

THE COACHWHIP SNAKE, *MASTICOPHIS FLAGELLUM*
(SHAW): TAXONOMY AND DISTRIBUTION¹

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ABSTRACT

The taxonomy and distribution of *Masticophis flagellum* (Shaw) are discussed. The use of the generic name *Masticophis* instead of *Coluber* and the relationship of

the species *flagellum* to the other species within the genus *Masticophis* are briefly considered.

Six subspecies recognized previously by other authors are retained, and *fuliginosus* Cope is resurrected from synonymy for another subspecies. The concept of the subspecies *cingulum* is modified. A discussion of color pattern variation is included under each subspecies heading. The types of variation illustrated by the

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color pattern are discussed, and so are intraspecific relationships.

The variation exhibited by the nonpattern characteristics is summarized and analyzed for sexual, ontogenetic, geographic, and individual significance.

Available information on distribution and habitat preference is reviewed.

INTRODUCTION

The coachwhip snake, *Masticophis flagellum*, is a wide-ranging North American species that exhibits considerable pattern variation. It has not been reviewed in its entirety since Ortenburger's (1928) revision of the genera *Masticophis* and *Coluber*. Ortenburger had approximately 400 specimens of *M. flagellum* available to him; in contrast I have examined more than five times as many. I recognize seven subspecies, three of which have been described since 1928. I have studied variation in most of the characters normally utilized in taxonomic work on snakes at the specific level, with emphasis on color pattern. These characters have been analysed for possible geographic, sexual, ontogenetic, and individual differences.

During the course of this study I have examined 2195 specimens of *Masticophis flagellum* from the following institutional and private collections:

AC	Alabama College
AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
ASDM	Arizona-Sonora Desert Museum
AU	Auburn University
BCB	Bryce C. Brown Collection, Strecker Museum, Baylor University
BYU	Brigham Young University
CAS	California Academy of Sciences
CHM	Charleston Museum
CM	Carnegie Museum
CU	Cornell University
DEH	Donald E. Hahn, private collection
EAL	Ernest A. Liner, private collection
FSU	Florida State University
HC	Howard College
INHS	Illinois Natural History Survey
JFC	Joseph F. Copp, private collection
JPC	Janalee P. Caldwell, private collection
JRD	James R. Dixon, private collection
KLW	Kenneth L. Williams, private collection
KU	University of Kansas Museum of Natural History
LACM	Los Angeles County Museum
LPI	Louisiana Polytechnic Institute

LSUMZ	Louisiana State University Museum of Zoology
MCZ	Museum of Comparative Zoology
MGFCM	Mississippi Game and Fish Commission Museum
MMH	M. Max Hensley, private collection
MISU	Mississippi State University
MSU	Michigan State University
NCSM	North Carolina State Museum
NLSC	Northeastern Louisiana State College
NMSU	New Mexico State University
NSU	Nevada Southern University
NTSU	North Texas State University
OSU	Oklahoma State University
PM	Philip Medica, private collection
RAT	Robert A. Thomas, private collection
SDSNH	San Diego Society of Natural History
SM	Strecker Museum
TCWC	Texas Cooperative Wildlife Collection
TNHC	University of Texas Natural History Collection
TU	Tulane University
UAHC	University of Alabama Herpetological Collection
UAZ	University of Arizona
UCM	University of Colorado Museum
UF	University of Florida Collections
UG	University of Georgia
UIMNH	University of Illinois Museum of Natural History
UM	University of Miami
UMMZ	University of Michigan Museum of Zoology
UNM	University of New Mexico
USL	University of Southwestern Louisiana
USM	University of Southern Mississippi
USNM	United States National Museum
UU	University of Utah

Scale counts were made in accordance with customary methods. Ventrals were counted using the method of Dowling (1951b), and so were scale reductions (Dowling, 1951a). Because of extreme variability in the temporal series, the number of scales on each side of the head was totaled as a single number.

Snout-vent length was measured from the tip of the snout to the posterior edge of the anal plate. Tail length was measured from the posterior edge of the anal plate to the tip of the tail.

Unless otherwise noted, the color pattern descriptions are based on preserved material, although I have made use of whatever living material was available.

Brackets are used in the text to indicate where a qualifying statement of mine has been made within a quotation.

I have used brief synonymies for the sub-

species discussed by Ortenburger (1928) and complete synonymies for those subspecies described since Ortenburger's work.

HISTORICAL SUMMARY

Coluber flagellum was described by Shaw (1802) from a plate in Catesby's "The Natural History of Carolina, Florida and the Bahama Islands." The provenance of the species was given as North America, and Shaw stated that it is "not uncommon in Carolina and Virginia." These states were regarded as the type locality by Ortenburger (1928). In 1823 Say described *Coluber testaceus* from the western portion of the range. Hallowell (1852) described *Psammophis flavigularis* from Cross Timbers, Oklahoma. The specific name *flavigularis* was used by Ortenburger for the western coachwhip, instead of *testaceus*, but most investigators have considered *flavigularis* to be a synonym of *testaceus*. Several subspecies have been described. Stejneger (1893) added *Bascanion flagellum frenatum*, from Mountain Spring, San Diego County, California. *Masticophis flagellum lineatulus* was described by Smith in 1941 from 11 miles north of San Buena Ventura, Chihuahua, Mexico. *Masticophis flagellum ruddocki* was described by Brattstrom and Warren in 1953 from Kern County, California. Lowe and Woodin added a sixth form, *Masticophis flagellum cingulum*, in 1954, based on specimens from Moctezuma, Sonora, Mexico.

Ortenburger (1928) was the first investigator to review the genus, and, in his excellent paper, he recognized three subspecies of *flagellum* (*flagellum*, *flavigularis*, and *frenatum*). He considered *piceus*, a name formerly applied to black individuals of *frenatum*, as a distinct species. But much more material has since accrued and three additional subspecies have been described. It is now possible to outline the range of each race with considerable accuracy, and to delineate the areas of intergradation between subspecies. Also, the considerably greater amount of specimens now available makes it possible to analyze the variation within the species with greater accuracy.

VALIDITY OF THE GENUS *Masticophis*

Considerable controversy exists in the literature as to whether or not the snakes

grouped under *Masticophis* should be considered as generically distinct from the snakes of the genus *Coluber*. In his monograph, Ortenburger (1928) discussed what he considered to be the distinguishing characteristics between *Masticophis* and *Coluber*. These included differences in the number of maxillary teeth, the type of scale reduction formula, the number of ventrals, subcaudals, and supralabials (including the number of supralabials entering the orbit, usually a function of the number of supralabials), certain characteristics of hemipenial structure, and the head width-head length ratio.

The severest critics of the use of the generic name *Masticophis* were Bogert and Oliver (1945). They cited Stuart's (1934) difficulty in deciding whether his new species *ortenburgeri* belonged to the genus *Masticophis* or *Coluber*. Stuart stated that the type specimen agreed with members of the genus *Masticophis* in having a similar scale reduction pattern, but, on the contrary, it agreed with members of the genus *Coluber* in its hemipenial structure. *Coluber ortenburgeri* has recently been shown to be the southernmost representative of and synonymous with *Coluber constrictor oaxaca* (= *C. c. stejnegerianus* auct.) (See Etheridge, 1952; Stuart, 1963; Wilson, 1966). In addition, during the preparation of my paper on Mexican *Coluber* (*op. cit.*), I examined the holotype of *Coluber ortenburgeri* and found it to be somewhat aberrant. The complete scale reduction in this specimen is:

$$\begin{array}{r} 19 \frac{3+4(5)}{3+4(5)} \quad 17 \frac{3+4(70)}{3+4(70)} \quad 15 \frac{6+7(129)}{6+7(139)} \\ \quad \quad \quad 14 \frac{\quad}{+7(129)} \quad 15 \frac{\quad}{\quad} \quad 14 \end{array}$$

This specimen has neither a typical *Coluber* nor a typical *Masticophis* scale row pattern, but it more closely resembles *Coluber constrictor*. Dunn (1933) believed that the specimen of *Coluber oaxaca* (= *C. c. oaxaca*) from Colima, Mexico that he discussed demonstrated a similarity to *Masticophis* in scale row reduction and number of supralabials. As I have stated previously (Wilson, 1966, p. 45), I believe this scale reduction pattern to be aberrant. The number of supralabials (eight) is, indeed, the

same as that seen in *Masticophis*, but eight supralabials is also characteristic of the western forms of *Coluber constrictor* (i.e., *mormon* and *oaxaca*); seven is characteristic of the more eastern forms. The mean number of supralabials increases gradually from east to west. Populations of *Coluber constrictor* in the eastern portions of Louisiana, for example, have a lower mean number of supralabials than those from the western portions of the same state (Wilson, unpublished manuscript). Use of characters exhibited in limited portions of the range of *Coluber constrictor* would not appear to be a valid criterion for demonstrating that *Masticophis* and *Coluber* are congeneric, nor are aberrant characters.

