Pattern Variation and Evolution of the Mountain Kingsnake, *Lampropeltis zonata*

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THE considerable variation in the color pattern of *Lampropeltis zonata*, its extensive geographic range, and its somewhat less extensive ecologic range provide excellent material for a simultaneous study of both the geographic and ecologic aspects of variation. Throughout much of its range, *L. zonata* occurs in local montane populations. When represented by a sufficient number of specimens, the pattern variation of each of these populations has been subjected to statistical analysis and compared with the others; this pattern variation has been studied from the point of view of both ecologic and phylogenetic relationships.

HISTORICAL SUMMARY

What may have been the first description of *Lampropeltis zonata* was that of Blainville (1835: 61) who described *Culuber zonatus* from California. However, the description of this form was so incomplete that, when the type specimen was lost, the species could no longer be identified with certainty.

The first name definitely associated with the
The mountain kingsnake is *Bpollophis zonatus* Lockington (1876: 52). Smith and Taylor (1945: 84) have reasoned that since Blainville's species is unidentifiable, Lockington is to be considered the author of the species, even though he apparently thought that he was merely placing Blainville's form in a new genus. A number of other authors have contributed to the discussion of the proper specific name for the mountain kingsnake (Burt, 1936; Peters, 1938; Klauber, 1943). The decision of Smith and Taylor, that *Lampropeltis zonata* (Lockington *ex* Blainville) is the proper name for the species, is followed in this paper. The form of citation is that of Smith and Taylor (1945: 84).

Since the description of *Bollophis zonatus*, four more names have been proposed which are considered here to be applicable to distinct subspecies of the mountain kingsnake. These are *Ophidopus gutulcus multicolor* Yarrow, 1882; *Coronella multicolor* Bocourt, 1886; *Lampropeltis herreræ* Van Denburgh and Slevin, 1923; and *Lampropeltis agalma* Van Denburgh and Slevin, 1923. Two additional subspecies are described in this account.

Klauber (1943) reviewed the species and proposed the recognition of coastal and Sierran races, and in addition removed the Baja Californian forms *herreræ* and *agalma* from synonymy, treating them as races of the mountain kingsnake.

**Pattern Variation**

The basic color pattern of *Lampropeltis zonata* consists of a series of alternating white and black rings, commencing with a white ring on the back of the head (Pl. I). Most of the black rings enclose red areas laterally, and the red may expand across the dorsum so that red rings are formed within the black, splitting the black into two rings. Any black ring, split or not by red, and bordered on either side by white, is called a triad.

Variation in the amount of red is most obvious, and this formed the basis for the first systematic recognition of subdivisions within the species (Van Denburgh and Slevin, 1923; Klauber, 1943). Any increase in the amount of red on the body is always at the expense of the black, the white rings remaining at a relatively constant width. The amount of red on the body may be roughly indicated by determining the percentage of body triads that have the lateral red areas confluent dorsally, splitting the black; short of actually counting the number of red scales, no better method has been devised.

The number of triads on the body is subject to considerable variation, and forms another variable that has been studied.

The first white ring, crossing the posterior portion of the head, may be complete or may be interrupted mid-dorsally. More important is its position relative to the last supralabial scale. In the anteriormost position, the white ring is sufficiently far forward that its posterior margin lies on, or rarely anterior to, the last supralabial (Fig. 1A). At the other extreme, the posterior margin is behind the angle of the mouth and may be as far as four scales back, the whole band being placed to the rear (Fig. 1C). While the distances involved are small, the differences are so constant for different geographic areas that I am inclined to give this character more weight as an indicator of relationships than is given to the other more highly variable characters. A third position of the first white ring is intermediate between the two extremes (Fig. 1B).
The color of the head scales anterior to the first white ring has been studied. In five of the races, these scales, the frontal, prefrontals and internasals in particular, are typically black; but in two races, there is commonly some light coloration, red in life, on these scales. Capitalized color names in the text have reference to Ridgway (1912) which was used as a standard for comparisons. Comparison of the sexes with respect to pattern characters has disclosed no significant difference between them. In view of the small samples available from some areas, this has been an advantage in allowing pooling of the sexes for statistical treatment.

**VARIATION IN SCUTELLATION.**

While this study has been primarily concerned with pattern variation, data on variation in numbers of ventrals, subcaudals and scale rows are also included. The author is indebted to Dr. L. M. Klauber who very kindly made available the majority of the data upon which the scale variation summaries are based.

**ACCOUNTS OF SUBSPECIES**

*Lampropeltis sonata multicincta* (Yarrow)

Plate I, A

*Xiphophorus setulus multicinctus* Yarrow (1882: 440), original description.

*Lampropeltis sonata*, Van Denburgh (1897: 167), part.


*Lampropeltis sonata multicincta*, Klauber (1943: 76), part.

**TYPE.**—Adult female, No. 11753, United States National Museum, collected by Gustav Eisen. The type locality was given as Fresno, California, but it is probably from the Sierra Nevada to the east of Fresno.

**DIAGNOSIS.**—Characterized by the following combination of characters: small amount of red on body, usually (90 percent of specimens) less than 60 percent of body triads dorsally split by red; first white ring in posterior position; snout black.

**VARIATION IN COLOR PATTERN.**—This diagnosis is based on 36 specimens. There are from 23 to 48 body triads, mean 35.88 ± 1.09. From none to 84 percent of the body triads are split dorsally by red, mean 25.08 ± 3.75. The first white ring is complete dorsally and in only one is the posterior margin as far forward as the angle of the mouth. The anterior head scales are normally black, without red markings. (Figs. 2–4; Table I.)

Color notes are available for a single specimen from Plumas County, California. The red of the triads of this snake was recorded as Carnelian Red (T. I. Storer, field notes).

**VARIATION IN SCUTELLATION.**—Eighteen males average 215.88 ± 1.16 ventrals, fourteen females, 216.28 ± 1.48. Nineteen males average 55.52 ± 0.68 subcaudals; thirteen females, 49.8 ± 0.81 (Table I). Close correspondence of the male and female ventral counts is evident, but the lower subcaudal counts of the females is correlated with their conspicuously shorter tails.

