumps of the perennial grass, mountain muhly (Muhlenbergia montana), occur; these are usually found where the canopy is more open. Occasional and widely-scattered individuals of madrone (Arbutus arizonica), gambel oak (Quercus gambeli), white pine (Pinus ayacahuite brachyptera), and Douglas fir (Pseudotsuga menziesi glauca) are present at this elevation. The white pine and Douglas fir become more conspicuous but never abundant on the south slopes at higher elevations. However, on north slopes above 7,500 feet elevation, on this mountain and others, they occur in association with white fir (Abies concolor) and corkbark fir (Abies lasiocarpa) in a distinctive fir forest that lacks yellow pine, and there they constitute important species of one of the facies of the Canadian Life-zone.

At 7,500 feet on south slopes, the yellow pine forest is of simple and open understory, as shown. This is characteristic of the sub-arid yellow pine forests of the inland southwest, which habitats

constitute a large proportion of the environment met by L. pyromelana. Yellow pine forest of increasingly mesic aspect continues upward on south slopes to the top of the mountain, while on north slopes it is replaced by fir forest.

As discussed below, the majority of observations of the Arizona mountain kingsnake have been made at elevations of between 6,000 and 7,500 feet elevation. Probably most of these have been made in habitats dominated wholly or in part by western yellow pine (Pinus ponderosa) in the southern portion of the geographic range of the snake, thus in the Transition Life-zone.

Fig. 2 is a photograph of evergreen woodland on the south face of the Santa Catalina Mountains at approximately 4,700 feet elevation. This is representative of the habitat near the lower elevational extreme for the species. The dominants are mainly oaks (Quercus arizonica and Q. emoryi), with a few scattered individuals of alligator juniper (Juniperus deppeana) and Mexican pinyon (Pinus cembroides). Several diverse shrub life-forms and grasses are present and contribute to a more dense and variable under-story than is present in the yellow pine forest. Mountain yucca (Yucca schotti) and beargrass (Nolina microcarpa) are clearly visible in the foreground. Golden-flowered agave (Agave palmeri), sotol (Dasylirion wheeleri), and a prickly pear (Opontia engelmanni) are present. Pointleaf manzanita (Arctostaphylos pungens) and skunkbush (Rhus trilobata) are the most abundant shrubs. Others present include holly-leaf buck-thorn (Rhamnus crocea ilicifolia) and wait-a-minute bush (Mimosa biuncifera), with quinine-bush (Garrya wrighti) and desert broom (Baccharis sarrothroides) along the drainages. Of the several

perennial grasses which contribute substantially to the relatively well-developed understory, the following natives are particularly abundant or conspicuous: sideoats grama (Bouteloua curtipendula), Santa Rita grama (B. eleudens), hairy grama (B. hirsuta), Texas bluestem (Andropogon cirratus), Andropogon hirtifloris, poverty threeawn (Aristida divaricata), beggarstick grass (A. orcuttiana), plains lovegrass (Eragrostis intermedia), and bullgrass (Muhlenbergia emersleyi).

This type of evergreen woodland, dominated mostly by species of oaks, and occupied by L. pyromelana at the lower limit of its ecologic distribution (4,500 - 5,000 feet elevation), is found over a considerable part of the southern portion of the geographic range of this kingsnake, viz., southern Arizona, southern New Mexico, and in northern Mexico. At similar elevations in northern New Mexico, northern Arizona, and in Colorado and Utah, the woodland vegetation is generally one of the facies of the well-known pinyon-juniper woodland. At elevations of over approximately 5,500 feet in the southernmost portions of the range, the vegetation is often the Mexican pine-oak woodland, characterized by Chihuahua pine (Pinus leiophylla chihuahuana) and Apache pine (Pinus engelmanni = P. latifolia auct.) which occur in association with several species of tree- and shrub-form oaks.

Another distinctive type of woodland inhabited is the largely deciduous riparian vegetation which occurs in the larger drainages in the Upper Sonoran and Transition life-zones, as well as in Lower Sonoran desert habitats. Varying somewhat in floral composition with shifts in elevation, it maintains its essentially deciduous tree-form character throughout. It is typified over a wide area in the inland southwest by plants such as cottonwood (Populus fremonti), sycamore

(Platanus racemosa wrighti), ash (Fraxinus velutina), walnut (Juglans major), and willows (Salix) at lower elevations, and by such plants as alder (Alnus oblongifolia), maple (e.g., Acer grandidentatum), box elder (Acer negundo interius), and willows (Salix) at the higher elevations. Many of these deciduous broadleafed trees overlap in ecologic tolerance and form widely varying associations at middle elevations (e.g. 5,000 - 7,000 feet) in the mountains.

A locality at approximately 6500 feet elevation in Ramsay Canyon on the east side of the Huachuca Mountains in southeastern Arizona was selected as a typical riparian habitat for this species, numerous individuals having been collected or observed by the author and others in this canyon between altitudes of 6000 and 7000 feet. Another was caught near the spot where plant samples had just been collected for this study. The woodland habitat here is surrounded by a pine forest climax. Dominants in the riparian vegetation are highly varied and there is a mixture of life-forms induced in part by the fingering down (= canyon effect) of species otherwise characteristic of higher elevations. As seen at this locality, the trees of such habitats commonly include individuals of broadleaved, and long and short needle-leaved evergreens, as well as broadleaved deciduous species. Conspicuous plants occurring in a transect across the bottom of the canyon are bigtooth maple (Acer grandidentatum), Arizona walnut (Juglans major), silverleaf oak (Quercus hypoleucoides), net-leaf oak (Quercus reticulata), alligator juniper (Juniperus deppeana), white pine (Pinus ayacahuite), white fir (Abies concolor), California buck-thorn (Rhamnus betulaefolia), mountain yucca (Yucca schotti), and the predominant needle grass (Stipa pringlei). The Huachuca Mountains,

rising to 9,445 feet and lying mostly in Cochise County, just north of the international boundary, constitute one of Arizona's southernmost mountain ranges and have a distinctive Mexican biotic component.

Elevation records for those specimens of L. pyromelana which had this data, together with several sight records, are shown in Table 1. The more frequent occurrence of this species at 7,000 ± 500 feet in its elevational range from approximately 4,500 to 9,000 feet is indicated by the predominance of these records in the table and is borne out by the field experience (in southern Arizona) by Mrs. John Healy, Dr. C. H. Lowe, Jr. and his students at the University of Arizona, the author, and others. It appears probable that L. pyromelana chiefly inhabits woodland habitats of the Upper Sonoran Life-zone in the northern portion of its range (north of central Arizona), and predominantly Transition Life-zone forest and riparian habitats in the southern portion of its range.

Occurrence and time of activity.-- Lampropeltis pyromelana occurs occasionally in shrubs and trees, although available records and personal experience indicate a predominance of activity on (or beneath) the ground. Gloyd (1937, p. 120), however, records an individual from the Huachuca Mountains "entwined in the lower branches of a small mountain mahogany shrub (Cercocarpus)..." A National Park Service ranger at Chiricahua National Monument, Cochise County, Arizona reported an individual in an oak tree near the headquarters buidding. This snake is an agile climber in captivity and it crawls without difficulty up the vertical trunks of rough-barked trees (e.g. oaks). The majority of specimens have been collected on the ground, in the vicinity of mountain trails or as they were crossing (or were found

TABLE 1

Elevation records for Lampropeltis pyromelana.

| 4500-5900 ft. | | | 6000-7500 ft. | | | 7600-9000 ft. | | |
|---|---|---|---|---|---|---|---|---|
| Specimen | Locality | Elev. | Specimen | Locality | Elev. | Specimen | Locality | Elev. |
| CHAS 14215 | Santa Rita Mts. | 4700 | CHAS 4010 | Huachuca Mts. | 6000 | LMK 8741 | Santa Catalina Mts. | 7900 |
| AMNH 57386 | Chiricahua Mts. | 5000 | MVZ 8086 | Chiricahua Mts. | 6000 | USNM 40063 | Mexico (Chihuahua, "Dist. Guerrero") | 7950 |
| WHW 40 | Santa Catalina Mts. | 5000 | WHW 856 | Huachuca Mts. | 6000 | CHL 6806 | Rincon Mts. | 8500 |
| sight record (Mrs. Healy) | Huachuca Mts. | 5375 | AMNH 62934 | Central Ariz. (Bradshaw Mts.) | 6300 | sight record (Mrs. Healy) | Huachuca Mts. | 9000 |
| MVZ 6310 | Central Ariz. (Sierra Ancha) | 5410 | USNM 44331 | Central Ariz. (Hualapai Mts.) | 6300 | | | |
| SD 16377 | Santa Catalina Mts. | 5500 | MVZ 8085 | Chiricahua Mts. | 6500 | | | |
| WHW 830 | Huachuca Mts. | 5500 | WHW 832 | Huachuca Mts. | 6500 | | | |

TABLE 1 (Cont'd)

| 4500-5900 ft. | | | 6000-7500 ft. | | | 7600-9000 ft. | | |
|---|---|---|---|---|---|---|---|---|
| Specimen | Locality | Elev. | Specimen | Locality | Elev. | Specimen | Locality | Elev. |
| USNM 44330 | Central Ariz. (Hualapai Mts.) | 5800 | sight record (W. H. Woodin) | Huachuca Mts. | 6500 | | | |
| WHW 831 | Huachuca Mts. | 5900 | AMNH 15086 | Huachuca Mts. | 6750 | | | |
| | | | CHAS 14220 | Huachuca Mts. | 6950 | | | |
| | | | CM 14480 | Central Ariz. (nr. Williams) | 7000 | | | |
| | | | AMNH 38174 | Utah (Beaver Co.) | 7000 | | | |
| | | | UCLA 280 | Central Ariz. (Flagstaff) | 7000 | | | |
| | | | SD 15836 | Chiricahua Mts. | 7500 | | | |
| | | | (Stebbins 1954) | Huachuca Mts. | 7500 | | | |

dead on) mountain roads.