Inger and Clark's (1943) attempt to subdivide the cumbersome genus *Coluber* (*sensu lato*) has also met with criticism. Bogert and Oliver (1945) stated that these authors "attempt to partition the genus *Coluber* (in its broadest sense) on the sole basis of scale reduction patterns." This is not strictly the case because Inger and Clark used the number of supralabials entering the orbit and the presence or absence of enlarged basal spines on the hemipenis as supportive characters. Although I would agree that the subdivision of or the erection of a generic taxon, if based on a single character, is ill advised, I also believe that Inger and Clark's system contributes to a better understanding of the relationships of this group of snakes. As I have stated (Wilson, 1967, p. 269), the genus *Coluber* (*sensu lato*) is an unwieldy assemblage of snakes, many of which are only distantly related to and are even generically distinct from *Coluber constrictor*, the type species of the genus. The range of characters exhibited collectively by the species now grouped in the genus *Coluber* is very wide and indicative of an unnatural grouping. The *Coluber* complex admittedly needs further study, and the relationships of its many components may not become clear until investigations are made on skeletal anatomy, hemipenial structures, blood proteins, and behavior on a world-wide basis. To retain the species of the genus *Masticophis* in the already unwieldy *Coluber* would require inclusion also of the other New World racer genera, i.e., *Dryadophis*, *Drymobius*, *Leptodrymus*, and *Dendrophidion*, which are certainly less distinct from

Masticophis and *Coluber constrictor* than are the Old World *Coluber dorri* and *Coluber dipsas*. For these reasons I continue to use the name *Masticophis* for the whip-snakes in general and for the species *flagellum* in particular.

THE *flagellum* GROUP OF *Masticophis*

In his review of *Masticophis* Ortenburger (1928) divided the genus into two sections, the *taeniatus* group and the *flagellum* group. His *taeniatus* group included *M. aurigulus*, *M. barbouri*, *M. lateralis*, *M. ruthveni* (= *M. taeniatus ruthveni*), *M. schotti* (= *M. taeniatus schotti*), *M. semilineatus* (= *M. bilineatus*), *M. taeniatus girardi*, and *M. taeniatus taeniatus*. This group is not pertinent to the present study and will not be discussed further.

Ortenburger's *flagellum* group included *M. anthonyi*, *M. flagellum flagellum*, *M. f. flavigularis* (= *M. f. testaceus*), *M. f. frenatum* (= *M. f. piceus*), *M. lineatus* (= *M. striolatus*), *M. mentovarius*, and *M. piceus* (= *M. f. piceus*). This arrangement has seldom been challenged, and I see no reason for changing it, except to shift some names because of priorities. Smith (1941), who discussed the Mexican forms of the genus, presented a phylogeny that did not differ significantly from that of Ortenburger insofar as the division of the constituent species into two groups is concerned. Smith, however, suggested that *mentovarius* is similar to the basic stock from which the remainder of the species developed. Ortenburger, on the other hand, postulated that the two groups arose from a "... hypothetical progenitor of the genus *Masticophis*." It is my opinion that a proto-*mentovarius* was not the basic form and that, furthermore, Smith's phylogeny represents the relationships of the species of the genus *Masticophis* at the present time level.

Without adequate paleontological data it is futile to speculate on the age of certain species, but it is more logical to assume a progenitor of the genus that diverged to form two groups: (1) a banded or unpatterned form (the *flagellum* group), and (2) a striped form (the *taeniatus* group). *Masticophis mentovarius* appears to be a derivative of *striolatus* that migrated southward to invade Central and South America. It is likely that the peculiar fusion of the



Figure 1. *Masticophis flagellum flagellum* (CHAS 6722) from Vaiden, Carroll County, Mississippi.

fourth and fifth supralabials is a derived character, inasmuch as all the other members of the genus have two supralabials entering the eye, as do the members of the genus *Coluber*.

A similarity in pattern ties *mentovarius* to *striolatus*. Most likely, another derivative of *striolatus* is *M. anthonyi*, found only on Isla Clarión in the Revillagigedo Island group (Ortenburger, 1928; Brattstrom, 1955). These three species form a compact group that is distinct from all the subspecies of *Masticophis flagellum*, except for *lineatulus*, in having a lineate dorsal pattern composed of a stripe (or a dot in the case of *anthonyi*) on each scale. The pattern of *lineatulus*, however, appears to have been derived separately from that of the *striolatus* subgroup, because the juveniles are typically banded across the neck, as is the case in the young of the other subspecies of *flagellum*. Juveniles of *lineatulus* are identical with juveniles of *M. f. testaceus* in this respect.

COMPOSITION OF THE SPECIES *Masticophis flagellum*

Smith and Taylor (1945) listed six subspecies of *Masticophis flagellum* (five Mexican subspecies and one extralimital form, *M. f. flagellum*). Since that time two additional subspecies (*cingulum* and *ruddocki*) have been described, and two subspecies have been removed. Bogert and Oliver (1945) demonstrated sympatry between *Masticophis striolatus* (= *Coluber striolatus striolatus* of Bogert and Oliver and *Mastico-*

phis flagellum lineatus of Smith and Taylor) and *Masticophis flagellum cingulum* (= *Coluber flagellum piceus* of Bogert and Oliver and *Masticophis flagellum piceus* of Smith and Taylor) in southern Sonora. They also stated that "the snake described by Smith (1943, p. 448) as *Masticophis flagellum variolosus*, if it proves to be valid, should be placed as a subspecies of *Coluber striolatus*." Zweifel (1960), in his study of the herpetofauna of the Tres Mariás Islands, discussed the validity of Smith's *variolosus* and concluded that "... differentiation in number of ventral scales alone is not an adequate basis for the recognition of an endemic insular subspecies. Whether *variolosus* should be recognized or not depends on the significance attached to slight but possibly consistent difference in lip pattern, in the apparent absence of more consistent differences. To recognize the subspecies would place undue emphasis on slight variation in a species not otherwise subject to variations sufficiently consistent for it to be considered polytypic, unless it proves to be conspecific with *M. mentovarius*. Hence, *variolosus* should be relegated to the synonymy of *lineatus*." Webb (1960) presented evidence confirming the specific status of *M. striolatus*. Further confirmation has been presented by Fugler and Dixon (1961) and Smith and Van Gelder (1955).

Thus, *Masticophis flagellum* presently contains six subspecies (*cingulum*, *flagellum*, *lineatulus*, *piceus*, *ruddocki*, and *testaceus*). *Masticophis striolatus* is now recognized as a distinct monotypic species. There remains,

however, the possibility that *striolatus* may be conspecific with *M. mentovarius* (Webb, 1960; Zweifel, 1960).

SUBSPECIES ACCOUNTS

Masticophis flagellum flagellum (Shaw) Eastern Coachwhip

- Coleiber flagellum* Shaw, 1802: 475
Coleiber testaceus: Harlan, 1826: 348
Psammophis flagelliformis: Holbrook, 1842: 11
Masticophis flagelliformis: Baird and Girard, 1853: 98
Masticophis flavigularis: Baird and Girard, 1853: 99 (part)
Herpetodryas flagelliformis: Duméril and Bibron, 1854: 210
Herpetodryas flavigularis: Günther, 1858: 118 (part)
Masticophis flagelliformis testaceus: Jan, 1863: 65 (part)
Bascanium flagelliforme flagelliforme: Cope, 1875: 40
Bascanium flagelliforme testaceum: Yarrow, 1875: 542 (part)
Bascanium flagelliforme: Cope, 1877: 64
Bascanium flagelliforme: Smith, 1882: 636
Coleiber flagelliformis testaceus: Garman, 1883: 43 (part)
Bascanium flagelliformis testaceus: Duméril and Bocourt, 1886: 705
Zamenis flagelliformis: Boulenger, 1893: 389 (part)
Zamenis flagellum flagellum: Cope, 1900: 789 (part)
Zamenis flagelliforme: Ditmars, 1912: 218
Coleiber flagellum flagellum: Stejneger and Barbour, 1917: 79 (part)
Masticophis flagellum flagellum: Ortenburger, 1923: 2

Holotype.—None designated. The original description by Shaw (1802) consisted primarily of information supplied by Catesby (1731-43). Shaw stated "it is a native of North America, and not uncommon in Carolina and Virginia." Schmidt (1953) restricted the type locality to Charleston, South Carolina.

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a dark to very dark brown anterior dorsal coloration and a tan to dark brown posterior dorsal coloration. The venter is dark brown anteriorly, grading to cream posteriorly (Fig. 1).

Range.—Southeastern United States from North Carolina south to and including all of Florida, west to eastern Texas, north to Missouri and southern Illinois, including the eastern half of Oklahoma and Kansas (Fig. 2).

Description.—The only information given

by Shaw (1802) was that this snake "is a very long and slender species, measuring from four to six feet or more in length: its color is a uniform dusky brown, palest beneath."

The following color pattern description is from a live female specimen (LSUMZ 9679) collected beside the Red River at the south city limits of Alexandria, Rapides Parish, Louisiana and measuring 1029 mm in head-body length. The anterior portion of the dorsum is very dark velvety brown. This color grades into pinkish brown on the posterior portion of the body and tail. Along the middle of the body, at intervals of about 100 mm, are a series of light bands about 40 to 50 mm long. They are orange brown dorsally and brownish gray laterally. There are about three or four of these bands, the last of which gives rise to a middorsal stripe-like area that is somewhat lighter than the lateral area. The venter is grayish brown on the neck with light orange flecks grading to cream posteriorly with an overtone of orange flecks. This orange coloration is darker on the lateral edges of the ventrals. The underside of the tail is pinkish orange. The head is dark velvety brown above. There is an orange spot on the right parietal. The lateral part of the head is grayish brown anteriorly, becoming brown on the temporals. There is a light spot on the upper preocular. The chin is grayish brown with white blotches on all scales. There are a few orange flecks on the gulars. The iris is dark brown except for an orange ring around the pupil.