There seems to be a clinal trend in numbers of ventrals, the larger numbers being more common in the more southerly areas. Eight specimens, both males and females, from Tulare County average 221.4 ventrals. From the next county to the north, Fresno County, seven specimens average 217.7. Eleven specimens from the Yosemite region of Mariposa County, roughly in the center of the Sierra Nevada, average 213.6. This trend is continued into the region of intergradation with *L. z. sonata* in northern California and southern Oregon. Intergradation with that subspecies is discussed in the account of *L. z. sonata*.

A maximum of 23 dorsal scale rows is reached by 28 of 33 specimens, the others having 25 (2) and 21 (3).

**HABITAT.**—The snakes of the Sierra Nevada seem to be restricted, or nearly so, to the yellow pine (*Pinus ponderosa*) belt. This situation has led to the supposition that the mountain kingsnake is a good indicator of the Transition Life-zone. Such may be true in the Sierra Nevada, but it is not so elsewhere.

Evidence seems to indicate that *Lampropeltis sonata* ranges little if any above the upper limits of the Transition Life-zone. A specimen (which I have not seen) from *"Hot Springs, Long Canyon, Mt. Whitney, 8000'"* constitutes the highest altitude record for *L. z. multicincta*. That this record is not inconsistent with the assumption that this race reaches its approximate upper limit at the upper border of the Transition Life-zone is shown by the following
Lampropeltis zonata: A—multicincta, Shasta Co., Calif., MVZ 15963; B—zonata, Lake Co., Calif., MVZ 14386; C—parvirubra, type specimen, San Gabriel Mountains, Los Angeles Co., Calif., MVZ 42407; D—agalma, Sierra Juarez, Baja California, México, MVZ 10493; E—multifasciata, Santa Cruz Co., Calif., MVZ 32243.
statement: “The lower part of Long Canyon is in the Transition Zone. At this point a considerable number of trees and shrubs reach their upper limits. Among these are incense cedar, yellow pine, silver fir, sugar pine, pinon pine, white alder, canyon live oak, California black oak. . . . The lodgepole pine does not range below this altitude.” (Elliot, 1904: 280).

**DISTRIBUTION.**—From eastern Shasta County, California, south along the western slopes of the Sierra Nevada at least to southern Tulare County and probably into northern Kern County (Fig. 5).

On the basis of the specimen from “Hot Springs, Long Canyon, Mt. Whitney, 8000’,” Blanchard thought that *L. zonata* ranged east of the Sierran Divide. However, this locality is west of the divide, in the drainage of the Kern River, as is shown on the map of the collector’s (Edmund Heller’s) itinerary (Elliot, 1904). The eastern escarpment of the Sierra Nevada is very steep, and the area in which *L. zonata* might be expected to occur is in consequence quite restricted. *L. zonata* may yet be found in some of the deep, well protected canyons along the eastern slope.

**LOCALITY RECORDS (ALL IN CALIFORNIA).**—

- **Shasta County:** Burney Creek, 0.5 mi. above Burney Falls. Plumas County: Keddie, 6 mi. N of Gurnay; Butte (Butt) Valley, 1 mi. below Butte Lake Dam. El Dorado County: Riverton Post Office; Fyffe. Calaveras County: Wolfboro, 6000’. Tuolumne County: Strawberry Lake, 5600’, 3 mi. E of Pine Crest. Mariposa County: Comet Mine, E of Mariposa; Tenaya Canyon; Yosemite Valley. Fresno County: 2.1 mi. SE of Pinehurst; 4 mi. W of Cedar Grove; 13 mi. from Cedar Grove; Kings River Canyon, 5000’.

- **Tulare County:** Smoky Valley, South Fork Kern River; Ash Mountain; Crystal Springs.
Trail, Sequoia National Park; between Trout Meadows and Little Kern River; Whittaker’s Forest, 10 mi. NE of Badger; General’s Highway near Slide Spring, Sequoia National Park; Giant Forest.

*Lampropeltis sonata zonata* (Lockington ex Blainville)

**Plate I, B**

*Bellophis sonatus* (Lockington 1876: 53), original description.

*Lampropeltis sonata*, Van Denburgh (1897: 167), part.


*Lampropeltis multicipincta*, Blanchard (1920: 5), part.

*Lampropeltis multicipincta multiferiata*, Klauber (1943: 76), part.

*Lampropeltis sonata zonata*, Klauber (1943: 76), part.

**Type.**—Formerly in the collection of the California Academy of Sciences, the type specimen (or specimens) was destroyed in the great fire of 1906. A personal communication from Van Denburgh was quoted by Blanchard (1921: 222): “the types... were two in number and were labeled Santa Barbara, but probably were collected in the mountains near there.” Lockington cited the type locality as “Northern California.” Reasons for rejecting Van Denburgh’s statement in favor of the type locality cited by Lockington are given below.

**Diagnosis.**—Anterior head scales dark; first white ring complete and in posterior position. Few body triads, 30 or less in four specimens examined; more than 60 percent of body triads dorsally split by red.

**Variation in color pattern.**—The four specimens upon which this race is based have 30, 28, 27 and 24 body triads. Respectively there are 90, 86, 63 and 96 percent of the triads split dorsally by red. (Figs. 2–3.) Despite this high percentage, these snakes are not so predominantly red as is *L. z. multifaciata* to the south. The posterior margin of the first white ring is from two to two and one-half scales back of the angle of the mouth. The anterior head scales are without light markings in all four specimens. (Figs. 2–4; Table I.)

**Variation in scutellation.**—The four specimens, one male and three females, have 216, 207, 209 and 218 ventrals. Subcaudals are 52, 49, 49 and 46. Maximum scale rows are 23 in all specimens. (Table II.)

**Geographic allocation of the type specimen.**—With respect to all pertinent characters, Lockington’s description of *Bellophis sonatus* disagrees with specimens from the Santa Barbara region and agrees with specimens from north of San Francisco Bay.