While logs and rocks on the woodland and forest floor are used as cover, rodent holes and other subterranean excavations appear to be more commonly used for retreat during the active season of the year as well as for hibernation. General surface activity in this species extends from April into October. All available capture or sight records fall into these seven months with one exception, LMK 41106, from the Barranca del Cobre region, Chihuahua, Mexico, collected on November 20, 1950.

No specimens have been found active at night. Fifteen records of times of activity for this species are during daylight hours, and range from approximately 7:00AM (Mrs. Healy, sight record, and others) to 6:00 PM (Donald Berlinski, University of Arizona, specimen CHL 6806). This snake does, however, appear to be abroad on rainy or overcast days (Woodin, 1953, p. 289; Stebbins, 1954, p. 402). Thus it appears that L. pyromelana is a distinctly diurnal species and in this regard is like the mountain dwelling Lampropeltis zonata of the Pacific coast region. L. pyromelana differs, however, from L. getulus of habitats (mainly desert and desert grassland in the inland southwest) at lower elevations, a king snake that is more often crepuscular and nocturnal than diurnal in areas where it occurs in association with L. pyromelana, as well as elsewhere over its much greater geographic range. The relationship of the diurnality of L. pyromelana to its adaptedness in the cooler and high mountain habitats is discussed under the section on reproduction.

Feeding habits.-- Stomach contents of freshly captured individuals of L. pyromelana from Arizona include the following: an unidentified bird (WHW 1351, Chiricahua Mountains), two mice (Peromyscus) (Woodin,

op. cit., p. 289-90; Huachuca Mountains), one skink (Eumeces skiltonianus GC R-373, in stomach of Grand Canyon specimen GC R-372), and a spiny lizard (Sceloporus jarrovi) (Stebbins, op. cit., p. 403; Huachuca Mountains). MNA Z7.8 (no data, presumably central Arizona) contained a lizard, Uta ornata, but it is not known whether this was a captive individual. In captivity this snake exhibits a marked preference for lizards, both living and dead. Individuals have been kept alive for several years on a diet of dead whiptail (Cnemidophorus) and zebra-tailed lizards (Callisaurus).

Reproduction.-- L. pyromelana is an oviparous snake, as are all king snakes. Measurements were made on July 1 of a clutch of four eggs laid on June 30. They were as follows: 2-1/4 x 5/8", 2-3/16 x 5/8", 2 x 3/4", and 2 x 3/4". Stebbins (op. cit., p. 403) records six ova, which appeared nearly ready for laying, found in a female from Nevada on June 12. They measured approximately 10 x 30 mm.

Three other snake genera, in addition to Lampropeltis, are represented in high mountain habitats in the inland southwest, living in coniferous forest regions at elevations over 8000 feet, and extending over all or most of the geographic range of L. pyromelana. These are Crotalus, Thamnophis, and Pituophis. Crotalus (rattlesnakes) and Thamnophis (garter snakes) are live-bearing, i.e., ovoviviparous. Thus Pituophis catenifer (the gopher or bull snake) is the only other high mountain egg-laying species which occurs over the geographic range of L. pyromelana. Pituophis catenifer is an unusually adaptable species with an ecological tolerance permitting it wide distribution from sea level to over 9000 feet elevation, and over a large part of the North American continent. However, the gopher snake is but an infrequent or rare component of the higher mountain coniferous forests.

L. pyromelana is the only egg-laying species over its geographic range which is limited to the higher mountains, i.e., occurring characteristically in coniferous forest habitats and extending its range to approximately 9000 feet elevation.

L. pyromelana is a distinctly diurnal species. As it is thus the only high mountain, egg-laying, diurnal snake occurring from the Rocky Mountains of Utah into the Sierra Madre System of Chihuahua-Sonora, certain conjectures may be warranted from the combination of ecologic and physiologic characteristics exhibited, and some lines for further fruitful exploration may be indicated. As in the high mountain dwelling snakes and lizards (e.g., species of Crotalus, Thamnophis, Phrynosoma, and Sceloporus), the body of the gravid female king snake may well serve as an incubator for the developing eggs. Thus there may exist a definite ratio between the length of time the eggs remain in the female and the time they remain in the ground prior to hatching; that is, a critical ratio permitting successful occupancy of the high mountain habitats in question. There may be a concomitant greater embryonic development prior to egg-laying in such a unique high mountain species, and there is most certainly indicated relatively high overall metabolic embryonic and adult rates, as compared, for example, with the lowland king snake, Lampropeltis getulus. A comparative study of the relative metabolism of Lampropeltis pyromelana with the gopher snake and with other mountain and non-mountain king snakes may well show an adaptive divergence favoring higher genetically controlled rates in the mountain forms, as well as an adaptively higher overall metabolic rate in L. pyromelana than in the sympatric egg-laying gopher snake, a species that is only occasional or rare in high mountain habitats.

Discussion.-- The apparent absence of L. pyromelana in many of the seemingly suitable mountain habitats in northern Sonora may be due only to lack of sufficient observation and collecting in this portion of the state. This snake may well have a considerably wide distribution over central and eastern Sonora; it is known from Sonora only from El Tigre Mountain near the Chihuahua border (Fig. 3, map). Incidentally, and probably significantly, this was also the only known locality in Sonora for the sympatric mountain rattlesnake, Crotalus w. willardi, until Lowe and Marshall (in press) found it not uncommon in several previously unexplored outlying ranges of the Sierra Madre Occidental in Sonora. Similar to L. pyromelana in some ecologic aspects of distribution, Crotalus willardi occurs in Mexican pine-oak woodland and in yellow pine forest. The rattlesnake is not known, however, from farther north than the Santa Rita and Huachuca mountains of extreme southern Arizona, whereas L. pyromelana extends northward into northern Utah.

## GEOGRAPHIC VARIATION

Lampropeltis pyromelana has been considered a monotypic species. Recently Tanner (1953), on the basis of approximately 81 specimens, described four subspecies, as follows: L. p. knoblochi from Chihuahua, L. p. pyromelana from central Arizona southeast into New Mexico and Chihuahua, L. p. woodini from southern Arizona southeast into Chihuahua, and L. p. infralabialis from Nevada, Utah, and southward to the northern rim of the Grand Canyon. This study is concerned with an analysis of certain morphological variables throughout the species as a whole, and is not concerned with the above-mentioned subspecies other than to include in the species pyromelana, as Tanner has done, the snake described by Taylor (1940) as Lampropeltis knoblochi.

The study of geographic variation considers four variables, as follows: the number of ventral scales, the number of white bands on the body, the amount of dorsal fusion of the black bands on the body, and the amount of lateral fusion of the white body bands. Some data are also presented regarding a fifth variable, the color of the bands. Body counts, rather than total counts, are used chiefly for two reasons: (1) the small number of specimens has made it desirable to combine the two sexes. There are sexual differences in tail length, and (2) there is a tendency toward pattern breakdown on the tail which renders several of these counts difficult to make accurately.

A total of 135 specimens were studied. Varying numbers were used in the different analyses, depending upon availability of data and completeness of the specimens. Data on 119 specimens were obtained from personal examination, information on the other 16 was

supplied through the kindness of several individuals or was taken from Blanchard (1921)[1]. The University of Utah specimens, numbering at least 5 from Utah, could not be obtained for this study. Also, no reply was received from Stanford University as regards their specimens; however, partial data for the latter were obtained from Blanchard (op. cit.).

Locality records are plotted in Fig. 3. The sixteen areas represented in this study, together with numbers of specimens from which data were taken, are as follows:

1. Nevada (near Lund, White Pine County): 2
2. Utah: 11
3. Grand Canyon (north rim), Coconino County, Arizona: 7
4. Central Arizona: 34
5. Pinos Altos Mountains, Grant County, New Mexico: 1
6. Graham (Pinaleno ) Mountains, Graham County, Arizona: 1
7. Santa Catalina and Rincon Mountains, Pinal, Pima and Cochise counties, Arizona: 10
8. Santa Rita Mountains, Pima and Santa Cruz counties, Arizona: 7
9. Pajarito Mountains, Santa Cruz County, Arizona: 1
10. Patagonia Mountains, Santa Cruz County, Arizona: 1
11. Huachuca Mountains, Santa Cruz and Cochise counties, Arizona: 39

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1. The former Brooklyn Museum specimens nos. 540 and 543 are now AMNH nos. 38174 and 38173 respectively, and the early UA specimen (unnumbered) from the Patagonia Mountains, the only one known from this range, has apparently been lost.

12. Bisbee, Cochise County, Arizona: 1

13. Chiricahua Mountains, Cochise County, Arizona: 10

14. Animas Mountains, Hidalgo County, New Mexico: 1

15. Big Hatchet Mountains, Hidalgo County, New Mexico: 1

16. Mexico: 7, as follows (from north to south on map, fig. 3):

Sonora

El Tigre Mountain, MMZ 78464

Chihuahua

San Diego, AMNH 3716

"Dist. Guerrero" (105 km. south of Nueva Casas Grandes), USNM 40063 (incomplete skin; counts not made on this specimen).

Mojarachi, EHT-HMS 23016-7, UI 17788

Barranca del Cobre region, LMK 41106

Santa Barbara, AMNH 68204

These divisions represent an attempt at roughly grouping the specimens on a geographical basis, without regard to the formal recognition of subspecies. It will be noted that while half of the localities listed above yield a sample of seven or more specimens, seven of the areas contain but one specimen each, and an eighth area includes but two. Specimens from these eight areas, yielding less than seven specimens each, do not appear in the statistical comparisons. It is believed that the most satisfactory groupings from the standpoint of geographic isolation may well be the southern Arizona and New Mexico mountain ranges. Included in this study are series from two such mountain ranges not examined by any previous authors (Santa Rita and Chiricahua mountains). Also, eight additional and previously unstudied specimens from the Santa Catalina and Rincon

mountains make a total of ten now available from this mountain area. Four CNHM specimens labeled "Tombstone" have been included with the group from the nearby Huachuca Mountains, a more likely locality.

SEXUAL DIMORPHISM.-- The presence or absence of sexual dimorphism in the number of ventral scales and white body bands was tested in one population (Huachuca Mountains). For ventral scales a comparison was made of 15 males and 12 females. The results are shown in Fig. 4. Results for the white body band counts of 14 males and 12 females are given in Fig. 5. There is no statistically significant difference between the sexes for either character.