Discussion.—Meristic and mensural data for this subspecies, based on 241 males and 207 females, may be summarized as follows: supralabials 7 to 9, infralabials 8 to 13, preoculars 2 or 3, postoculars 1 to 3, loreal 0 to 3, ventrals in males 188 to 212, ventrals in females 186 to 207, subcaudals in males 100 to 122, subcaudals in females 91 to 123, dorsal scale rows 19-17-11 to 19-17-15. Body length in males of all ages ranges from 291 to 1600 mm, in females of all ages 331 to 1520 mm. Total length in males of all ages ranges from 373 to 2074 mm, in females of all ages 436 to 1983 mm. Tail length/total length ratios in males ranges from 0.220 to 0.275, in females 0.217 to 0.300.

There is a considerable amount of pattern

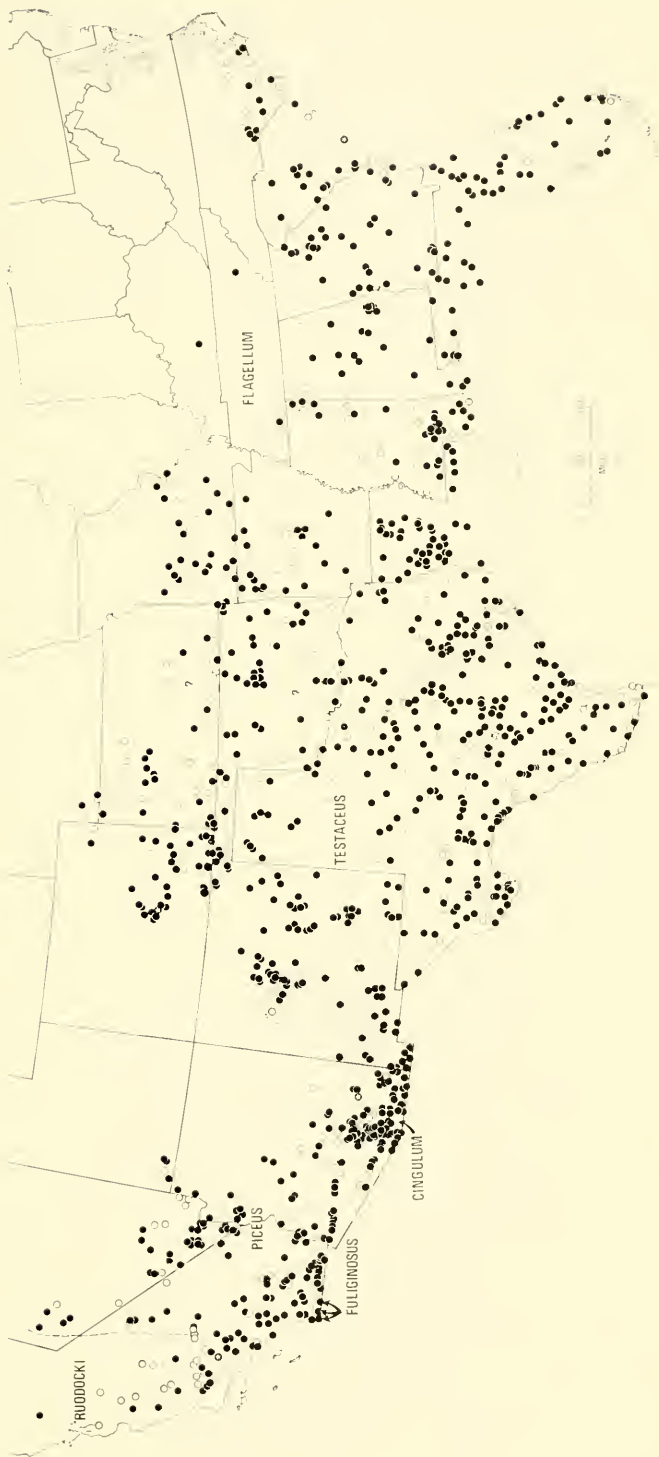


Figure 2. Distribution of *Masticophis flagellum* in the United States. Solid circles represent localities for specimens examined, open circles literature records, and stars type localities.

variation in the nominate subspecies. This subspecies exhibits an ontogenetic color change. Juveniles of *M. f. flagellum* have a pattern similar to the young and adults of *M. f. testaceus*. The dorsum is some shade of tan with narrow brown to dark brown bands on the neck and forebody, which diminish gradually in intensity posteriorly. The head is light brown or tan, with white outlining the dorsal scales, and with a dark brown area on the posterior portion of the internasals and prefrontals, on most of the supraoculars and frontal, and on the anterior, lateral, and posterior portions of the parietals. The side of the head is light brown to tan with cream spots on most scales. The chin is cream, with light brown pigment between the junction of the infralabials and the chin shields. The venter is uniform cream, except for a double row of brown spots on the neck.

As the snake increases in size the dorsal pattern on the anterior part of the body becomes uniformly dark as the result of a darkening of the existing brown or tan coloration on each scale and the invasion of the pale lateral areas of each scale by the same color. The dorsal surface of the head becomes uniformly dark by loss of the white scale borders and by a darkening of the light areas on the head. The side of the head becomes darker in an anterior to posterior direction. The chin becomes uniformly dark by the deepening of the existing brown color and a progressive invasion of that color into the light cream areas. The spots situated on the anterior portion of the venter begin to darken and enlarge. As the snake grows older and larger, these spots fuse together and still later they fuse with the lateral extension of the dorsal ground color to form the uniformly dark, anterior ventral coloration of the adult.

This description of the ontogenetic color pattern changes in *flagellum* is generalized; some individuals of this subspecies may reach a certain level in the development of the color pattern at a smaller or larger size than others. For example, in LSUMZ 16772 from Caddo Parish, Louisiana (625 mm in snout-vent length), and LSUMZ 16773 from Sabine Parish, Louisiana (621 mm), the former is much paler dorsally than the latter. The juvenile markings are still evident on the head of LSUMZ 16772 and the

spotting on the venter is more clearly defined. These two snakes were collected only a few miles apart.

A juvenile *flagellum* (OSU 483) with a curious pattern is available from Lake Carl Blackwell in Payne County, Oklahoma. This specimen, which measures 540 mm in total length, entirely lacks the typical neck bands. Instead, each of the dorsal scales, especially on the anterior portion of the body, has a concentration of darker pigment toward the center of the scale, giving the impression of a broad, diffuse stripe on each dorsal scale row.

The dorsal coloration of adults of *Masticophis f. flagellum* ranges from a completely pale tan dorsum with narrow, dark brown crossbands to one almost completely black dorsally. The most widespread type of coloration has been described above.

There are disjunct populations in northern and central Florida and southern Georgia, the adults of which are characterized by a pale tan dorsum with narrow, dark brown crossbands. A specimen of this phase (LSUMZ 18527) that I collected on 30 March 1968 on St. George Island, Franklin County, Florida, was tan dorsally with very dark brown pigment on the posterior edges of the internasals and prefrontals, the posterior one-half of the frontal, most of the supraoculars except for the extreme anterior portion, and the anterior and posterior portions of the parietals. There is some dark brown pigment on the neck arranged in the form of indistinct bands. The first band is the best developed and is about four scales wide. Ventral coloration is cream with a triangular extension of the dorsal ground color onto the lateral edges of the ventrals and some tan and dark mottling on the neck. The chin is white, heavily mottled with tan and dark brown pigment. The specimen is an adult male, measuring 1280 mm in snout-vent length.

This color phase is known from the following localities in Florida (Fig. 4): Alachua County, 1 mi. NE Archer (UF 9656); Clay County, 3 mi. S Middleburg (UIMNH 25699), Gold Head State Park (TCWC 10781); Duval County, near Jacksonville (UMMZ 67807); Escambia County, Pensacola (MCZ 98); Franklin County, St. George Island (LSUMZ 18527); Gulf County, 2 mi. S Wewahatchka (UF 6546);



Figure 3. Distribution of *Masticophis flagellum* in Mexico. Explanation as for Figure 2.