*Lockington’s type had 32 white rings on the body and tail, therefore probably not more than 27 body triads. This agrees well with the condition observed in northern California specimens, but is ten triads fewer than the mean for seven snakes from Santa Barbara and Ventura counties and is well below the minimum of 35 exhibited by them. The type of *Bellophis sonatus*...*"*
Fig. 5. Distribution and locality records of Lampropeltis zonata. The estimate of total range was derived from personal observation, data accompanying specimens, and pertinent literature (Grinnell, 1935; Bailey, 1936; Jansen, 1947).
had a black snout, while all seven specimens from Santa Barbara and Ventura counties have some light markings anterior to the first white ring. More important, however, is the position of the first white ring. In the southern California snakes, the ring is in the anterior position. While Lockington did not specifically relate the position of the ring to the supralabials, he did mention that the first black ring commences back of the parietals, which indicates that the white ring was well back on the head, as is some with the typical pattern of *L. z. zonata* and some typical of *L. z. multiciptta*. As these two races have been defined, *multiciptta* typically has less than, and *zonata* more than, 60 percent of the body triads dorsally split by red. This plainly allows no room for intermediacy on the part of individuals, but a comparison of the ranges of variation and means of the populations in question shows that, as a whole, the northern California and Oregon snakes stand roughly intermediate (Figs. 2–3). The zone of

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Ventrals</th>
<th>Subcaudals</th>
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<tbody>
<tr>
<td><em>multiciptta</em></td>
<td>18♂️, 202–225 (215.88 ± 1.16)</td>
<td>19♂️, 49–61 (55.52 ± 0.68)</td>
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<td>14♀️, 209–227 (216.28 ± 1.48)</td>
<td>13♀️, 46–55 (49.84 ± 0.81)</td>
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<td>All, 202–227 (216.06 ± 0.95)</td>
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<tr>
<td><em>multiciptta x zonata</em> (intergrades)</td>
<td>9♂️, 203–214 (208.44 ± 1.47)</td>
<td>9♂️, 49–54 (51.40 ± 0.51)</td>
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<td>3♀️, 210–211 (210.33)</td>
<td>3♀️, 46–48 (46.33)</td>
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<td>All, 203–214 (209.08 ± 1.11)</td>
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<td><em>zonata</em></td>
<td>1♂️, 216</td>
<td>1♂️, 52</td>
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<td></td>
<td>3♀️, 207–218 (211.3)</td>
<td>3♀️, 46–49 (48.0)</td>
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<td>All, 207–218 (212.5)</td>
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<td><em>multifasciata</em></td>
<td>9♂️, 205–219 (211.33 ± 2.2)</td>
<td>8♂️, 55–61 (58.12 ± 0.69)</td>
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<td>8♀️, 206–224 (208.2 ± 3.0)</td>
<td>8♀️, 52–62 (52.29 ± 2.1)</td>
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<td>All, 205–224 (209.88 ± 1.68)</td>
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<tr>
<td><em>parvirubra</em></td>
<td>19♂️, 204–220 (212.24 ± 1.01)</td>
<td>17♂️, 54–60 (56.70 ± 0.53)</td>
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<td>25♀️, 204–216 (209.72 ± 0.71)</td>
<td>24♀️, 48–56 (53.54 ± 0.56)</td>
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<td>All, 204–220 (211.02 ± 0.65)</td>
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<tr>
<td><em>pulchra</em></td>
<td>16♂️, 198–210 (206.43 ± 1.02)</td>
<td>15♂️, 51–59 (55.2 ± 0.72)</td>
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<td>18♀️, 194–220 (205.11 ± 1.63)</td>
<td>16♀️, 47–58 (52.44 ± 0.87)</td>
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<td>All, 194–220 (205.73 ± 0.96)</td>
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<td><em>agalma</em></td>
<td>1♂️, 213</td>
<td>1♂️, 56</td>
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<td>3♀️, 207–210 (208.6)</td>
<td>3♀️, 50–55 (52.3)</td>
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<td>All, 207–213 (209.7)</td>
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<tr>
<td><em>herrerae</em></td>
<td>8♂️, 217–220 (218.7 ± 0.42)</td>
<td>7♂️, 57–59 (58.28 ± 0.38)</td>
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<tr>
<td></td>
<td>1♀️, 216</td>
<td>1♀️, 53</td>
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typical of the northern snakes. Lockington further states that "the black rings become wider on the center of the back, approaching, and in most cases, joining each other in pairs." It seems probable that if the type did come from northern California, it came from the area of intergradation between *L. z. zonata* and *L. z. multiciptta*, so the assignment of the name *zonata* to the more westerly race is somewhat arbitrary.

**INTERGRADATION WITH OTHER SUBSPECIES.**—Ten specimens from southwestern Oregon and northern California have been available, intergradation evidently extends from northern Mendocino County, California, into the Rogue River Valley of Oregon and east throughout the Siskiyou region in California. Within the area outlined, there is no consistent geographic arrangement of the two pattern types evident in the material available. (An explanation for this situation is offered in a subsequent section on dispersal and evolution.)

The five northernmost specimens, from Klickitat County, Washington, represent a similar situation, both pattern types being represented.
HABITAT.—There seem to be no published data on the habitat of this subspecies. One of the localities, four miles southwest of Lakeport, Lake County, California, is in the chaparral zone.

DISTRIBUTION.—Specimens are known from the mountains of Napa, Lake, southern Mendocino and Sonoma counties in west-central California (Fig. 5).


LOCALITIES IN THE ZONE OF INTERGRADATION.
—CALIFORNIA.—Siskiyou County: Callahan; Beaver Creek, mouth of Dutch Creek; Klamath River, mouth of Clear Creek. Del Norte County: East Fork, Illinois River, ¾ mi. S of Oregon State Line. Mendocino County: near Covelo.

OREGON.—Jackson County: Little Applegate River, 7 miles above mouth; 7 mi. SE of Brownsboro; McLeod; Rogue River; 4 mi. S of Ashland. Josephine County: near Wolf Creek. Curry County: 3 mi. N of Ilahe; W side Rogue River, 3 mi. above Agness. Washington.—Klickitat County: 1 mi. W of White Salmon; Bingen.