COLOR.-- A thorough color analysis was not possible due to the limited number of live individuals available. However, five snakes representing four distinct geographic areas have been available simultaneously, an unusual circumstance. Color notes were recorded for them. They are from the following localities (all in Arizona): central Arizona (Prescott Mountains), Santa Catalina Mountains, Huachuca Mountains, and Chiricahua Mountains (2 specimens). Colors of the red and white bands of the dorso-lateral surface were checked, with the aid of Maerz and Paul (1930), and are summarized in Table 2. When these individuals are simultaneously compared, very little variation in color can be detected (with the exception of the specimen from the Santa Catalina Mountains), either among the different snakes or within a single individual. In general, there is a very slight lightening of the red and white from the mid-dorsal line to the ventral scales, and a slight lightening of the red anteriorly (the first red band is frequently suffused with lighter coloring on its lateral surfaces, and the same is true for much of the red throughout the ventral surface).

The individual from the Santa Catalina Mountains has much whiter

TABLE 2

Colors on the dorso-lateral surface of Lampropeltis pyromelana from Arizona. Colors are from Maerz and Paul (1930).

| Locality | Band type | Color at neck | Color at mid-body | Color near vent |
|---|---|---|---|---|
| Prescott Mts. (ASDM 1070) | red | Pl. 4 I12 (Nasturtium) | Pl. 5 I12 | Pl. 5 I12 |
| | white | Pl. 10 C1 (Marguerite Yellow) | Pl. 10 C1 (Marguerite Yellow) | Pl. 10 D1 |
| Santa Catalina Mts. (ASDM 1069) | red | Pl. 3 E12 (Burnt Orange) | Pl. 3 H12 | Pl. 5 I12 |
| | white | Pl. 9 B1 | Pl. 9 B1 | Pl. 9 B1 |
| Huachuca Mts. (ASDM 667) | red | Pl. 5 F12 (Burnt Sienna) | Pl. 5 I12 | Pl. 5 I12 |
| | white | Pl. 11 D1 | Pl. 11 E1 | Pl. 11 E1 |
| Chiricahua Mts. (ASDM 1013) | red | Pl. 5 I12 | Pl. 5 J12 (Monterey) | Pl. 5 J12 (Monterey) |
| | white | Pl. 11 D1 | Pl. 11 E1 | Pl. 11 E1 |
| Chiricahua Mts. (WHW 1351) | red | Pl. 5 I12 | Pl. 5 I12 | Pl. 5 I12 |
| | White | Pl. 10 C1 (Marguerite Yellow) | Pl. 10 C1 (Marguerite Yellow) | Pl. 10 C1 (Marguerite Yellow) |

bands than any of the other snakes examined. This is clearly shown in the photograph (fig. 11) of this specimen. The red bands are also somewhat more orange in color than those of the other snakes. Another individual from the Santa Catalina Mountains (CHL 3588), which was compared by C. H. Lowe, Jr. (field notes, 1951) with a specimen from the Chiricahua Mountains (CHL 3587), was also found to have noticeably whiter bands; dorsal color at mid-body corresponding to Oyster White (Plate 10 B1). He also noted that the red bands of the Catalina individual were lighter than those of the Chiricahua specimen, colors at mid-body being as follows: Catalina specimen - Tile Red to Burnt Orange (Plate 3 D12 - E12), Chiricahua specimen - Tomato Red to Bittersweet (Plate 3 I12 - J12). The Chiricahua specimen had apparently considerably more orange bands than those examined in this study, and may have been similar to another Chiricahua individual (AMNH 57386) examined several years previously, whose bands had a noticeably orange color. This individual is the lower snake in the frontispiece; the upper snake (WHW 1351) is also from the Chiricahua Mountains and exhibits the more usual darker color.

No live snakes from Utah were examined, but Tanner (op. cit.) gives dorsal red coloration of a Utah individual as Scarlet (Ridgeway, 1912). Scarlet is Plate 1 L12 in Maerz and Paul; this is a very different shade of red from that of any snakes of this species examined in this study, and may indicate significant geographic variation.

why not compare directly with Ridgeway?

PATTERN.-- The basic dorsal pattern of Lampropeltis pyromelana is a series of red, black and white bands so oriented that the red bands are bordered by a black one on each side. This pair of black bands split with red is normally called a triad, but for simplification in

this study the various bands are referred to by their colors and the term "triad" is avoided. The pattern is broken up on the belly, which may vary in color from predominantly red to solid black. Due to the difficulty of accurate analysis and description, ventral pattern is not considered in the analyses here presented.

Dorsal fusion of black bands (body).-- Counts were made on 119 specimens for the number of occurrences of two black bands fused or meeting along the dorsal mid-line. Such fusion is one of the most obviously apparent variables to one familiar with mountain king snakes, and was successfully used by Zweifel (1952) as a measure of determining the amount of red area in Lampropeltis zonata of the Pacific Coast region.

This variation is not clinal, appears to be random, and is not generally concordant with that for other characteristics of pattern nor with the variation in ventral scales, as discussed below. A summary is given in Table 3 and is shown in Figs. 6 and 7. The wide variation in fusion among snakes from a single area may be seen in Fig. 6. There is some degree of uniformity only in the sample from the Santa Catalina and Rincon mountains, and in the Mexican group, with the exception of one specimen (the southernmost individual).

White bands (body).-- The number of white bands occurring on the body (not including head) were counted on a total of 131 specimens. A statistical summary for this characteristic is given in Table 4 and Fig. 8. The range is from 26 (Arizona, Bisbee) to 61 (Arizona, Catalina-Rincon Mountains sample, 3 specimens).

Fig. 8 shows the variation to be segregated into some rather distinctive geographic groups and not forming a "smooth" cline. Two major groups of similar samples appear, viz., (1) the Nevada, Utah,

TABLE 3

Percentage of dorsal fusion of black body bands in Lampropeltis pyromelana.

| Locality | N | Range | Mean |
|---|---|---|---|
| Nevada | 2 | 37.8 - 78 | 57.9 |
| Utah | 10 | 0 - 95 | 54.7 |
| Grand Canyon | 7 | 2.8 - 80.5 | 33.6 |
| Central Arizona | 33 | 0 - 96.4 | 47.3 |
| Pinos Altos Mts. | 1 | 21.7 | 21.7 |
| Graham Mts. | 1 | 61.5 | 61.5 |
| Catalina-Rincon Mts. | 10 | 62.7 - 96.8 | 83.5 |
| Santa Rita Mts. | 6 | 0 - 65.8 | 42.7 |
| Pajarito Mts. | 1 | 76.2 | 76.2 |
| Huachuca Mts. | 29 | 0 - 89.6 | 44.7 |
| Bisbee | 1 | 0 | 0 |
| Chiricahua Mts. | 8 | 0 - 91.5 | 64.1 |
| Animas Mts. | 1 | 97.7 | 97.7 |
| Big Hatchet Mts. | 1 | 72.1 | 72.1 |
| Mexico | 7 | 0 - 66 | 17.1 |

TABLE 4

Comparisons of number of white body bands of Lampropeltis pyromelana. A value for P of .01 or less indicates significant variation.

| Locality | N | Range | Mean ± S.E. | t | P |
|---|---|---|---|---|---|
| Utah | 10 | 31 - 44 | 38.3 ± 1.47 | .42 | .7 |
| vs. | | | | | |
| Grand Canyon | 7 | 33 - 41 | 37.4 ± 1.18 | | |
| Grand Canyon | 7 | 33 - 41 | 37.4 ± 1.18 | 4.50 | .001 |
| vs. | | | | | |
| Central Arizona | 34 | 34 - 57 | 46.3 ± .84 | | |
| Central Arizona | 34 | 34 - 57 | 46.3 ± .84 | 2.56 | .01 |
| vs. | | | | | |
| Catalina-Rincon | 10 | 42 - 61 | 51.6 ± 2.40 | | |
| Catalina-Rincon | 10 | 42 - 61 | 51.6 ± 2.40 | 2.95 | .01 |
| vs. | | | | | |
| Santa Rita | 7 | 32 - 55 | 39.4 ± 3.14 | | |
| Catalina-Rincon | 10 | 42 - 61 | 51.6 ± 2.40 | 7.31 | .001 |
| vs. | | | | | |
| Huachuca | 38 | 27 - 47 | 38.1 ± .68 | | |
| Catalina-Rincon | 10 | 42 - 61 | 51.6 ± 2.40 | .71 | .5 |
| vs. | | | | | |
| Chiricahua | 10 | 38 - 58 | 49.3 ± 1.95 | | |
| Santa Rita | 7 | 32 - 55 | 39.4 ± 3.14 | .61 | .5 |
| vs. | | | | | |
| Huachuca | 38 | 27 - 47 | 38.1 ± .68 | | |
| Santa Rita | 7 | 32 - 55 | 39.4 ± 3.14 | 2.65 | .02 |
| vs. | | | | | |
| Chiricahua | 10 | 38 - 58 | 49.3 ± 1.95 | | |

TABLE 4 (Cont'd)

| Locality | N | Range | Mean ± S.E. | t | P |
|---|---|---|---|---|---|
| Huachuca | 38 | 27 - 47 | 38.1 ± .68 | 6.60 | .001 |
| vs. | | | | | |
| Chiricahua | 10 | 38 - 58 | 49.3 ± 1.95 | | |
| Mexico | 6 | 30 - 59 | 46.5 ± 4.61 | 1.01 | .9 |
| vs. | | | | | |
| Catalina-Rincon | 10 | 42 - 61 | 51.6 ± 2.40 | | |
| Mexico | 6 | 30 - 59 | 46.5 ± 4.61 | 3.28 | .001 |
| vs. | | | | | |
| Huachuca | 38 | 27 - 47 | 38.1 ± .68 | | |
| Mexico | 6 | 30 - 59 | 46.5 ± 4.61 | 1.20 | .9 |
| vs. | | | | | |
| Santa Rita | 7 | 32 - 55 | 39.4 ± 3.14 | | |
| Mexico | 6 | 30 - 59 | 46.5 ± 4.61 | .60 | .6 |
| vs. | | | | | |
| Chiricahua | 10 | 38 - 58 | 49.3 ± 1.95 | | |

extreme northern Arizona (Grand Canyon) plus the Santa Rita and Huachuca samples and (2) the Catalina - Rincon plus the Chiricahua and possibly the Mexico sample, which actually overlaps both groups. The central Arizona sample appears to be intermediate; as close to the Santa Rita as it is to the Catalina - Rincon. It will be noted that in three adjacent samples, the rectangles, representing $2\sigma_m$, do not overlap. These are the Grand Canyon and Central Arizona, the Catalina - Rincon and Santa Rita, and the Huachuca and Chiricahua samples.