Jackson County, 1.5 mi. W Campbellton (AU 2037); Lake County, Tavares (UF 113), Leesburg (UF 2456); Leon County, east of Tallahassee (FSU 116); Liberty County, 6 mi. S, $\frac{1}{2}$ mi. E Bristol (UF 10083-1, 10083-2); Marion County, Fort McCoy (AMNH 23100); Orange County, Orlando (SDSNH 36740); Putnam County, road between Interlachen and Grandin (MCZ 67179); Washington County, 1 mi. N Ebro (LSUMZ 16860). In addition, Charles W. Myers (*in litt.*) informed me that two similar pale-phased specimens of *flagellum* escaped from him at the two following localities: Franklin County, 6 mi. S, $9\frac{1}{2}$ mi. W Carrabelle, near Green Point, and Liberty County, 18 mi. NNW Carrabelle on Florida Hwy. 67. The following records are available from Georgia: Baker County, near Newton, Pineland Plantation (CM 40196-7), 3 mi. N Newton (BYU 22188), Itchwa Plantation (UG 206); Baldwin County, Milledgeville (MCZ 286); Brantley County, 20 mi. SE Waycross (UMMZ 92793); Decatur County, 4 mi. SW Bainbridge (INHS 7612); Long County,

10 mi. SE Thomasville (TCWC 11945), 1 mi. S Thomasville (TCWC 11943), 3 mi. NW Metcalf (TCWC 11944); Wilcox County, Benhill Fishery (UG 262). Charles W. Myers also informed me (*in litt.*) that he saw a DOR specimen of this phase $9\frac{1}{2}$ mi. N, 5 mi. W Bainbridge on U.S. Hwy. 27, Decatur County, Georgia. He stated that the specimen "was also uniformly light colored but probably not as pale as those from Florida . . ." In addition, I have seen one specimen of this phase (NCSM 1966) from Rose Hill, Duplin County, North Carolina.

Even excluding this pale phase, the dorsal coloration of adults tends to be paler in Florida than in other portions of the range (Fig. 5); the darkest animals occur in Missouri, northwestern Arkansas, and eastern Oklahoma (Fig. 6). In dealing with an animal that has a color pattern consisting of an evenly graded change in color from one end of the body to the other it is difficult to devise an objective system for evaluating this color pattern. Variation in *M. f. flagellum*, therefore, is more difficult to discuss

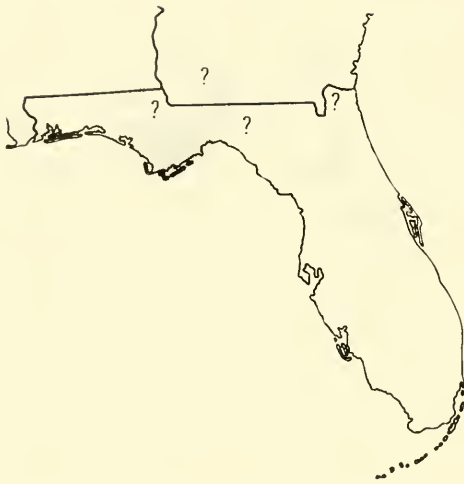


Figure 4. Distribution of the pale phase of *Masticophis flagellum flagellum* in Florida and surrounding areas.

than that of any other subspecies. In recording color notes on specimens, I have made an arbitrary judgment regarding the intensity of the color present and the extent to which the anterior portion of the body is covered by dark pigment.

An estimate of the amount of dark pigment was made on the basis of a fraction of the total body length, i.e., 1/4, 1/3, 1/2, 2/3, or 3/4. In terms of this crude method the following statements can be made (Table 1). Specimens from Florida are pre-

TABLE 1

Percentage of specimens of *Masticophis f. flagellum* exhibiting various amounts of dark pigment on the anterior portion of the body. The amount is expressed as a fraction of the total length.

Area	Fraction of Body Covered by Dark Pigment				
	1/4	1/3	1/2	2/3	3/4
Florida	68	16	16	0	0
North and South Carolina	12	71	17	0	0
Georgia, Alabama, and Mississippi	26	39	30	0	5
Louisiana, Kentucky, Tennessee, and eastern Texas	0	20	50	20	10
Arkansas, eastern Oklahoma, eastern Kansas, and Missouri	0	5	48	33	14

dominantly pale, usually one fourth or less of the body is covered with dark pigment. The extent of dark pigment on the body increases clinally from Southeast to northwest, those specimens from Arkansas, Oklahoma, Kansas, and Missouri being darkest. In addition, there is also a tendency for specimens from the southeastern and eastern portions of the range to be tan on the posterior portion of the body and for those from the northwestern and western portions of the range to be reddish brown to dark reddish brown on the posterior portions of the body (Table 2). The color of the pos-



Figure 5. *Masticophis flagellum flagellum* from Sanibel Island, Lee County, Florida.

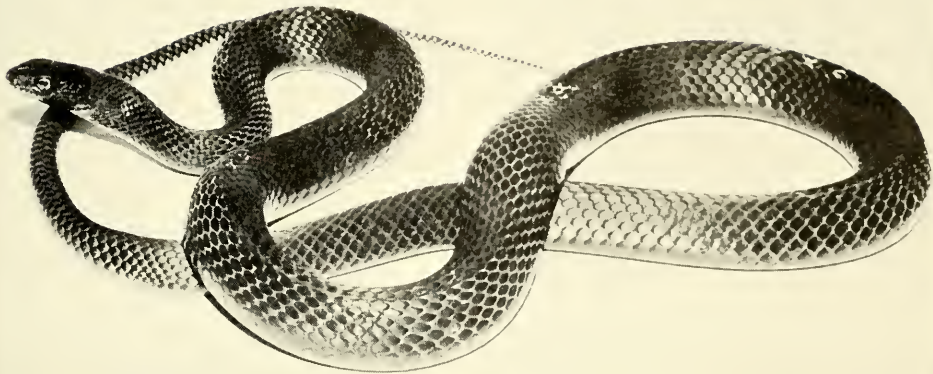


Figure 6. *Masticophis flagellum flagellum* from Salina Creek, 2 miles S Salina, Mayes County, Oklahoma.

terior portion of the body normally ranges from tan through light brown, brown, and dark brown to black. I have seen only one specimen, however, that was black posteriorly (OSU 3244 from Okmulgee County, Oklahoma).

Occasional specimens throughout the range of *flagellum* have a series of light bands across the body (Fig. 7). These bands range from four to ten scales in length and range in number from one to eight in any one snake. Some specimens (especially several from Mississippi, Louisiana, North

Carolina, and eastern Texas) have very distinct bands that are tan in color in contrast with the dark to very dark brown areas that surround them and extend completely across the dorsum. These bands may be either unicolorous or bisected transversely by a narrow dark brown band through the center. Other specimens show only slight evidence of this light banding, which is confined to the mid-dorsal and one or two paravertebral rows of dorsal scales. I have seen banded specimens from every state within the range of *flagellum* except South Carolina, Kentucky, and Illinois (only one adult from each of the last two states). There is no geographical continuity to this type of pattern, inasmuch as specimens from the same general area may be banded or nonbanded. For example, in a series of twelve adults from Bladen, Hoke, Richmond, and Scotland counties in south-central North Carolina, eight specimens are banded and four are not.

My interpretation of the zone of intergradation between *M. f. flagellum* and *M. f. testaceus* is at variance with that given by Brown (1950). Examination of the material from eastern Texas demonstrates that the southern portion of the intergrade zone (Fig. 2) is fairly wide, as indicated by Brown, but lies farther to the east. My reason for this conclusion is that specimens from Colorado County (KU 1459, 1463), and Matagorda County (MCZ 19895,

TABLE 2
Percentage of specimens of *Masticophis f. flagellum* exhibiting various colorations of the posterior portion of the body.

Area	Tan	Light brown	Brown	Dark brown
Florida	91	9	0	0
Georgia	58	31	11	0
Alabama	41	41	18	0
Mississippi	83	13	4	0
South Carolina	80	20	0	0
Kentucky, Tennessee, and Illinois	75	25	0	0
Louisiana	47	16	35	2
Eastern Texas	19	33	31	17
Arkansas	19	25	37	19
Eastern Oklahoma	2	28	42	28
Eastern Kansas	0	66	17	17
Missouri	10	19	52	19

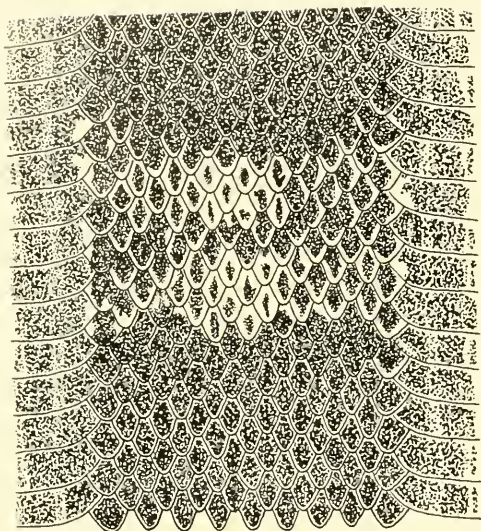


Figure 7. Pattern at midbody of *Masticophis flagellum flagellum*, (CM 24649) from 1.7 miles S Boles, Scott County, Arkansas.