Lampropeltis sonata multifasciata (Bocourt)

Plate I, E

Coronella multifasciata Bocourt (1886: 616), original description.

Coronella sonata, Boulenger (1894: 202).

Lampropeltis sonata, Van Denburgh (1897: 167), part.

Lampropeltis pyrrhomelaena multicincta, Stejneger (1902: 153), part.

Lampropeltis multicincta, Blanchard (1920: 5), part.

Lampropeltis multifasciata, Klauber (1943: 76), part.

Lampropeltis sonata sonata, Klauber (1943: 76), part.

TYPE.—In the Paris Museum, collected in California by M. de Cessac.

DIAGNOSIS.—Large amounts of red on body and on anterior head scales, particularly prefrontals, characterize this subspecies. The only other race regularly having red on snout, L. s. agalma of Baja California, has 41 or more body triads. There are less than this number in 19 of 21 specimens of L. s. multifasciata.

VARIATION IN COLOR PATTERN.—Twenty-two specimens of this race have been examined. The body triads range in number from 26 to 45, mean 35.4 ± 0.96. The great amount of red on the body is reflected in the percentage of body triads split dorsally; range 72–100 percent, mean 93.9 ± 2.2. There are red markings in the snout region in 17 of 19 specimens checked for this character. (Figs. 2–4; Table I.) The position of the first white ring varies geographically. In the northern specimens, from the Santa Cruz Mountains, the posterior margin of the ring is near the rear edge of the last supralabial or on the scale following it, so that the condition for the population as a whole is intermediate between the anterior and posterior positional extremes. All specimens of L. s. multifasciata from south of Monterey Bay have the ring in the anterior position.

While the greatest number of body triads for this race was recorded for a rather northerly locality (Carmel Highlands, Monterey County), there seems to be a trend toward higher triad counts at the southern end of the range in Santa Barbara and Ventura counties. Ten snakes from the Santa Cruz Mountains have an average of 32.6 ± 1.28 body triads (range 26–38), while seven specimens from Santa Barbara and Ventura counties have from 35 to 43 triads, mean 37.6 ± 1.0.

The specimens from Santa Barbara and Ventura counties have, on the average, less red on the anterior head scales than is usual in the more northerly snakes. This represents an approach to the forms of southern California south of Ventura County.

Color notes are available for two living individuals of this race, both from the Santa Cruz Mountains. The red areas of one specimen were near English Red dorsally and Grenadine Red ventrally (Thomas Rodgers, field notes). In the other specimen, the areas were between English Red and Grenadine Red. The notes on the latter specimen were taken shortly after it had shed. Many of the scales in the white rings of this snake were tipped with gray.

VARIATION IN SCUTEILLATION.—Nine males have from 205 to 219 ventrals, mean 211.33 ± 2.2. Eight females average 208.2 ± 3.0, range 206–224. Males average 58.12 subcaudals, females 52.29. The range of the females (52–62) completely overlaps that of the males (55–61). (Table II.)

INTERGRADATION WITH OTHER SUBSPECIES.—A single specimen from Mount Hamilton, Santa Clara County, has been interpreted as an inter-
grade between *L. z. zonata* and *L. z. multifasciata*. This individual has a black snout, but light markings are present on the supraoculars. The first white ring is in the posterior position, agreeing in this respect with *L. z. zonata*. All the body triads are widely split by red. This specimen is unique among all mountain kingsnakes examined in that it possesses only 19 body triads. In the sum of its characters, it appears nearer to *L. z. zonata*, despite its closer geographic proximity to *L. z. multifasciata*.

It is possible that other small endemic populations of kingsnakes await discovery in the area surrounding San Francisco Bay, and that they may prove subspecifically distinct.

**Geographic Allocation of the Type Specimen.**—Bocourt's (1886) figure of the type clearly shows a considerable amount of light color in the snout region. The difficult accessibility of the range of the only other light-snouted race, *L. z. agalma* of Baja California, together with the type locality cited for *L. z. multifasciata* (“Californie”), favors the assignment of Bocourt's name to the California subspecies.

**Habitat.**—The Big Basin area of the Santa Cruz Mountains, where a number of specimens have been taken, is the site of one of the most extensive redwood forests south of San Francisco Bay. Farther south, in the Santa Ynez Mountains of Santa Barbara County, the snakes live in chaparral where the mountains closely approach the ocean.

**Distribution.**—The southern limit is reached in the mountains of Ventura and Santa Barbara counties, California. The Santa Clara River forms the dividing line between *L. z. multifasciata* and the races to the south. There is a gap of over 150 miles to the nearest records to the north, in Monterey County. It is probable that future collecting will only partly bridge this gap, as much of the intervening territory appears to be unsuited to this species. There is little doubt that the population of the Santa Lucia Mountains in Monterey County is completely disjunct from that of the Santa Cruz Mountains north of Monterey Bay. The northern extremity of the range is in the Santa Cruz Mountains of Santa Cruz and Santa Clara counties (Fig. 5).

**Locality Records.**—All in California. *Santa Clara County*: Wright's Station. *Santa Cruz County*: Near Zayante; Big Basin State Park; Ben Lomand; Boulder Creek (also 2 mi. W; 2 mi. N); Santa Cruz (also 2 mi. N). *Monterey County*: Fern Canyon Road, Carmel Highlands; Pine Valley, head of Carmel River; Big Sur. *Santa Barbara County*: Bluff Camp, 4500'; summit San Marcos Pass; San Marcos Ranch; Mono Flat, 8 mi. NE of Santa Barbara; Santa Ynez Grade, 4 mi. S of Santa Ynez. *Ventura County*: Matilija; Red Reef Canyon, 16 mi. NE of Ojai.

**Lampropeltis zonata parvirubra**, subsp. nov. Plate I, C

*Lampropeltis zonata*, Van Denburgh (1897: 167), part.


*Lampropeltis zonata multicincta*, Klauber (1943: 76), part.

**Type.**—Adult male, No. 42407, Museum of Vertebrate Zoology, collected by Robert C. Stebbins on May 8, 1946, ¼ mi. NW of Falling Springs Resort, 2 mi. SW of Crystal Lake Park, San Gabriel Mountains, Los Angeles County, California.