It appears that the two major statistical groups constitute four natural evolutionary segregates which may be geographically delineated as follows: (1) Nevada, Utah, northern Arizona (Grand Canyon), (2) central Arizona (and possibly Santa Catalina and Rincon mountains), (3) Santa Rita Mountains, Huachuca Mountains, and (4) Chiricahua Mountains, and Mexico. There is a general lack of concordance between this variation and that for ventral scales as well as other characteristics of pattern.

Variation in white bands is shown in Figs. 12 and 13 which compare individuals from two adjacent mountain ranges in southeastern Arizona (Chiricahua and Huachuca mountains). Specimens from the Chiricahua Mountains have not been previously studied.

Lateral fusion of white bands (body).-- A principal feature of the snakes from southwestern Chihuahua (originally described as L. knoblochi Taylor) is the lateral fusion of the white bands in an irregular line along the sides of the body. Sporadic fusion of this type occurs in snakes from farther north, where it usually appears as a rather even band somewhat lower down on the sides. This pattern may be described as a lateral extension of the white bands, usually

located at about the edge of the ventral scales, and having above it some elements from the bordering black bands, so that a lateral view gives the impression of a red area bordered on both sides and below by a black and white band (and enclosed above by black also, if dorsal fusion of the black bands occurs); see Fig. 14 (left). In southern individuals of the "knoblochi" form, this lateral white band fusion typically takes place on about the 3rd and 4th scale rows and the area below this is broken with irregular black elements (see Fig. 16).

Determination of the number of occurrences of lateral fusion of two white body bands were made on 119 specimens (Table 5, Fig. 9). It will be seen that while such fusion occurs throughout the entire geographic range of the species, it is predominant in only one mountain range outside of Mexico, viz., the Chiricahua Mountains of southeastern Arizona. Fig. 14 (left) is a photograph of a specimen from the Chiricahuas showing extreme fusion, and Fig. 15 shows an individual from the Santa Catalina Mountains exhibiting a majority of the white bands similarly fused. Fig. 14 (right) exhibits an opposite extreme to the fused band condition, wherein the pattern on the lateral surfaces is nearly obsolete. Both specimens in Fig. 14 are from the Chiricahua Mountains.

The last two columns in Table 5 show the greater incidence of lateral white band fusion in the more southerly populations. The Chiricahua Mountains of Arizona harbors today the only population outside of Mexico that is known to have an individual (CHL 3587) in which all of the white bands of the body are fused laterally. As seen in the table, there is a disparity between 3 bands fused and 7 fused, i.e., no animals are known that have 4, 5, or 6 bands fused. A new

TABLE 5

Lateral fusion of white body bands in Lampropeltis pyromelana.

| Locality | N | Number of bands fused | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4-6 | more than 6 (not all) | all |
| Nevada | 2 | 1(50%) | 1(50%) | 0 | 0 | 0 | 0 | 0 |
| Utah | 10 | 5(50%) | 2(20%) | 3(30%) | 0 | 0 | 0 | 0 |
| Grand Canyon | 7 | 6(85.7%) | 1(14.3%) | 0 | 0 | 0 | 0 | 0 |
| Central Arizona | 33 | 25(75.8%) | 5(15.2%) | 2(6.1%) | 0 | 0 | 1(2.9%) | 0 |
| Pinos Altos Mts. | 1 | 0 | 0 | 1(100%) | 0 | 0 | 0 | 0 |
| Graham | 1 | 1(100%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Catalina-Rincon | 10 | 6(60%) | 3(30%) | 0 | 0 | 0 | 1(10%) | 0 |
| Santa Rita | 6 | 5(83.3%) | 0 | 1(16.7%) | 0 | 0 | 0 | 0 |
| Pajarito | 1 | 0 | 0 | 1(100%) | 0 | 0 | 0 | 0 |

TABLE 5 (Cont'd)

| Locality | N | Number of bands fused | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4-6 | more than 6 (not all) | all |
| Huachuca | 29 | 17(58.6%) | 6(20.7%) | 3(10.3%) | 1(3.5%) | 0 | 2(6.9%) | 0 |
| Bisbee | 1 | 1(100%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Chiricahua | 8 | 2(25%) | 1(12.5%) | 1(12.5%) | 0 | 0 | 3(37.5%) | 1(12.5%) |
| Animas Mts. | 1 | 1(100%) | 0 | 0 | 0 | 0 | 0 | 0 |
| Big Hatchet Mts. | 1 | 0 | 1(100%) | 0 | 0 | 0 | 0 | 0 |
| Mexico | 7 | 0 | 1(14.3%) | 0 | 0 | 0 | 2(28.6%) | 4(57.1%) |

plateau is reached at 7 or more bands fused. Included in this latter category is 1 (2.9%) of the central Arizona specimens, and 3 of the southern Arizona specimens outside of the Chiricahua Mountains (viz., Huachuca Mountains, 2 (6.9%) and Santa Catalina and Rincon mountains, 1 (10%)). Three (37.5%) of the Chiricahua specimens are in this category.

While this characteristic is expressed to some extent largely throughout the geographic distribution of the species (Table 5, columns 0, 1, and 2), in its well-developed form (Table 5, last 2 columns) it does not appear north of the forested Mogollon Rim country of central Arizona. It is of interest that here, in a mountain dwelling reptile, is found the "Mexican influence" (in more or less "pure" form) reaching to the Mogollon Rim of central Arizona; this is true of certain of the characteristics of numerous lowland species.

It is seen that two significant shifts of frequency occur in this character along a north-south line; one of these is at the Chiricahua Mountains in the southeastern corner of Arizona and the other is in the Mogollon country of central Arizona.

VENTRAL SCALES.-- The analysis of number of ventral scales is based on counts taken from a total of 132 specimens. A summary is given in Table 6 and Figure 10. The range in number of ventrals is from 198 (Utah; Stockton, Tooele County) to 239 (Arizona, Santa Catalina Mountains).

Fig. 10 and Table 6 show that of the geographically adjacent populations that are compared, a statistically significant difference occurs only between the central Arizona and the Catalina-Rincon Mountains series. It is to be noted here that the Catalina - Rincon sample is, however, not significantly different from the adjacent

TABLE 6

Comparisons of number of ventral scales of Lampropeltis pyromelana. A value for P of .01 or less indicates significant variation.

| Locality | N | Range | Mean ± S.E. | t | P |
|---|---|---|---|---|---|
| Utah | 11 | 198 - 226 | 216.5 ± 2.79 | | |
| vs. | | | | 1.80 | .9 |
| Grand Canyon | 6 | 220 - 229 | 224.0 ± 1.44 | | |
| Grand Canyon | 6 | 220 - 229 | 224.0 ± 1.44 | | |
| vs. | | | | .54 | .6 |
| Central Arizona | 33 | 205 - 234 | 222.5 ± 1.12 | | |
| Central Arizona | 33 | 205 - 234 | 222.5 ± 1.12 | | |
| vs. | | | | 2.90 | .01 |
| Catalina-Rincon | 10 | 222 - 239 | 229.6 ± 2.10 | | |
| Catalina-Rincon | 10 | 222 - 239 | 229.6 ± 2.10 | | |
| vs. | | | | 1.83 | .10 |
| Santa Rita | 7 | 221 - 228 | 224.4 ± 1.07 | | |
| Catalina-Rincon | 10 | 222 - 239 | 229.6 ± 2.10 | | |
| vs. | | | | 1.81 | .10 |
| Huachuca | 38 | 220 - 235 | 226.5 ± .66 | | |
| Catalina-Rincon | 10 | 222 - 239 | 229.6 ± 2.10 | | |
| vs. | | | | 2.49 | .02 |
| Chiricahua | 10 | 210 - 227 | 222.6 ± 1.66 | | |
| Santa Rita | 7 | 221 - 228 | 224.4 ± 1.07 | | |
| vs. | | | | 1.28 | .03 |
| Huachuca | 38 | 220 - 235 | 226.5 ± .66 | | |
| Santa Rita | 7 | 221 - 228 | 224.4 ± 1.07 | | |
| vs. | | | | .78 | .50 |
| Chiricahua | 10 | 210 - 227 | 222.6 ± 1.66 | | |

TABLE 6 (Cont'd)

| Locality | N | Range | Mean ± S.E. | t | P |
|---|---|---|---|---|---|
| Huachuca | 38 | 220 - 235 | 226.5 ± .66 | 2.48 | .02 |
| vs. | | | | | |
| Chiricahua | 10 | 210 - 227 | 222.6 ± 1.66 | | |
| Mexico | 7 | 223 - 233 | 226.7 ± 1.57 | .96 | .9 |
| vs. | | | | | |
| Catalina-Rincon | 10 | 222 - 239 | 229.6 ± 2.10 | | |
| Mexico | 7 | 223 - 233 | 226.7 ± 1.57 | .12 | .9 |
| vs. | | | | | |
| Huachuca | 38 | 220 - 235 | 226.5 ± .66 | | |
| Mexico | 7 | 223 - 233 | 226.7 ± 1.57 | 1.12 | .9 |
| vs. | | | | | |
| Santa Rita | 7 | 221 - 228 | 224.4 ± 1.07 | | |
| Mexico | 7 | 223 - 233 | 226.7 ± 1.57 | 1.62 | .9 |
| vs. | | | | | |
| Chiricahua | 10 | 210 - 227 | 222.6 ± 1.66 | | |

Santa Rita Mountain series. And the Santa Rita series is not significantly different from any others with the exception of the Utah sample.