UIMNH 28508, USNM 32770-71) show no approach to *flagellum* in coloration. Also, I have seen three specimens from Galveston Island, two of which (UIMNH 25811, UNM 8849) are typical *testaceus* whereas the other (UIMNH 28510) shows some influence from *flagellum*. Specimens from Bell County, from which Brown listed one specimen with no specific locality, are typical *testaceus* (KU 72914, SM 7009 and 7033, UNM 9207). Another specimen (KU 72915) from Bell County may show some influence from *flagellum*. On the eastern edge of the intergrade zone two specimens (TCWC 196, TNHC 33876) from Harris County are intergrades and two others (ANSP 10871, LSUMZ 14146) show no approach to *testaceus*. Most of the 14 specimens from Brazos County that I have examined are *flagellum*, but five (TCWC 195, 2482, 4751, 14522; UAZ uncatalogued) show influence from *testaceus*. North of Dallas and Tarrant counties the zone of intergradation apparently becomes very narrow. I have seen a single specimen from Wise County (USNM 83127), most likely the same specimen examined by Brown, and I agree with him that it is a *testaceus* showing no approach to *flagellum*. I have been fortunate in having available a series of recently collected specimens from

Denton County. All four adults from this county (NTSU 193, 238, 268; TNHC 26773) definitely have a *flagellum* pattern with no influence from *testaceus*. One juvenile (NTSU 223) is unquestionably a *flagellum* as it has already begun development of the typical adult pattern of this subspecies. Two other juvenile specimens (NTSU 186, 207) look like *testaceus*. Neither specimen, however, has the dark head markings of juvenile *flagellum*. I do not know if juveniles of the two races can be distinguished in an area of intergradation.

The zone of intergradation between *flagellum* and *testaceus* in Oklahoma and Kansas is largely conjectural. A single specimen (KU 8389) from Love County, Oklahoma, is a *flagellum*. I have seen no specimens between this county and Payne County, Oklahoma, to the north. Most of the specimens I have seen from Payne County are *flagellum*, but four (MCZ 61175; OSU 482, 485-86) show influence from *testaceus*. The sample from Noble County to the north includes some of the darkest specimens of *flagellum* that I have examined. I have seen no intergrade specimens from Kansas, and the zone of intergradation that I depict (Fig. 2) is based on Smith (1950).

The zone of intergradation follows approximately the ecotone between the pine and hardwood forests of eastern Texas and the prairie and hardwood forests of east-central Texas (Austroriparian and Texan biotic provinces of Raun, 1965). According to Raun the major trees of the Austroriparian biotic province include longleaf pine (*Pinus palustris*), loblolly pine (*Pinus taeda*), yellow pine (*Pinus echinata*), post oak (*Quercus stellata*), blackjack oak (*Quercus marilandica*), red oak (*Quercus falcata*), sweetgum (*Liquidambar styraciflua*), and wax myrtle (*Myrica cerifera*). The major trees of the Texan biotic province are post oak, blackjack oak, and hickory (*Carya* spp.), and mesquite (*Prosopis juliflora*), a recent invader.

Masticophis flagellum testaceus (Say)
Western Coachwhip

Coluber testaceus Say, 1823: 48

Psammophis flavigularis Hallowell, 1852: 178
(type, ANSP 5388, Cross Timbers, Oklahoma)

Masticophis flavigularis: Baird and Girard, 1853: 99 (part)

Herpetodryas flagelliformis: Günther, 1858: 118 (part)
Coryphodon testaceus: Günther, 1858: 108
Masticophis testaceus: Baird, 1859: 43
Masticophis flagelliformis testaceus: Jan, 1863: 65
Masticophis flagelliformis testacea: Jan, 1867: livr. 20, pl. 6, fig. 2
Bascanium flagelliforme testaceum: Yarrow, 1875: 542 (part)
Bascanium flagelliforme bicinctum Yarrow, 1883: 153 (type, USNM 11814, Old Fort Cobb, Texas)
Coluber flagelliformis testaceus: Garman, 1883: 43 (part)
Bascanium flagelliformis: Duméril and Bocourt, 1886: 705 (part)
Zamenis flagelliformis: Boulenger, 1893: 389 (part)
Zamenis flavigularis: Günther, 1895: 120 (part)
Bascanium flagelliforme: Dugès, 1896: 481
Zamenis flagellum flagellum: Cope, 1900: 799 (part)
Bascanium flagellum: Bailey, 1905: 46
Bascanium flagellum frenatum: Bailey, 1913: 35
Coluber flagellum flagellum: Stejneger and Barbour, 1917: 79 (part)
Masticophis flagellum flavigularis: Ortenberger, 1923: 2
Coluber flagellum picus: Van Denburgh, 1924: 217

Holotype.—Lost. Originally in the collection of the Academy of Natural Sciences of Philadelphia. Type locality: junction of Turkey Creek with the Arkansas River, 12 mi. W Pueblo, Pueblo County, Colorado (Maslin, 1953).

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a light tan or light brown (Fig. 8) to pinkish red dorsum with darker narrow crossbands on the neck and a double row of dark spots on the otherwise immaculate cream belly.

Range.—South-central United States from western Kansas, extreme southwestern Nebraska, and eastern Colorado, south through eastern New Mexico and all of Texas except for the eastern pine forest. In Mexico the western coachwhip occurs in eastern Coahuila, Nuevo León, Tamaulipas, eastern San Luis Potosí, and extreme northern Veracruz (Figs. 2 and 3).

Description.—The following description is based on LSUMZ 18688, an adult female from 10 miles SE Colorado Springs on the grounds of Fountain Valley School, El Paso County, Colorado, collected 18 May 1967 by Robert M. Stabler. This specimen is from relatively near the type locality. Scutellation: supralabials 8-8, 4th and 5th entering the

orbit; infralabials 11-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 6-6; scale reduction pattern

$$\begin{array}{r} 19 \frac{3+4(9)}{3+4(10)} \quad 17 \frac{3+4(121)}{3+4(116)} \\ 15 \frac{7+8(134)}{7+8(131)} \quad 13 \frac{7=7+8(138)}{7+8(131)} \\ 14 \frac{7+8(141)}{\quad} 13; \end{array}$$

ventrals 197; tail incomplete. Head-body length 1159 mm.

The dorsum is Dragon's-blood Red (color terminology based on Ridgway, 1912) on the nape grading to Light Coral Red posteriorly. The dark crossbands on the neck are near Liver Brown. The venter is Light Coral Red. The spots on the ventral surface of the neck are Dragon's-blood Red, the remaining spots are yellowish cream. The top of the head is near Hay's Russet (reddish brown). The anterior edge of each dorsal head scale is lighter (pink). The side of the head is reddish brown and the temporals are outlined with pink. A cream spot is present on the upper preocular. The chin is white with mustard yellow and reddish orange blotching.

Discussion.—Meristic and mensural data for this subspecies, based on 365 males and 313 females, may be summarized as follows: supralabials 7 to 9, infralabials 8 to 12, preoculars 2 or 3, postoculars 1 to 3, loreal 1 to 2, ventrals in males 173 to 204, ventrals in females 180 to 203, subcaudals in males 95 to 121, subcaudals in females 93 to 117, dorsal scale rows 19-17-12 to 19-17-15. Body length in males of all ages ranges from 263 to 1480 mm, in females 279 to 1270 mm. Total length in males of all ages from 375 to 1780 mm, in females 376 to 1655 mm. Tail length/total length ratios in males range from 0.195 to 0.272, in females 0.224 to 0.272.

Maslin (1953) noted the presence of red individuals of *Masticophis flagellum* in the Arkansas River Valley of eastern Colorado. He stated that this phase occupied a distinct area in Colorado and demonstrated that the name *Coluber testaceus* Say, 1823, was applicable to this form. Prior to this date,

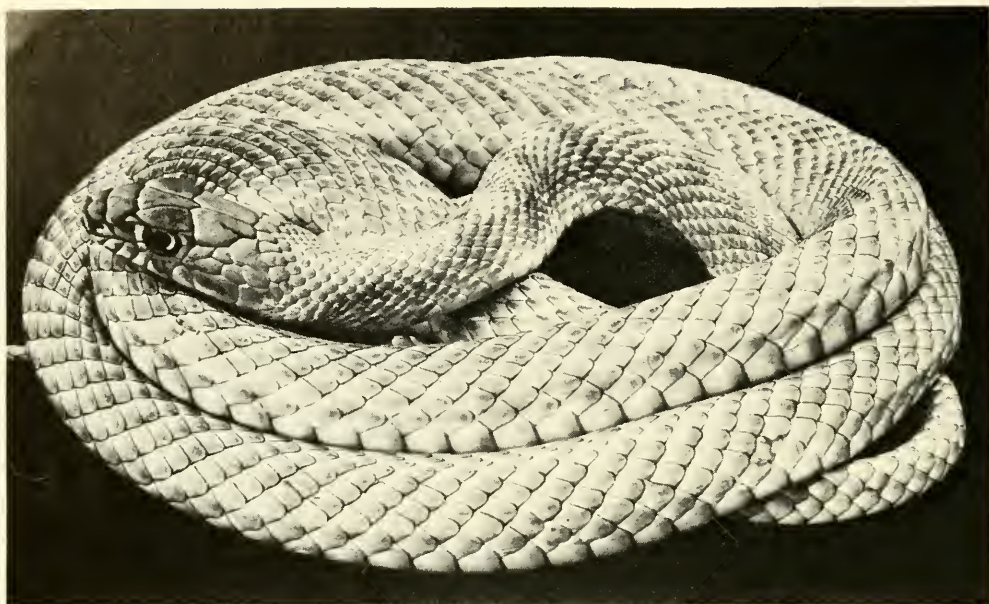


Figure 8. *Masticophis flagellum testaceus* (LSUMZ 12878) from Meade County State Lake and Park, Meade County, Kansas.

however, Schmidt and Smith (1944) and Jameson and Flury (1949) had noted the presence of red specimens of *Masticophis flagellum* in Trans-Pecos Texas. Schmidt and Smith (*loc. cit.*) stated "the red racer is a familiar snake on the desert areas surrounding the Chisos [Mountains]." Jameson and Flury (*loc. cit.*) also stated that "two of our specimens have a distinct reddish color anteriorly and ventrally while another is dark red." They noted, however, that "other specimens show the more typical yellow-tan dorsal color." Minton (1959) and Axtell (1959) likewise noted the presence of reddish-colored whipsnakes in the Big Bend National Park and the Black Gap Wildlife Management Area in Brewster County, Texas.