**Description of Type Specimen.**—Snout-vent length 590 mm., tail length 118 mm.; 212 ventrals, 57 subcaudals; dorsal scale rows 21-21-17; supralabials 7/7, infralabials 9/9. Forty-three body triads, of which five (11.6 percent) are split dorsally by red. The first white ring is incomplete dorsally with the posterior margin on the last supralabial. The dorsal surface of the head anterior to the first white ring is black.

**Diagnosis.**—The combination of characters that distinguishes this race from the others is as follows: first white ring in anterior position; high triad count, 37 or more in 90 percent of specimens; snout dark; relatively little red on body.

**Variation in Color Pattern.**—Sixty-one specimens exhibit the following variation: body triads 35-48, mean 41.16 ± 0.44; percentage body triads with red dorsally confluent, 3.5-100, mean 33.9 ± 2.64. Three specimens have the posterior margin of the first white ring one-half scale back of the angle of the mouth; the
rest have it on the last supralabial scale. (Figs. 2-4; Table I.)

Color notes have been taken from three living specimens of this subspecies, all from the San Gabriel Mountains of Los Angeles County, California. The red of the anterior rings of one specimen was between Flame Scarlet and Mars Orange; the posterior rings were closer to Flame Scarlet. Two other specimens had almost identical colors, anterior rings between Scarlet and Brazil Red, posterior rings slightly deeper. *L. s. parvirubra* seems to resemble the other southern Californian race, *L. s. pulchra*, more closely than it does *L. s. multicincta* with respect to the shade of red.

**VARIATION WITHIN A SINGLE BROOD.**—Through the courtesy of Dr. L. M. Klauber, I have been able to examine a brood of eight snakes hatched from eggs laid at the San Diego Zoo by a snake from Seven Oaks, San Bernardino Mountains. The body pattern of the father is unknown; that of the mother is decidedly unusual for this subspecies. She has the greatest amount of red on the body of all *parvirubra* examined, and has a triad count only one above the minimum recorded for the race. The brood differs from the mother in varying degrees (Fig. 6), showing a correlation of low triad count with increased red, as well as the converse.

**VARIATION IN SCUTELLATION.**—Nineteen males average 212.24 ± 1.01 ventrals, range 204–220; 25 females average 209.72 ± 0.71, range 204–216. The absence of significant differences in numbers of male and female ventrals noted for other subspecies is again suggested. Males average 56.70 ± .53 subcaudals, females 53.54 ± .56. (Table II.) Thirty-three specimens have a maximum of 21 scale rows, eight have 23 scale rows. In number of scale rows, *L. s. parvirubra* differs from *L. s. multicincta* which usually has 23 as the maximum, and which superficially resembles *parvirubra* in body pattern.

**INTRASUBSPECIFIC TRENDS.**—While only 13.5 percent of the snakes from the San Bernardino Mountains have the first white ring interrupted, it is broken dorsally in 45 percent of the specimens from the San Gabriel Mountains of Los Angeles County. This seems to be a tendency toward the condition in the snakes of the coastal Santa Monica Mountains (*L. s. pulchra*) where 81 percent of 18 specimens have the ring broken.

Seven specimens from the San Jacinto Mountains, Riverside County, have an average of 38.4 body triads, 2.8 fewer than the mean for the race as a whole. In addition the San Jacinto snakes average fewer ventrals than the race as a whole, 206.25 as contrasted to 211.02 for all males and females. Both of these trends are in the direction of *L. s. pulchra*. Larger numbers of specimens might prove it better to recognize the snakes of the San Jacinto Mountains as intermediate between *pulchra* and *parvirubra*.

**HABITAT.**—The altitudinal range is from about 1000 to 9000 ft., the lower extreme being reached along the southern face of the San Gabriel Mountains, Los Angeles County, California, and the higher extreme in the San Jacinto Mountains, Riverside County. At higher altitudes it is commonly associated with yellow-pine (*Pinus ponderosa*) and incense cedar (*Libocedrus decurrens*). At lower elevations bigcone spruce (*Pseudotsuga macrocarpa*) and various canyon chaparral species are common associates. Records for altitudes above 6000 ft. are scarce. From the Lake Arrowhead region of the San Bernardino Mountains, elevation 4000–5500 ft., ten specimens have been available, but from nearby Big Bear Lake, elevation 6700 ft., which is also a popular collecting and resort site, none has been reported.

**DISTRIBUTION.**—Found in the San Gabriel, San Bernardino and San Jacinto mountains in southern California (Fig. 5).

**LOCALITY RECORDS.**—All in California. *Riverside County* (San Jacinto Mountains): Strawberry Valley; Idyllwild; Mt. San Jacinto, 9000’;
Fern Valley. San Bernardino County (San Bernardino Mountains): Cable Canyon near Verdumont; 1 mi. E of Cedar Pines Post Office; Crestline; near Thousand Pines; Blue Jay; Lake Arrowhead; Santa Ana River, 5600'; Barton Flats; Forest Home; Seven Oaks; Water Canyon near Banning (may be in Riverside County); Whitewater Wash, 6000'; (San Gabriel Mountains) Lytle Creek, 6000'. Los Angeles County (San Gabriel Mountains): Head of Mescal Gulch, Pig Pines; Swartout; 1/4 mi. NW of Falling Springs Resort; Monrovia Canyon; mouth Arroyo Seco Canyon; Arroyo Seco Canyon; Monrovia Peak; Santa Anita Canyon; Altadena; Bell Canyon; Bailey Canyon; Wintergreen Canyon; Fish Canyon; Mount Wilson; West Fork San Gabriel River, 1.0 mi. E of Red Box Divide; Glendora; La Cañada; Eaton Canyon; Big Tujunga Canyon; Pacoima Canyon; Placerita Canyon; 2 mi. S of Newhall.

_Lampropeltis zona_ pulchra_, subsp. nov.