Although there is a significant difference between the Utah sample and that from Mexico, and the Arizona material (with the exception of the Catalina - Rincon sample) falls geographically and morphologically between these extremes, Fig. 10 does not appear to show a cline in ventral scale numbers.

Among additional statistical probabilities depicted in Fig. 10 it is found (1) that over the geographic distribution of L. pyromelana from the Santa Catalina Mountains of Arizona to southern Chihuahua the species is without statistically significant variation in ventral scale number, (2) that the central Arizona material and the northern Arizona (Grand Canyon) sample differ in similar degree from the Utah series, and (3) that the northern Arizona (Grand Canyon) sample is not significantly different from any of the mountain populations of southern Arizona, or from Mexico.

Finally, it is of interest to note that there is a general lack of concordance between the variation in ventral scales and pattern, as has been discussed above. The Utah sample has low counts in both ventral scales and white bands, while the central Arizona group occupies an intermediate position with regard to both of these variables. The population from the Santa Catalina and Rincon mountains is unique in having both a high ventral and white band count, a high degree of dorsal fusion of black bands, and perhaps some difference in color of white bands as well.

DISCUSSION.-- From the foregoing analysis of pattern variation and scutelation in Lampropeltis pyromelana it is apparent (1) that no

population is unique in its characteristics, (2) that significant geographic variation occurs, and (3) that this variation is seldom consistent with respect to the various characters analyzed. One might consider formal recognition of a number of subspecies and/or species on the basis of this pattern and scale variation, and this has been attempted (Taylor, op. cit.; Tanner, op. cit.). However, the consideration of more than a single species in this complex can be readily dispensed with as an artificial taxonomic conclusion resulting from earlier lack of material permitting critical analysis. As for recognition of subspecies, from the present analysis it is clear that (1) in such event, the number of subspecies recognized would necessarily result from arbitrary decision, (2) the geographic limits would be arbitrarily drawn, and (3) the statistical parameters would be arbitrarily set. It is concluded that formal recognition of subspecies in Lampropeltis pyromelana is, in the final analysis, largely an academic exercise in drawing arbitrary lines. However, this conclusion and the data upon which it rests should not, and cannot properly, be construed as evidence in any sense vitiating either the reality of subspecies or the concept that subspecies should not be formally recognized in systematics, either in this or in any other polymorphic species; such proposals have been recently published by Wilson and Brown (1953), and others.

# SUMMARY AND CONCLUSIONS

Lampropeltis pyromelana is a diurnal, oviparous snake which is ecologically restricted to cooler and more mesic environments in the inland southwest, viz., pinyon-juniper, oak, Mexican pine-oak, and riparian woodlands; yellow pine forest, and possibly the lower portions of fir forest. Throughout its geographic range, it appears to be most abundant between 6000 and 7500 feet elevation, reaching the extremes of approximately 4500 to 9000 feet. The ecologic tolerance of this species falls within the limits of the Upper Sonoran and Transition life-zones.

Aspects of behavior, food habits, and reproduction are treated, followed by a discussion of possible adaptations to a high mountain environment with respect to metabolic rate and egg retention.

Geographic variation in ventral scales, color, and several aspects of color pattern are analyzed. Certain characters appear to be random in distribution, others exhibit geographic variation but usually inconsistently so with respect to each other. It is concluded that there is such general lack of concordance in the distribution of these characteristics over the geographic range of this species that recognition of subspecies may not be warranted.

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Abbreviations used are as follows:

| | |
|---|---|
| AMNH | American Museum of Natural History |
| ASDM | Arizona-Sonora Desert Museum |
| CHAS | Chicago Academy of Sciences |
| CHL | Charles H. Lowe, Jr. |
| CM | Carnegie Museum |
| CNHM | Chicago Natural History Museum |
| EHT-HMS | Edward H. Taylor - Hobart M. Smith |
| GC | Grand Canyon National Park |
| LMK | Laurence M. Klauber |
| MNA | Museum of Northern Arizona |
| MVZ | Museum of Vertebrate Zoology, University of California |
| SD | San Diego Society of Natural History |
| UA | University of Arizona |
| UCLA | University of California, Los Angeles |
| UI | University of Illinois |
| USNM | United States National Museum |
| WHW | William H. Woodin |

There are many specimens of this
snake in Calif. Acad. Sciences!
C.L.C.

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Fig. 1. Habitat of Lampropeltis pyromelana in the Santa Catalina Mountains, Pima Co., Arizona, at an elevation of 7500 feet.

Fig. 2. Habitat of Lampropeltis pyromelana in the Santa Catalina Mountains, Pima Co., Arizona, at an elevation of 4700 feet.

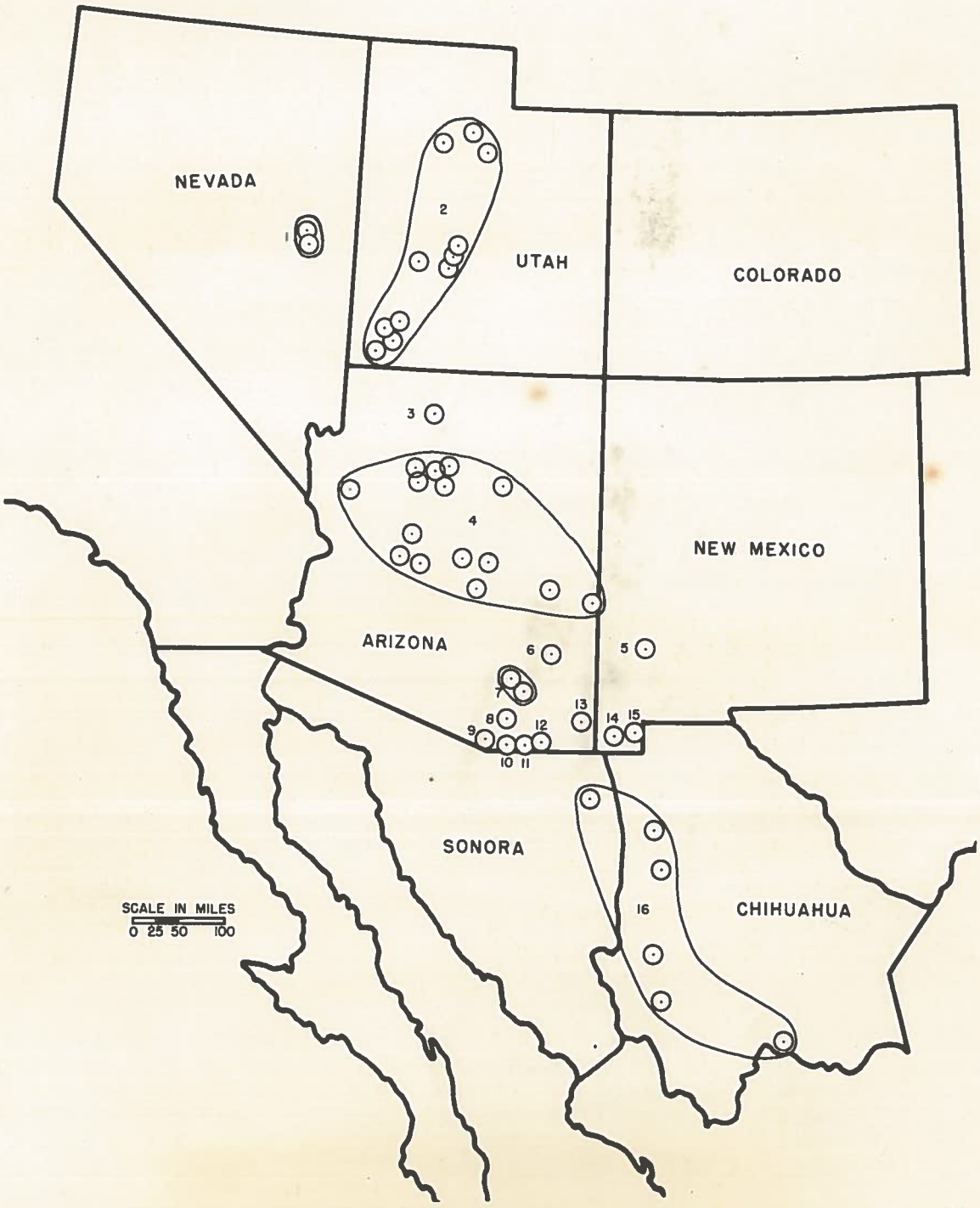


Fig. 3. Locality records of Lampropeltis pyromelana. Those areas considered as groups are enclosed by a line.

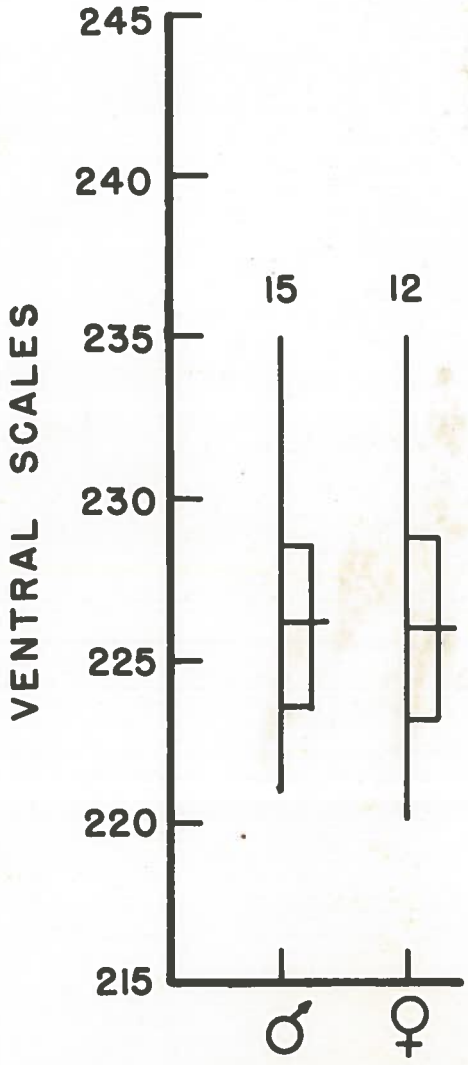


Fig. 4. Ventral scales of males and females of Lampropeltis pyromelana from the Huachuca Mountains, Cochise Co., Arizona.