Recently, I became aware of a similar population of red *testaceus* in eastern New Mexico. I have seen specimens from ¼ mile N Logan (JRD 9518) and the vicinity of Tucumcari (UAZ uncatalogued), Quay County, 10 miles NW Ramon (UNM 172) and 8 miles ENE Vaughn (JRD 9519), Guadalupe County, and about 65 miles NW Roswell, Lincoln County (NMSU 2213). I examined the University of Arizona specimen just a few days after it was preserved.

The dorsum was reddish orange with about ten narrow darker bands on the neck and forebody. The venter was cream with a light reddish orange overtone and a double row of indistinct reddish orange spots on the neck.

The existence of these disjunct populations (Fig. 9) of reddish-colored individuals in eastern Colorado, eastern New Mexico, and western Texas, and the presence of normally pigmented individuals in at least the Trans-Pecos populations, makes Maslin's (1953) arrangement untenable. The name, therefore, of the wide-ranging tan form (as well as the red phase of this subspecies) should be *Masticophis flagellum testaceus* (Say).

The factors responsible for the existence of these red whipsnakes in at least three disjunct areas remain obscure. The shortgrass prairie of eastern Colorado and eastern New Mexico, and the desert scrub and barren flats of the Big Bend region would seem to have little in common. Thus, the occurrence of the red color phase seems not to be correlated with any vegetation type.

Considering the disjunct nature of the range of the red populations, there is no alternative to recognizing them as represent-

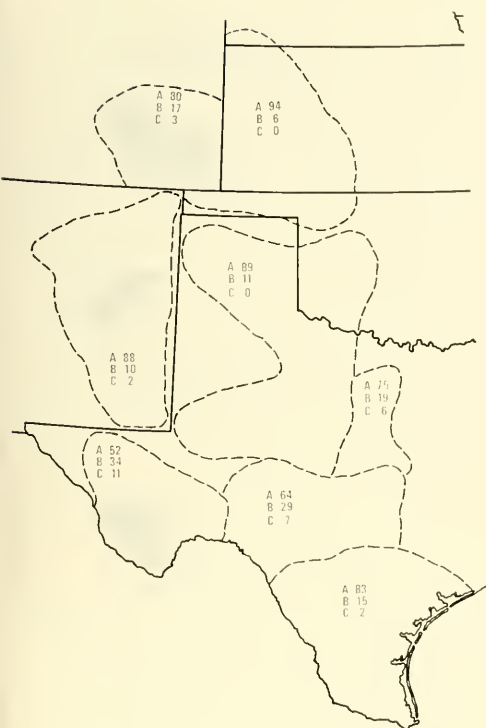


Figure 9. Distribution of the phases of *Masticophis flagellum testaceus* in the United States. Striped areas indicate the range of the red phase and the numbers within the areas outlined by a dashed line are the relative percentage values of the three pattern types of *M. f. testaceus*.

ing a color phase of the subspecies *testaceus*. The exact limits of the range of this form are difficult to plot inasmuch as the red coloration fades in preservative to the tan of typical *testaceus*. Maslin (1959) listed specimens from Baca, El Paso, Fremont, Kiowa, Las Animas, Otero, and Prowers counties, all in southeastern Colorado. In addition, Maslin (*in litt.*) stated that they occur in Bent County. In New Mexico it is known from the three counties listed above. In Texas it is found in Presidio and Brewster counties (Fig. 9).

In contrast to the pink or red coloration, the tan coloration occurs virtually throughout the range. A snake with this type of coloration was described by Hallowell (1852) as *Psammophis flavigularis*. The name *flavigularis* was used for the western coachwhip by Ortenburger (1928), who

thought that Say's (1823) description of *Coluber testaceus* as a "pale sanguineous or testaceous" snake too uncertain to warrant the use of this name. Klauber (1942, p. 93, footnote) expressed a contrary opinion, however, when he stated, "I cannot see by what line of reasoning the name *testaceus* is not applicable to this subspecies [the western coachwhip]. At the time the type specimen was collected (about July 18, 1820) the Long Expedition was at the foot of the Rocky Mountains, toward the headwaters of the Arkansas River. The description, though brief, fits no other snake found in that region. It does not fit the prairie racer, usually referred to as *C. f. flavigularis*, and this snake does occur in that vicinity. I am therefore of the opinion that the prairie subspecies should be known as *Coluber flagellum testaceus* Say, 1823."

Ortenburger (1928) noted three basic types of coloration in *M. f. testaceus*. These were: "(1) a very light brown ground color with no indication of a pattern; (2) the same general light brown ground color with numerous narrow, darker crossbands (two to three scales in width), which extend for a considerable portion of the body length; (3) few wide, dark crossbands (ten to fifteen scales in width) on either a light or dark brown ground color." Ortenburger further noted (p. 102):

"Variation in color and pattern is probably greater in this form than in any other member of the genus. When the actual distribution of the types of pattern was studied, it was found that there is a definite relation between the types of pattern and distribution. To the east throughout the region between the ranges of *flagellum* and *flavigularis* it was noticeable that there is a much greater number of specimens which possess the pattern composed of a few wide stripes. Toward the center of the range and south the unicolor light form is more numerous; to the west this again is gradually replaced by the form with many narrow stripes. Southeastern Texas seems to be the only region which does not hold to this type of distribution, as here one finds (if we can trust the locality records) a veritable mixture of all three forms. At present it does not seem that these forms should

be considered as distinct, since there are no structural characters which will support the color pattern differences, and it is believed that the locality records for southeastern Texas, if accurate enough, would show that these forms are found in distinct habitats. While lack of data at present precludes the possibility of determining definitely what it is that actually causes these differences of color pattern, there can be no doubt that definite relations of pattern to environment will be shown when the necessary data are available."

My data suggest a somewhat different interpretation. Contrary to what Ortenburger contended, the three color pattern phases of *testaceus* do not occupy discrete areas within the total range of the subspecies. Figures 9 and 10 show that the narrow-banded phase (A) is by far the most common in all areas within the range. The incidence of occurrence of this pattern type ranges from 52% to 94%. It is highest in Kansas and lowest in Trans-Pecos Texas. The incidence of the unicolor phase (B) ranges from 6% to 34%. It is lowest in Kansas and highest in Trans-Pecos Texas. The incidence of the widebanded phase (C) ranges from 0% to 20%. No specimens of this phase were found in the material from Kansas, Nebraska, Oklahoma, or the panhandle of Texas. The percentage of this phase is highest in Coahuila and Nuevo León. There are no areas other than the ones mentioned above where all three of the phases fail to occur. All three phases were present in several collections from a single county. All three pattern phases undoubtedly do occur in the red phase of this subspecies also, however, I have not seen unicolor specimens which were red at the time of examination. I have seen unicolor specimens from within the ranges of the red phase and these specimens may have been red in life.

The following is a description of the color pattern of the narrow-banded phase (based on notes made on a living specimen, now in the private collection of Janalee P. Caldwell, collected 5.8 miles NW Cotulla on Hwy. 468, LaSalle County, Texas). The dorsum is tan with a slight pink wash on the nape. The neck bands are brown, 1 to 1½ scales wide and separated by 2½ to 3 scales. The venter is cream (light yellow on

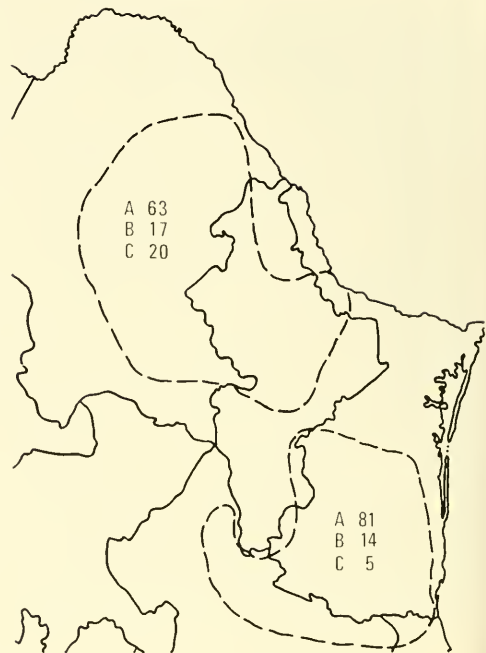


Figure 10. Percent frequency of the three pattern types of *Masticophis flagellum testaceus* in Mexico.

neck) with a double row of light brown spots on the neck. The head is tan dorsally, the scales outlined with white. The lateral area of the head is also tan with light yellow blotching on some of the scales. The chin is white with light brown blotching.