**Type.**—Adult male, No. 38667 in the collection of Laurence M. Klauer, collected near Crater Camp, Santa Monica Mountains, Los Angeles County, California. Crater Camp lies at an altitude of 450 ft., about 10 miles WNW of the city of Santa Monica.

**Description of the type specimen.**—Snout-vent length 545 mm., tail length 101 mm.; 217 ventrals, 57 subcaudals; dorsal scale formula 21-21-17; supralabials 7/7, infra labials 9/9. Thirty-two body triads, of which 22 (68.7 percent) have the lateral red areas dorsally confluent. The first white ring is incomplete dorsally with the posterior margin on the last supralabial. The anterior head scales are dark, except for a small white fleck on the frontal.

**Diagnosis.**—Distinguished by the following combination of characters: no red on snout; fewer than 39 body triads; first white ring in anterior position; relatively large amount of red per triad.

**Variation in color pattern.**—There are from 27 to 38 body triads, the mean for the 50 specimens being 32.24 ± 0.38. There is considerable variation in the amount of red on the body, from 15 to 100 percent of the triads being split dorsally. The mean for this character is 69.16 ± 2.8 percent.

Color notes are available for three living specimens. An individual from the Santa Monica Mountains had red areas which were Dragon's Blood Red anteriorly and Brazil Red toward the tail. Another from the Santa Monica Mountains was Brazil Red in both the anterior and posterior rings. Klauer (1943: 80) records a snake from San Diego County which had Scarlet rings anteriorly and Brazil Red toward the tail. The white rings tend toward Cream color.

The first white ring may be complete or may be broken along the mid-dorsal line. In the Santa Monica Mountains of Los Angeles County, 81 percent of 18 specimens have the ring broken, while to the south in San Diego County the incidence of incomplete rings is about 60 percent. In only one of 50 specimens is the posterior margin of the first white ring behind the angle of the mouth, and in that one it is only one-half scale back. (Figs. 2–4; Table I.)

**Variation in scutellation.**—As in other races, there is no significant difference between the male and female ventral counts. Males average 206.43 ± 1.02, females 205.11 ± 1.63. _L. z. pulchra_ has the lowest average ventral count of any of the races of _zonata_, but the overlaps are too extensive to permit the use of the scale counts as a key character. In subcaudals, males average 55.2 ± 0.72, females 52.44 ± 0.87. Twenty of 33 specimens have 21 dorsal scale rows, 13 have 23 rows. (Table II.)

**Habitat.**—The altitudinal range is from within a few feet of sea level to over 5000 feet. Where the maximum elevation is attained, in San Diego County, the snake probably does not range below 4000 feet. To the north, in the Santa Monica Mountains, the range extends from about 3000 feet (the maximum elevation of the mountain range) to within a few feet of sea level at the mouths of the larger canyons.

In the Santa Monica Mountains the plant associates are typical of canyons in the chaparral: _Quercus agrifolia_, _Platanus racemosa_, _Juglans californica_, _Rhus ovata_, _Rhus laurina_ and _Rhus diversiloba_. In the mountains of San
Diego County this subspecies apparently ranges little if any below the yellow pine (Pinus ponderosa) belt.

**Distribution.**—Known from the Santa Monica Mountains, Verdugo Hills, Santa Ana Mountains and the mountains of San Diego County in southern California (Fig. 5).

**Locality Records.**—Los Angeles County (Santa Monica Mountains): Saddle Peak; Crater Camp; Topanga Canyon; Pacific Palisades; Rustic Canyon; Stone Canyon; Beverly Glen Canyon; Mulholland Drive; Griffith Park; (Verdugo Hills) Glendale. Orange County: Santa Ana Mountains, Santiago Canyon; 2 mi. S of Irvine. This latter locality is not in the mountains, but is on the coastal plain, well out of the usual habitat. Perhaps the specimen is a flood-transported waif. San Diego County: Palomar Mountain; Iron Spring, Palomar Mountain; Laguna Junction; Laguna Mountain; Julian; Pine Hills; Green Valley; Cuyamaca Mountain; Gustay; Pine Valley.

_Lampropeltis sonata agalma_ Van Denburgh and Slevin

Plate I, D

_Lampropeltis sonata agalma_ Van Denburgh and Slevin (1923: 2), original description.

_Lampropeltis sonata_, Linsdale (1932: 378).

_Lampropeltis multifasciata agalma_, Klauber (1943: 76).

_Lampropeltis sonata agalma_, Klauber (1943: 76).

**Type.**—Adult male, No. 56856, California Academy of Sciences, collected by J. R. Slevin on South Todos Santos Island, Baja California, México, May 23, 1923.

**Diagnosis.**—Distinguished from almost all mainland snakes by the lack of red in the pattern. From the occasional black and white _L. s. multifasciata_, the snakes of South Todos Santos Island are distinguished by the position of the first white ring, the posterior margin of which is rarely back of the angle of the mouth, whereas it is in the posterior position in the Sierran snakes.

**Variation in Color Pattern.**—There is almost complete suppression of red, that color being represented by brownish patches laterally placed on some of the anterior triads. In ten specimens, the number of body triads ranges from 36 to 41, mean 38.2 ± 0.63. The first white ring tends to be a little farther back on the head than in the other southern races, but in only one specimen is the posterior margin as far back as one-half scale behind the angle of the mouth. (Figs. 2-4; Table I.)

**Variation in Scutellation.**—Eight males average 218.7 ± 0.42 ventrals, the single female has 216. The males have from 57 to 59
subcaudals, mean 58.28 ± 0.38, the female has 53. All have a maximum of 23 dorsal scale rows, a condition not in line with the usual reduction in scale rows in more coastaly located areas. (Table II.)

HABITAT.—South Todos Santos Island is one and one-quarter miles long, has a maximum altitude of 315 feet, and is covered with low brush and cactus. The specimens collected by Mr. Slevin were abroad on a cloudy day. Probably abundant fogs are an important factor in permitting the existence of this species at such a low altitude and latitude.

DISTRIBUTION.—This race appears to be restricted to the type locality, South Todos Santos Island, which is three miles from the tip of Punta Banda, the nearest point on the mainland of Baja California. The island is 11 miles WSW of the town of Ensenada (Fig. 5).