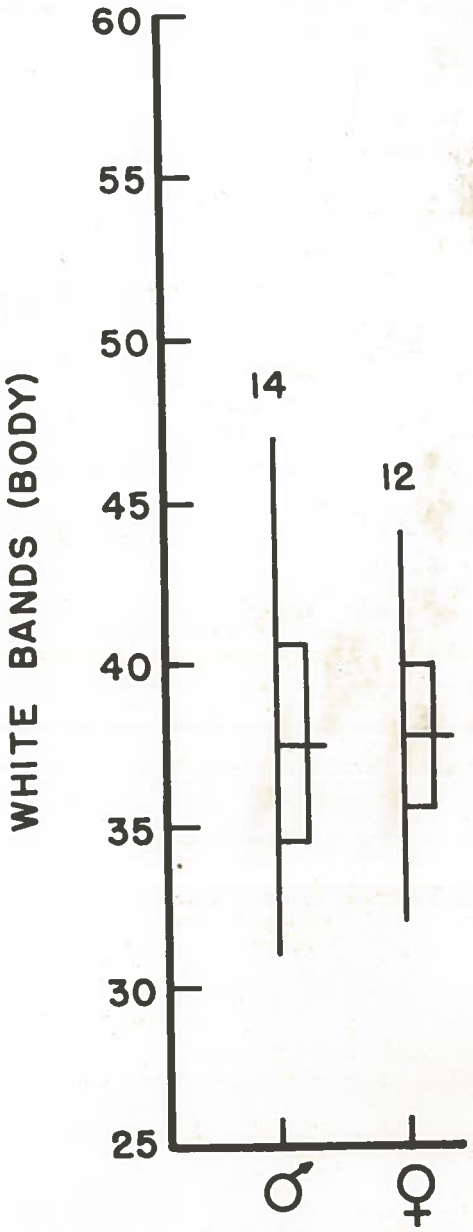


Fig. 5. White body bands of males and females of Lampropeltis pyromelana from the Huachuca Mountains, Cochise Co., Arizona.

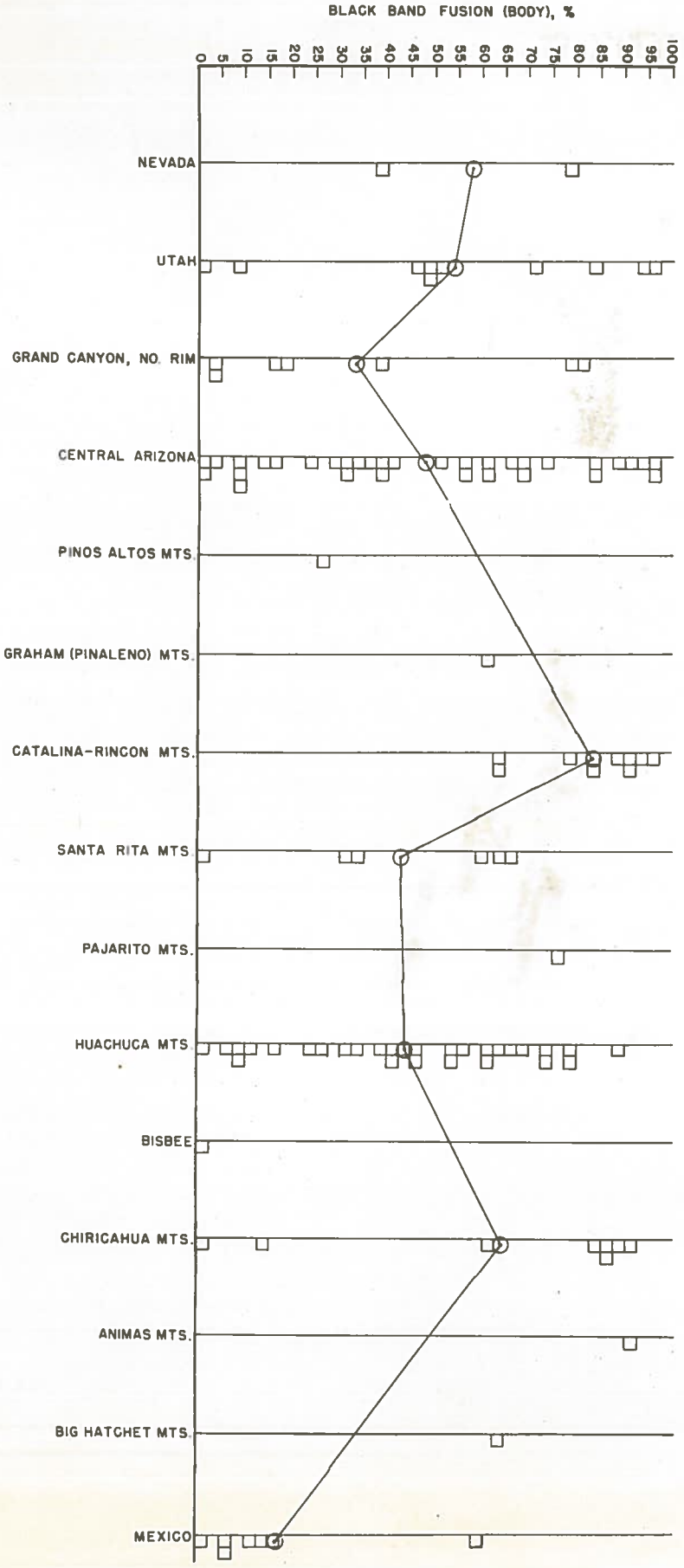


Fig. 6. Geographic variation in the degree of dorsal fusion of black body bands in Lampropeltis pyromelana. The line connects the means for this character as determined for specimens from those localities represented by more than one individual.

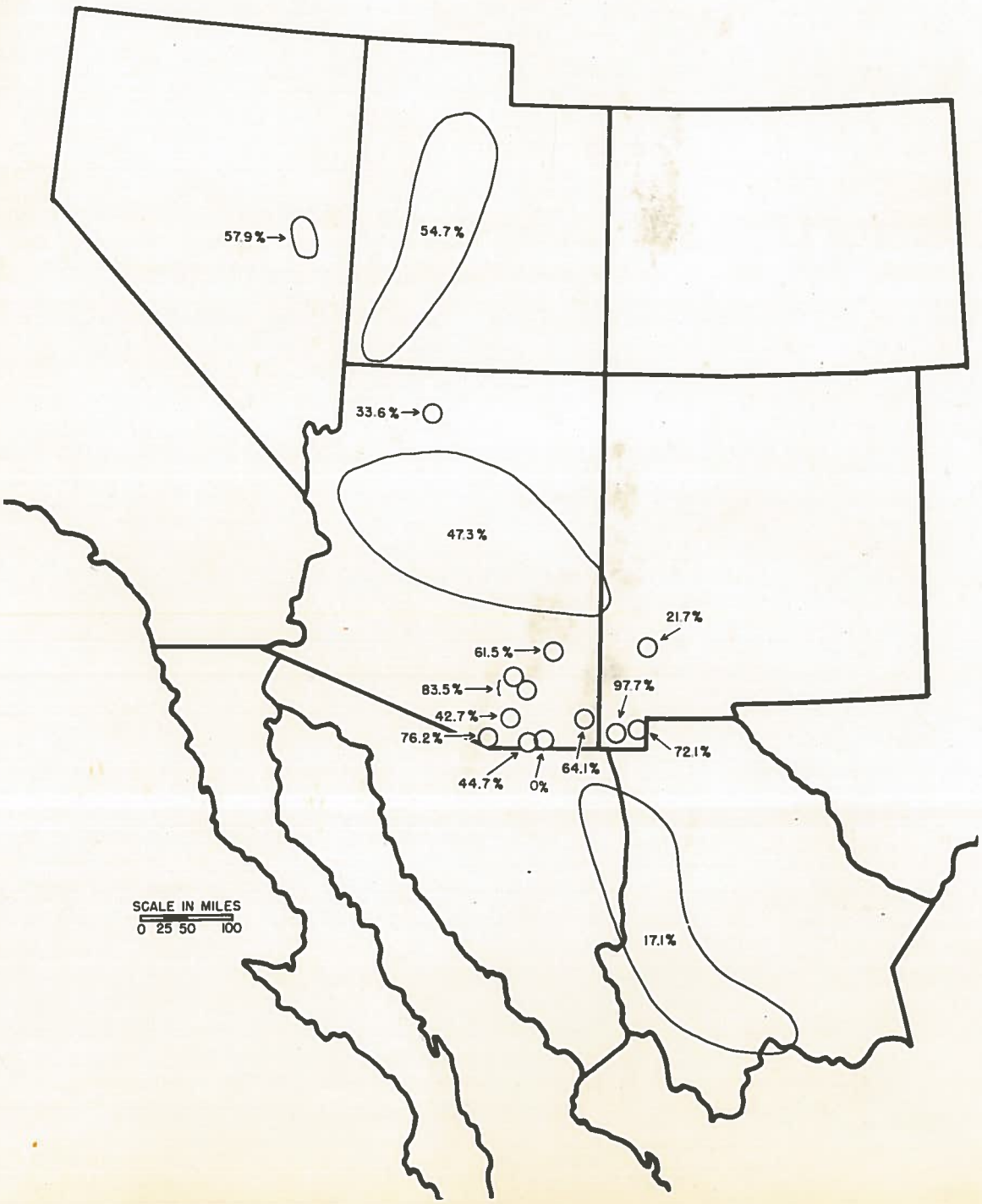


Fig. 7. Dorsal fusion of black body bands in Lampropeltis pyromelana. The mean percentage of fusion is given for each locality.