The unicolor phase is uniform light tan dorsally and cream ventrally with a double row of brown spots on the neck and forebody.

The following description is of the widebanded phase (based on TNHC 30448 from 4 miles SSW Cuatro Ciénegas, Coahuila, Mexico; Fig. 11). The dorsum is tan with about 6 brown bands, 12 to 14 scales in width. Each of these long brown bands has several narrower, darker bands within it. The throat is dark brown and there is a double row of brown spots extending posteriorly from this area. The posterior portion of the venter is cream. The chin is dark brown with cream spotting.

I can find no basis for Klauber's (1942, p. 93) statement that "*C. f. flavignularis* . . . tends to produce black (especially anteriorly) specimens in parts of New Mexico

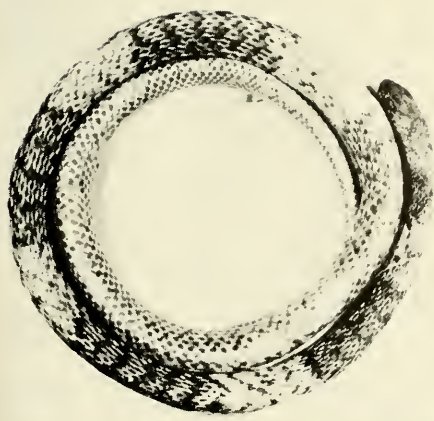


Figure 11. *Masticophis flagellum testaceus* (TNHC 30448) from 4 miles WSW Cuatro Ciénegas, Coahuila, Mexico.

and Oklahoma . . . ” Dr. Klauber stated (*in litt.*) that although he had no memory of these specimens, perhaps some note of this characteristic might have been made on his original data sheets that I sent me. Upon looking through his data I find no mention of any *testaceus* from Oklahoma having this coloration. Two specimens, however, which may have been in the University of New Mexico collection (the designation used for the specimens is “N.M.,” no numbers are given) from Bernalillo County, New Mexico, are described as “grayish black” and “light brown, somewhat darker on the head.” I have examined the entire University of New Mexico collection and have seen no specimens fitting such descriptions. Possibly fading may have taken place as it often does in snakes that have long been preserved.

Masticophis flagellum lineatulus Smith
Lined Whipsnake

Bascanium flagelliforme testaceus: Cope, 1886: 284 (part)
Masticophis flagellum flavigularis: Ortenburger, 1928: 102 (part); Dunkle and Smith, 1937: 4; Gloyd and Smith, 1942: 233
Masticophis flagellum lineatulus Smith, 1941: 394, 1943: 446; Taylor, 1944: 185, 1949: 170, 1952: 811; Smith and Taylor, 1945: 95, 1950: 327; Brown, 1950: 168; Schmidt, 1953: 189; Stebbins, 1954: 495, 1966: 150; Conant, *et al.*, 1956: 12, 1965: 18; Grant and Smith, 1959: 55; Cochran, 1961: 196; Fowle, 1965: 71

Holotype.—USNM 105292. Type locality: 11 miles N San Buena Ventura, Chihuahua, Mexico.¹

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a tan or light gray dorsum with each dorsal scale on the anterior portion of the body having a central longitudinal dark streak (Fig. 12). The posterior portion of the venter and the underside of the tail are salmon pink (this color does not fade in preservative).

Range.—Extreme southwestern New Mexico and southeastern Arizona south through most of Chihuahua (except the southwestern portion), southwestern Coahuila, eastern Durango, northern Zacatecas, and western San Luis Potosí (Figs. 2 and 3).

Description of Holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 9-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 7-8; scale reduction pattern

$$\begin{array}{rcl} & 3 + 4 \text{ (11)} & 3 + 4 \text{ (119)} \\ 19 \frac{\quad}{3 + 4 \text{ (13)}} & 17 \frac{\quad}{3 + 4 \text{ (121)}} & \\ & 7 + 8 \text{ (120)} & 7 + 8 \text{ (142)} \\ 15 \frac{\quad}{\quad} & 14 \frac{\quad}{\quad} & \\ & 6 + 7 \text{ (173)} & \\ 13 \frac{\quad}{\quad} & 12; & \end{array}$$

ventrals 195; tail incomplete. Body length is 1616 mm (Smith reported 1481 mm, apparently in error), the incomplete tail measures 335 mm.

Smith (1941) described the color pattern of the holotype as follows: “Head light yellowish brown, darker toward posterior sutures; sides of head light yellowish brown, with a lighter area in the preocular, loreal, nasal and rostral; a dark, rounded spot in center of nasal [I find this spot to be in the rostral, not the nasal]; supralabials white below a line about even with posterolateral border of seventh labial and middle of subocular labials.

“Dorsal ground color light yellowish brown, becoming more reddish toward middle of body, posteriorly mostly salmon red; all anterior dorsal scales with a central longitudinal black streak, which becomes

¹ Original description stated “south” (Cochran, 1961, p. 196).

more spot-like on scales in middle of body, barely indicated on posterior scales, as the black spots become less distinct, the red areas become more distinct, the posterior scales being mostly red (with a little black near tip), with a white (cream) base; dorsal surface of the tail is even more strongly marked with salmon red.

"Posterior edge of mental and broad areas near the sutures between the infralabials and chin shields, black-marked brown; a double row of black spots beginning with anterior ventral scales; posteriorly these spots becoming mixed with red and soon mostly red and very little black; anterior ground color of belly yellow, this color extending onto lower dorsal scale rows; toward middle of belly this color is largely replaced by salmon red, and posteriorly the belly is entirely red, with the double row of black spots faintly indicated; ventral surface of tail mostly red, the bases of the scales lighter (cream)."

Discussion.—Meristic and mensural data for this subspecies; based on 29 males and 20 females, may be summarized as follows: supralabials 8 or 9, infralabials 9 to 12, preoculars 2, postoculars 2, loreal 0 to 3, ventrals in males 183 to 199, ventrals in females 185 to 197, subcaudals in males 99 to 109, subcaudals in females 95 to 103, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from 249 to 1270 mm, in females 290 to 1281 mm. Total length in males of all ages ranges from 332 to 1650 mm, in females 386 to 1616 mm. Tail length/total length ratios in males range from 0.213 to 0.262, in females 0.207 to 0.260.

I have examined the entire type series of this subspecies and find that some comment is necessary. Seven of the specimens (USNM 14279, 104675, 104676, 105292, 1988, 14283, 46355) are typical *lineatulus*. Two (USNM 12676, 26151), from Guanajuato and "Mexico," respectively, are juvenile *Masticophis striolatus*. Another specimen (USNM 8429) from "New Mexico," considered by Smith (1941) to be a possible intergrade between *lineatulus* and *flavigularis* (= *testaceus*), is a juvenile and cannot be allocated to subspecies. Smith apparently considered USNM 1989 from Co-bre Mines, New Mexico, as typical of the subspecies; I would identify it as an intergrade between *lineatulus* and *testaceus*, as

I would USNM 4388 from Laguna, Valencia County, New Mexico. Both have striping on the dorsal scales but lack red color of the posterior ventrals and the subcaudals.

There is very little pattern variation in adults of this subspecies, in marked contrast to all other subspecies of *Masticophis flagellum* with the exception of *M. f. rud-docki*. The color pattern of the specimens I have examined conforms very closely to the description given by Smith (1941). He failed to mention, however, the coloration of the nape, which is light yellow to yellowish-tan. This coloration occupies an area of from six to twelve scales posterior to the parietals. This area is distinctly set off from the lineate coloration which follows it. There is some slight variability in the anterior extent of the salmon red ventral coloration and the extent of coverage of individual ventrals. In some specimens the posterior half of each ventral is salmon red or pink and the anterior half is cream. In others the whole scute is salmon pink or red. The ventral, as well as the dorsal, coloration varies ontogenetically and is discussed below.

Specimens from Zacatecas are not so brightly colored as those from Durango, Coahuila, and San Luis Potosí. All three of the adult specimens I have seen (UMMZ 123251-52; AMNH 82156) lack bright yellow coloration on the anterior ventrals, and the salmon pink coloration on the posterior portion of the body and underside of the tail is not nearly so bright or extensive in distribution. The nape band, which is light yellow in more typical adult *lineatulus*, is yellowish tan in the Zacatecas specimens. Conant (1965) also mentioned this in his discussion of AMNH 82156, which he reported as the first record for the state of Zacatecas.

The record for this subspecies from 6 miles S Artesia, Eddy County, New Mexico (Gehlbach, 1956), obviously is an error, inasmuch as the area is inhabited by *testaceus*.

Juveniles of *Masticophis flagellum lineatulus* are indistinguishable from those of *M. f. testaceus*, that is, in both races the dorsal pattern consists of narrow (less than one scale long to one scale long), uniformly dark bands separated by lighter interspaces of variable length (usually 2 to 3 scales in

length). This differs from the type of color pattern seen in juveniles of the *piceus* group, in which the bands are longer (usually about 3 scales long) and are bounded anteriorly and posteriorly by an irregular, narrow dark line. The dorsal surface of the head in juvenile *lineatulus* is relatively uniform in coloration (unlike the head pattern of *flagellum*, and the other subspecies in the *testaceus* group), and the anterior portion of the venter is marked with a double row of brown spots. There is a nonbanded area of variable length (9 to 11 scales long) on the nape.