KEY TO THE SUBSPECIES OF *Lampropeltis sonata*

Excluding snakes from the areas of intergradation, the following key will properly allocate 89 percent of the specimens examined by the author.

A. Posterior margin of first white ring back of angle of mouth
   B. Posterior margin of first white ring on or anterior to last supralabial
   C. Sixty percent or more of body triads with lateral red areas dorsally confluent, splitting triads
   D. Less than 60 percent of body triads with red areas dorsally confluent, snout black
   E. Snout with red markings, especially on internasals and prefrontals; black of triads greatly restricted laterally
   F. Snout dark, without red markings; black of triads usually more than one scale wide laterally
   G. 36 or fewer body triads
   H. 37 or more body triads

*CORRELATION OF VARIATION AND HABITAT*

*Lampropeltis sonata* is found in a number of different plant associations such as chaparral, yellow pine, border-redwood and redwood, but it is not evenly distributed throughout all of these associations. For example, in the south it is found in the chaparral only in montane situations subject to the mollifying influence of the ocean. Again, it apparently does not penetrate the redwood forests north of San Francisco Bay.

There seems to be little correlation between color pattern and habitat. *L. s. pulchra* is found in the chaparral of the Santa Monica Mountains; but farther to the south, in the mountains of San Diego County, the populations here recognized as the same race are restricted to the yellow pine belt. Here the mountains are farther inland, and the habitat is at a higher elevation. Similarly, *L. s. parvisurina* inhabits the chaparral-covered south face of the San Gabriel Mountains and extends up to an elevation of over 6000 feet in the yellow pine belt of that mountain range.

The redwood forests of the Santa Cruz Mountains and the chaparral of the Santa Ynez Mountains are both included within the range of *L. s. multifasciata*.

*L. s. multicincta* appears to be restricted to the yellow pine belt of the Sierra Nevada, but in Oregon, in the Rogue River Valley area of intergradation with *L. s. sonata*, snakes with the typical pattern of *L. s. multicincta* may be found in areas “where Garry oak, golden oak, madrone, or chaparral are dominant” (Fitch, 1936: 646).

There appears to be little or no correlation between the amount of red and the habitat. Snakes with a high percentage of red are found in the moist redwood areas of the Santa Cruz Mountains, in the chaparral of the Santa Ynez Mountains and in the rather arid yellow pine belt of the Sierra San Pedro Martir. Similarly, snakes with the amount of red greatly reduced occur in the yellow pine belt of the Sierra Nevada, in the pines and chaparral of the San Gabriel Mountains and on tiny South Todos Santos Island off the coast of Baja California.

Nor does the number of body triads correlate with any particular habitat. For example, in one general area in the southern Sierra Nevada, snakes of the race *L. s. multicincta* show a range in number of body triads which nearly equals that for the entire species.

Variation in the position and continuity of the first white ring also shows no correlation with variation in habitat.
Although the range of the species extends through almost nine thousand feet of altitude and through a number of major plant communities, there is no phenotypic evidence of ecotypic differentiation. Probably the ecological distribution, as well as the geographic distribution, is a reflection of individual tolerance and of behavioral adaptation, rather than physiological adaptation of ecological races to a series of narrow sets of environmental conditions. The snakes are exploiting a part of the environment, utilizing from the range of conditions offered by a region only those suited to their needs and rejecting the remainder by retreating below ground or into other shelter.

The basic ringed pattern of *L. zonata* has a disruptive effect when observed in nature. Vivid though the snake appears when removed from its native environment, while it is on the forest floor the broken coloration renders it difficult to discern. However, while the basic pattern would seem to be adaptive, no adaptive significance can be detected in the geographic variation in the pattern.

**Interspecific Relationships**

Within the *doliata* group of kingsnakes, there are four forms that resemble *L. zonata* sufficiently closely to have received consideration as being close relatives of this species. These are *L. doliata gentilis*, *L. pyromelana*, *L. knoblochi* and *L. ruthveni*.

One of these, *L. ruthveni*, is known only from Michoacán, México, quite remote geographically from *L. zonata*. From a purely geographical standpoint, it seems unlikely that *L. ruthveni* is a direct ancestor of *L. zonata*. More probably the resemblance is fortuitous. When the great range of pattern variation within *L. zonata* is considered, it does not seem remarkable that another member of the *doliata* group should, purely by chance, come to resemble one of the races of *L. zonata*. The problem is to separate such probably fortuitous similarity from resemblance stemming from closer genetic relationship. Geographic considerations should help in this respect.

If it can be assumed that the type ancestral to *L. zonata* originally entered the Pacific Coast region from the east, then a form resembling *L. zonata* and with a range directly to the east of the present range of *L. zonata* may be close to the ancestral type. Both *L. pyromelana* and *L. doliata gentilis* fulfill these requirements.

*L. pyromelana* resembles *L. zonata* in the body pattern but, particularly in its white snout, has a distinctly different head pattern. It resembles *L. zonata* in having a maximum of 23 dorsal scale rows, but has higher ventral and subcaudal scale counts. Blanchard (1921: 234) found *L. pyromelana* to have a proportionately longer tail and a relatively wider head than *L. zonata*. He also noticed more specialized dentition in *L. pyromelana*. On the basis of these specializations, deviations from the mode of the group as a whole, he considered it unlikely that the more generalized *L. zonata* had descended from the more specialized *L. pyromelana*. *L. knoblochi* of the Sierra Madre Occidental of Mexico is probably conspecific with *L. pyromelana*.

The resemblance of certain individuals of *L. d. gentilis* to *L. zonata*, particularly the race *L. z. multicincta*, is striking. Only a lower ventral scale count and a slight tendency for the white rings to expand at the border of the ventrals serve to distinguish such *L. d. gentilis* from *L. z. multicincta*, at least among preserved specimens. A specimen of *gentilis* from Utah had light rings that were straw yellow dorsally (R. C. Stebbins, field notes), while the rings of *L. zonata* are much whiter, without any yellow color present. It is perhaps significant that the most westerly specimens of *L. d. gentilis*, examined from Colorado, Utah and Arizona, resemble *L. zonata* much more closely than do the *L. d. gentilis* from the plains to the east. No such geographic trend toward *L. zonata* has been noted in *L. pyromelana*.