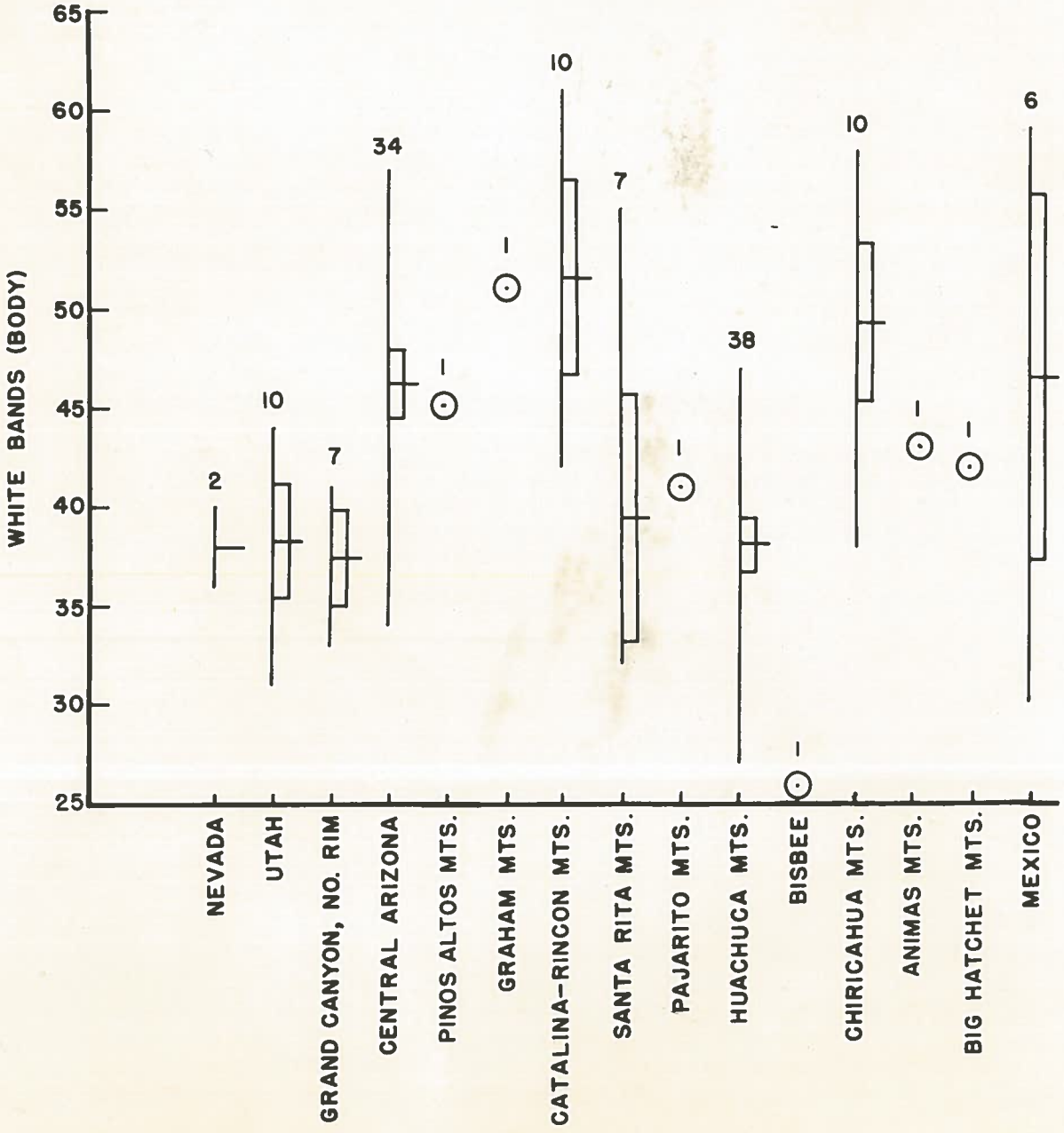


Fig. 8. Geographic variation in the number of white body bands in Lampropeltis pyromelana.

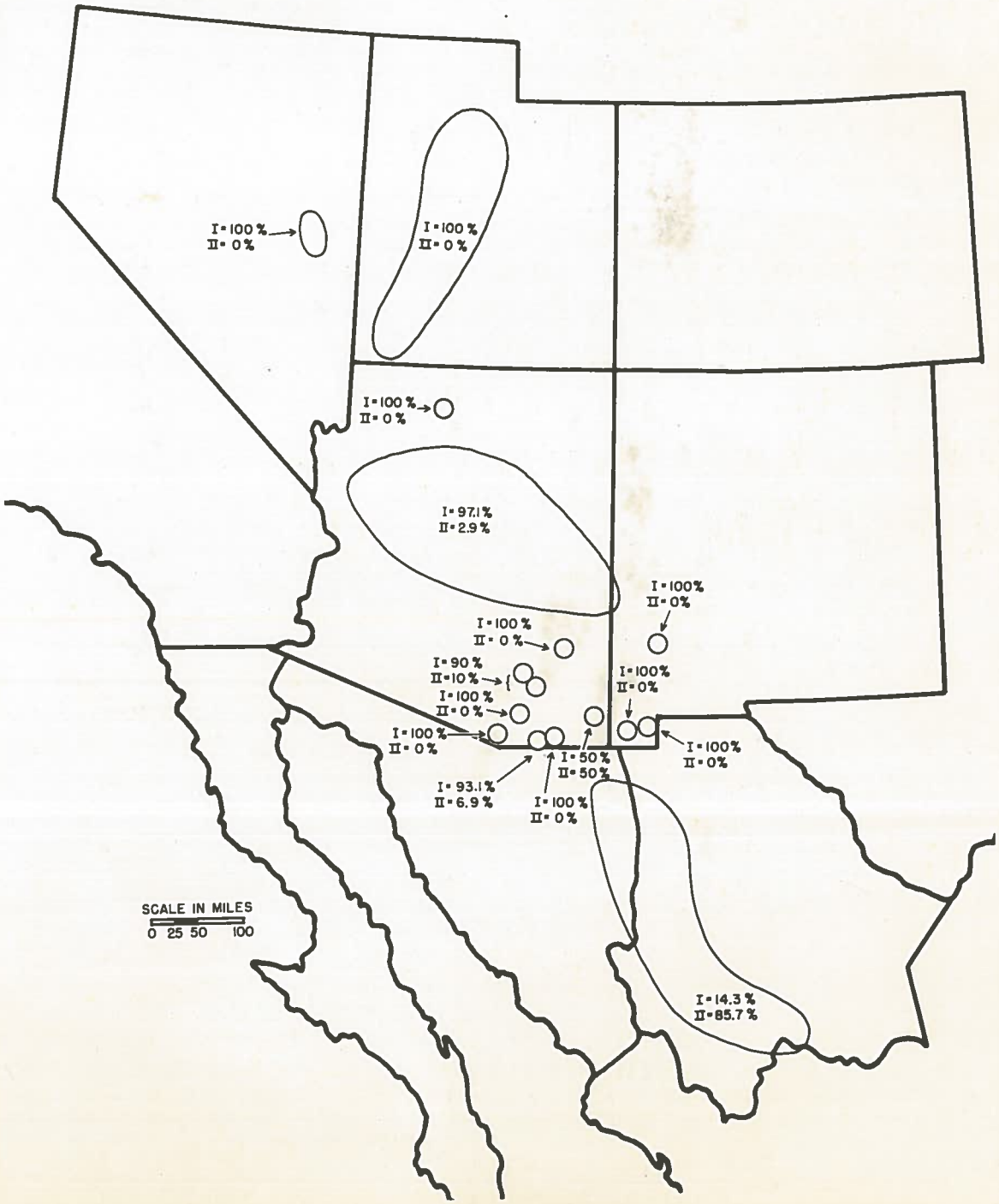


Fig. 9. Lateral fusion of white body bands in Lampropeltis pyromelana. Group I includes those specimens having 0 - 3 bands fused; Group II individuals have more than 3 bands fused.

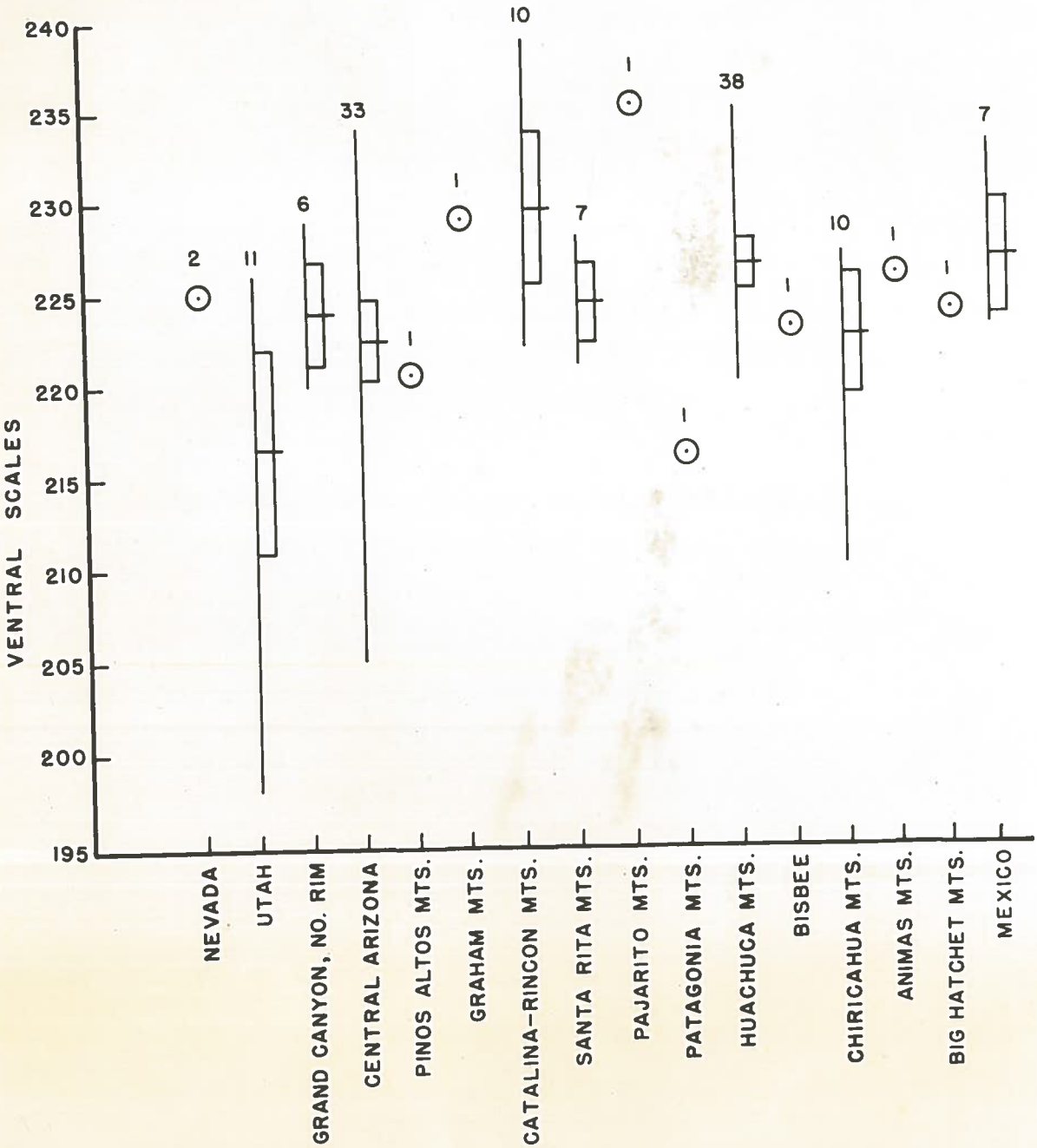


Fig. 10. Geographic variation in the number of ventral scales in Lampropeltis pyromelana.

Fig. 11. Lampropeltis pyromelana from the Santa Catalina Mountains, Pima Co., Arizona (ASDM 1069).

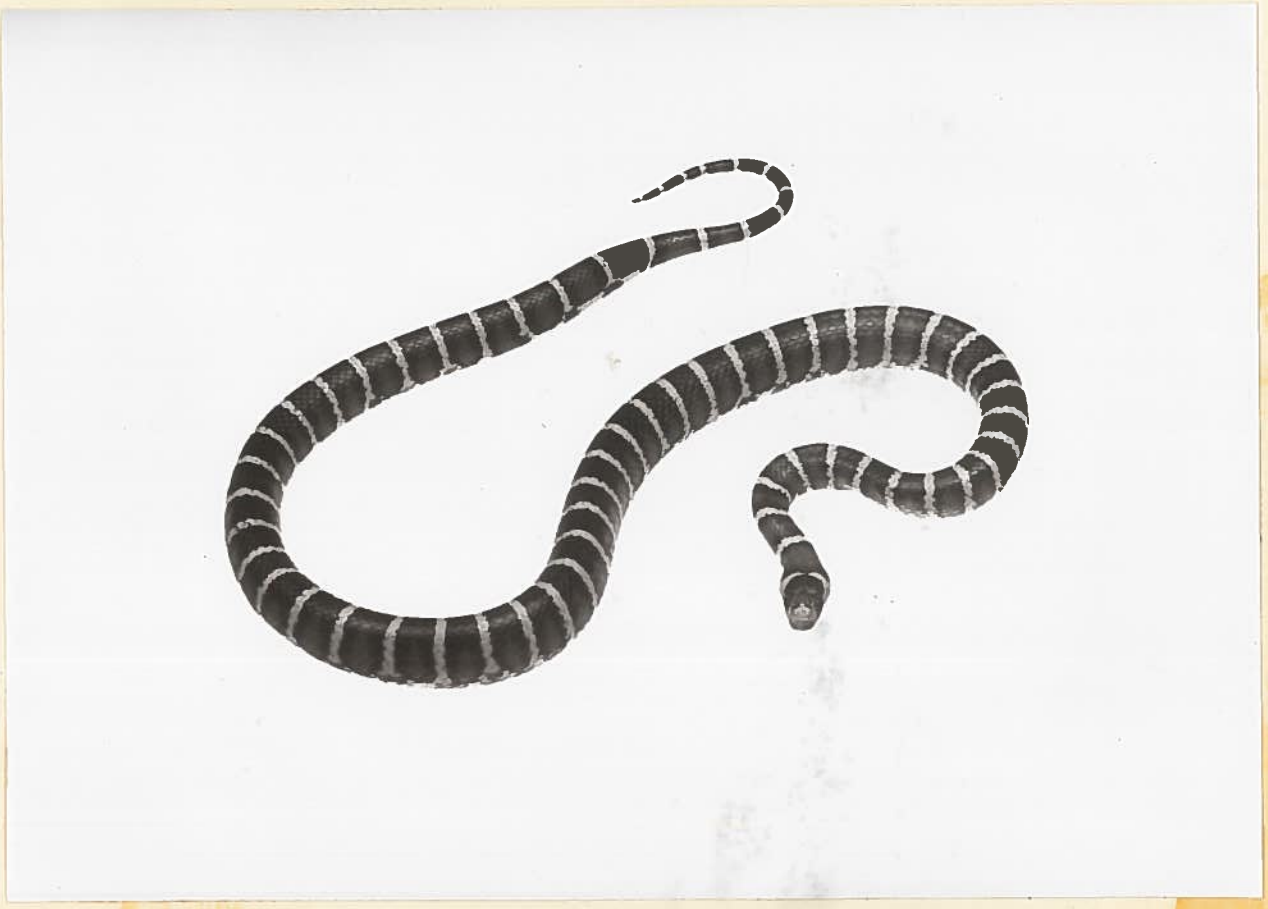

Fig. 12. Lampropeltis pyromelana from the Chiricahua Mountains, Cochise Co., Arizona (WHW 1351).

Fig. 13. Lampropeltis pyromelana from the Huachuca Mountains, Cochise Co., Arizona (ASDM 667).

Fig. 14. Specimens of Lampropeltis pyromelana from the Chiricahua Mountains, Cochise Co., Arizona, showing variation in lateral fusion of white bands. Left, CHL 3587; right CHAS 3937.

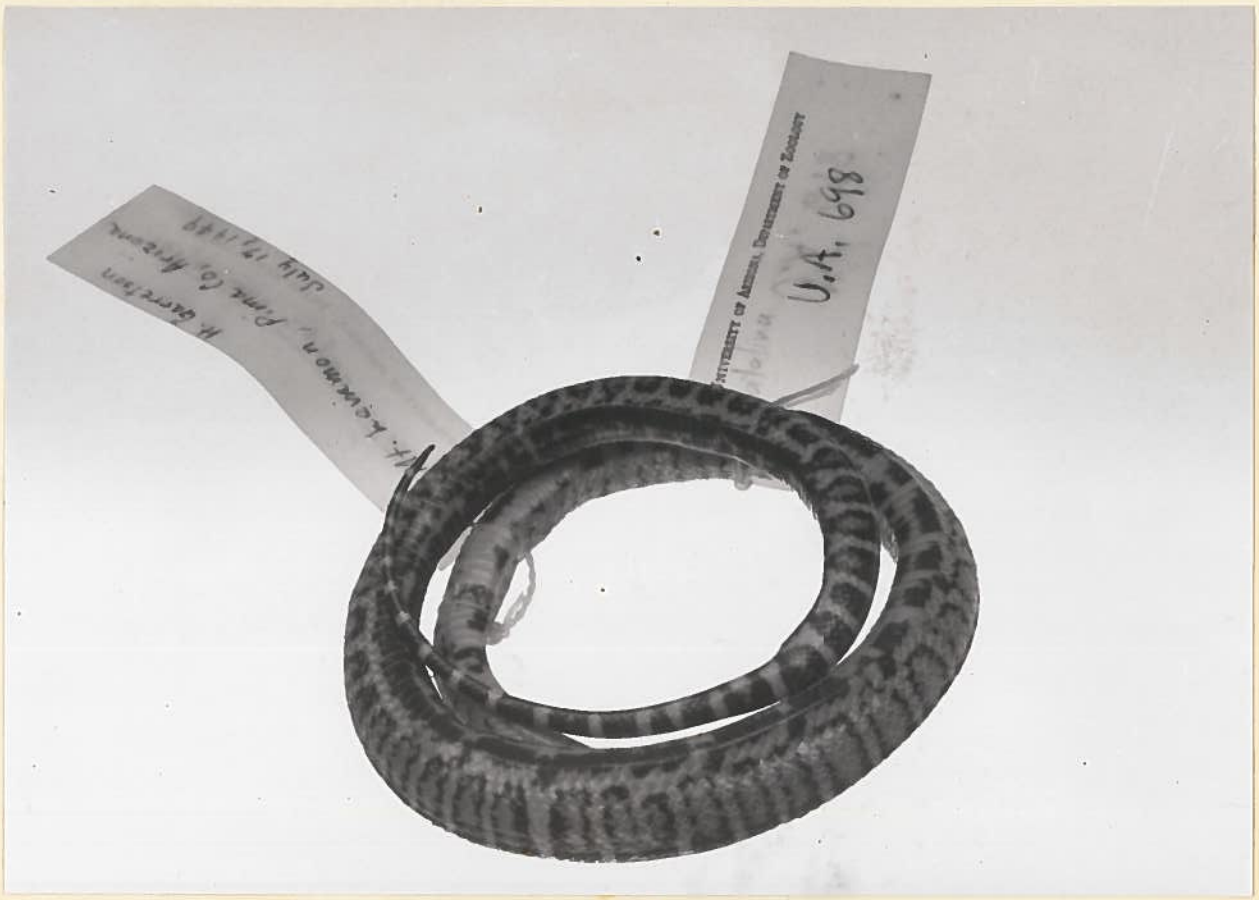


Fig. 15. Lampropeltis pyromelana from the Santa Catalina Mountains, Pima Co., Arizona (UA 698), showing extensive lateral fusion of the white bands.

Fig. 16. Lampropeltis pyromelana (previously described as L. knoblochi) from Mojarachi, Chihuahua, Mexico (UI 17788).