Blanchard (1921: 227) considered it possible, but unlikely, that *L. d. gentilis* could have been modified to *L. zonata* upon reaching the Pacific Coast region. Smith (1942: 197) grouped *L. zonata* together with *L. ruthveni*, *L. pyromelana* and *L. knoblochi* in an evolutionary line separate from the northern races of *L. doliata*.

The opinion of the author is that *L. zonata* is closely related to, and perhaps even conspecific with, *L. doliata gentilis*. The differences between the two forms are slight and appear even more insignificant when the geographic separation is considered. The ranges of the two forms are now known to be separated by a minimum of 220 miles of rather arid country in the Great Basin and Mojave Desert. Further col-
lecting may narrow both the geographical and morphological gaps.

**SPECULATION ON DISPERAL AND EVOLUTION**

Since *L. dolius* exhibits an east-west geographic trend toward *L. zonata*, and *L. d. gentilis* most closely resembles the race of *L. zonata* inhabiting the Sierra Nevada, the Sierran race (*L. z. multicincta*) seems to be a logical candidate for the ancestral position with regard to the other races of *L. zonata*.

It is highly unlikely that the mountain kingsnake has ever dispersed across the great central valley of California, except perhaps at the extreme northern end. The invasion of the coastal and southern California regions from a Sierran foothold might be expected to have taken one or both of two routes: the mountain ranges at the northern or southern ends of the great central valley.

To the north, *L. z. multicincta* and *L. z. zonata* resemble each other in that the first white ring is in the posterior position. This character is given more weight as an indicator of relationships than is given to the more highly variable body pattern characters, and is considered to indicate a close relationship between these forms. The zone of intergradation between *L. z. multicincta* and *L. z. zonata* occupies much of northern California and southwestern Oregon. Whether or not there is a continuous population north into southern Washington (the northernmost verified locality) is not known. The Washington population may have been derived from the Blue Mountains to the east, where mountain kingsnakes are suspected to occur (Johnson, 1939: 2). The more northerly intergradient populations of northern California and southwestern Oregon probably represent a relatively recent northward expansion of the zone of direct intergradation between the two forms, and thus owe their intermediacy not directly to intergradation between *L. z. zonata* and *L. z. multicincta*, but rather to the characteristics of the intergradient population which supplied the dispersants.

The population of the Santa Cruz Mountains (*L. z. multifasciata*) south of San Francisco Bay forms a connecting link between the two extremes of position of the first white ring. All *L. z. multifasciata* from south of this area conform to the anterior position.

To the south, *L. z. parvirubra* was previously considered to be conspecific with *L. z. multicincta* of the Sierra Nevada (Klauber, 1943: 78). This interpretation finds support in a number of other distributions disjunct between the Sierra Nevada and the mountains of southern California. Examples include *Thamnophis elegans elegans*, *Charina bottae*, *Scoloporus gracilus* and the salamander *Ensatinia eschscholtzi* (races *platensis*, *croceater* and *klauberi*). *L. z. parvirubra* was grouped with *L. z. multicincta* on the basis of similar amounts of red on the body; but in the nature of the first white ring, *parvirubra* allies itself with *L. z. multifasciata* rather than with the Sierran type. In view of the great variability observed throughout the species with respect to the amount of red, it is my opinion that the more conservative character, the position of the first white ring, is a truer indicator of relationships.

These observations suggest a pattern of dispersal from a Sierran foothold across the northern end of California and southward along the parallel Sierra Nevada and Coast Ranges. In line with this suggestion, the southern California and northern Baja California snakes may be considered derivatives primarily of the coastal, rather than of the Sierran, complex. It is difficult to picture conditions sufficiently altered to permit migration between the Sierra Nevada and the mountains of southern California that would not permit a far greater volume of exchange with the coastal region to the north.

The invasion of southern California by the north coastal (and Sierran?) prototype must have taken place when conditions were more humid than at present, possibly during a glacial maximum. Following this, increasing aridity restricted the snakes to areas possibly smaller than those now inhabited. The differentiation now evident would have been initiated in all the southern subspecies at about the same time. Each of the different geographic units went its own evolutionary way, proceeding with its own random, seemingly adaptively neutral pattern variation. Alternating arid and humid cycles have allowed some gene exchange between the various populations, but for the most part they have remained separate, a reflection of the remarkable efficiency of even small areas of
unsuited terrain in preventing dispersal of this species.

Genetic drift in small populations is an obvious mechanism suggesting explanation for the apparently randomly fixed variation in the color pattern of the races which inhabit the smallest areas, the races of southern California and Baja California. Adaptive neutrality of the variation has allowed the survival of these widely differing types.

An alternative explanation for the derivation of the pattern of *L. z. herrerai* may be offered. On the basis of area inhabited, hence population size, this race, of all the races of *L. zonata*, could most logically be expected to have acquired its pattern characters by random fixation, inhabiting as it does an island only a little over a mile long. *L. z. herrerai* is phenotypically very similar to *L. getulus californicae* (ringed phase) and occurs in a habitat much more like that of *getulus* than is typical for *zonata* as a whole. It is conceivable that the *getulus* type of pattern is favored by selection in a habitat such as that of *L. z. herrerai* on South Todos Santos Island.

**Summary**

*Lampropeltis zonata* is a complex of seven subspecies extending discontinuously between northern Baja California, México, and the southern border of the state of Washington. The variation in pattern is considerable, and seems to show no consistent association with variation in habitat. The closest interspecific relationship appears to be with *L. doliata gentilis* to the east. Dispersal is presumed to have been southward along the parallel Sierra Nevada and Coast Ranges of California. The snakes of southern California and Baja California have closest relationship with those of the California Coast Ranges. Genetic drift in relatively small populations that have become restricted with climatic change may be responsible for the apparently random nature of the variation.

Two new subspecies from southern California are described and five previously named forms are redefined.

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