By the time the animal has reached a snout-vent length of approximately 500 mm, the adult pattern has begun to develop. The unique subcaudal and posterior body color is one of the first of the adult characteristics to appear (indications of this coloration are shown by AMNH 82154 which has a snout-vent length of only 305 mm). The salmon color develops first along the posterior edge of the subcaudals and posterior ventrals. Also, the yellow coloration of the anterior region of the venter develops at about 500 mm.

The lineate pattern of the dorsum of the adults develops from the banded juvenile pattern by an intensification of the dark markings on the scales within the juvenile bands and by the progressive development of longitudinal stripes on the scales between the bands. Therefore, as the animal matures the salmon color becomes brighter, covers more area on each scale, and progressively obscures the banded juvenile pattern.

As the lineate pattern of the dorsum becomes more well defined, the nape area becomes more noticeable by its lack of pattern. Also, it is dull yellow in contrast to the brown ground color of the dorsum.

At about 900 mm the dorsum of the posterior region of the body is infused with the same salmon color that is found on the posterior ventrals. This salmon color occupies the posterior half of each scale, leaving the anterior half tan in coloration.

In adult animals (above 950 mm) each ventral on the posterior portion of the body is almost completely covered with salmon pink pigment. The posterior half of each subcaudal is also salmon-colored, the anterior half being white. The remainder of

the venter, except for the first few ventrals (which are cream) is bright yellow. Each of the dorsal scales has a more or less centrally located black stripe. The nape is dull yellow.

Intergradation between *M. f. lineatulus* and *M. f. testaceus* in New Mexico takes place over a broad area from Valencia and Bernalillo counties southwestward to southern Catron County and southeastward to western Otero County. The southern limits of this intergrade zone are unknown because of a lack of specimens from northwestern Chihuahua. Within New Mexico, however, there is decreasing indication of the *lineatulus* pattern to the north. Specimens from Hidalgo, Luna, and Dona Ana counties show a great amount of influence from *lineatulus* to the south.

The following color pattern is of a living specimen from Las Cruces, Dona Ana County (LSUMZ 10519). The dorsum is brownish gray anteriorly, grading to brown posteriorly. A series of indistinct bands is present on the neck and forebody. Each scale on the anterior portion of the body has a black line extending through the center. The lateral edges of the posterior body scales are yellow. There is also an indistinct broken line on scale row 2 on the posterior portion of the body. The base of the scales in row 1 is tinged with orange. The nape has a distinct yellowish tinge. The venter is cream to white with a double row of dark brown spots that become diffuse on the forebody and are gradually replaced by light orange. This coloration becomes more prominent posteriorly, and on the posterior portion of the body and tail forms the posterior border of each scale. The head is light brownish gray above with darker blotching on some head scales. The lateral area of the head is similarly colored with light yellow blotches on the posterior nasal, loreal, and upper preocular. The supralabials are white except for the posterodorsal corner of each, which is grayish brown. The chin is white with brown blotching.

Some New Mexico specimens from Dona Ana County show no pink or orange coloring on the ventrals or subcaudals and so approach *testaceus* in this respect. A single specimen from Catron County (UNM 9312) has no pink on the subcaudals but has the typical *lineatulus* striping on the

dorsum. A specimen from Grant County (UNM 8422) is similar but has a pink tinge on the posterior edge of the subcaudals. A specimen from Otero County (NMSU 1796) has only slight indications of striping on the dorsum and is otherwise like *testaceus*. A single specimen from Sierra County (UNM 435) has light dorsal streaking and some light pink coloration on the posterior ventrals and subcaudals.

Specimens from Socorro, Valencia, and Bernalillo counties show a varying degree of influence from *lineatulus*. Some specimens more closely resemble *testaceus*, others *lineatulus*. From its description, the specimen (TNHC 4487) discussed by Gehlbach (1965) appears to be an intergrade. He stated "the recent specimen, an adult male, 1070 mm in total length, has longitudinal lines on the dorsal scales but retains anterior crossbands and lacks the diagnostic red subcaudal color."

Specimens from El Paso County, Texas, also show characteristics of both *lineatulus* and *testaceus*. I have seen two such specimens (KU 72910, UMMZ 117769). Robert G. Webb stated (*in litt.*) "strangely, the coachwhips in the El Paso area are hard to come by—the only one I have seen, which was a DOR, and is now a skeleton in our collections, I would call an intergrade; although the specimen was torn up badly, the posterior part of the body (dorsally and ventrally) had the characteristic magenta color of *lineatulus*. This DOR specimen is from Jueco Tanks, about 25 miles east of El Paso." Also, Strecker (1915) gave the following information: "Several coachwhips from El Paso County combine the characters of the two western subspecies, *frenatum* and *piceus*, having narrow crossbands in front and the underparts bright pink in color." These words, written twenty-six years before *lineatulus* was described, give a fairly accurate and succinct description of a *lineatulus* $\times$ *testaceus* intergrade.

In Arizona the intergrade zone becomes narrower and more complex as three subspecies intergrade in southern Cochise, southern Pima, and Santa Cruz counties, *M. f. lineatulus* from the southeast, *M. f. cingulum* from the south, and *M. f. piceus* from the north. Influence from *lineatulus* is seen in specimens from the vicinity of

Portal and Rodeo on the eastern side of the Chiricahua Mountains. These individuals do not differ essentially from specimens seen from Hidalgo County, New Mexico. A specimen from 5-8 miles S San Simon in the San Simon Valley (UAZ uncatalogued) is similar to those from near Portal and Rodeo except that it lacks the salmon subcaudal color, and the lines on the dorsal scales are not particularly dark. It does not, however, show any influence from *piceus*. I have seen specimens from the Sulphur Springs Valley and one from the San Bernardino Valley which show influence from *lineatulus* and a varying amount of influence from *piceus* and *cingulum*. Two specimens (both uncatalogued specimens in the UAZ collections) appear to be intergrades between *piceus* and *lineatulus*. A specimen from 28 miles NW Willcox, at the north end of the Sulphur Springs Valley (UAZ uncatalogued), shows more influence from *lineatulus* than from *piceus*. The following description is of this specimen, seen soon after it had been preserved. The dorsum is brown with a dark streak down the center of each scale. Posteriorly these streaks become less prominent. There is an indication of banding on the neck as in *piceus*. The venter is white anteriorly grading to cream. The posterior edge of the ventrals of the posterior region of the body and the subcaudals are salmon pink.

The other specimen is from the Willcox Playa and shows more influence from *piceus*. Its color pattern (in preservative) consists of a brown dorsum (more reddish brown on the neck and forebody) with a few of the dorsal scales having *lineatulus*-type striping. Neck bands are of *piceus* type. The venter is cream anteriorly with a double row of dark brown spots grading to light rust on the posterior portion of the body and the underside of the tail. The head has a typical *piceus* coloration.

A specimen from 4 miles S Dos Cabezas (ASDM 655) looks very similar to typical banded *cingulum*, but there is a slight indication of *lineatulus* influence in neck banding. Another specimen from 5.6 miles N Bernardino (AMNH 75130) has a *lineatulus* nape band and a *piceus*-type head pattern. Banding of a *piceus* type is present on the neck but *lineatulus* striping is also present. Lowe (1964: 20) mentioned the intrusion of typical Chihuahuan Desert

vegetation into parts of the San Simon and Sulphur Springs valleys and it is evidently through these avenues that the influence of *lineatulus* has spread into Cochise County.

M. f. piceus and *M. f. cingulum* intergrade along the area of contact between the elements of the Sonoran Desert and the Desert-Grassland ecotone (see Lowe, 1964). Intergrades have been examined from the Palo Alto Ranch, along the Tucson-Nogales Highway (U.S. 89) and from about Continental south to Arivaca Junction. I have also seen intergrades from the eastern slope of the Huachuca Mountains, and specimens which look like *cingulum*, *piceus*, and *cingulum* × *piceus* intergrades from the region of Fort Huachuca.

Masticophis flagellum cingulum is known in Arizona from several localities in the oak woodland between the Patagonia and Pajarito mountains and occurs as far north in Santa Cruz County as Tubac (SDSNH 32504). I have seen one specimen from Peña Blanca in the foothills of the Pajarito Mountains, also an oak woodland habitat. Another specimen was examined from 8 miles S Arivaca (UAZ uncatalogued), and I collected a DOR specimen 11 miles NNE Arivaca, Pima County, in mesquite grassland. *M. f. cingulum* is also found in desert grassland near Sonoita between the Santa Rita and the Patagonia mountains. It is also found in the region between Palominas and Douglas.

Masticophis flagellum piceus is an inhabitant of the Sonoran Desert in Arizona and its distribution conforms well to the outline of that vegetational complex as described by Shreve and Wiggins (1964), except that it occurs somewhat farther east and south. It also extends north into the Mohave Desert. The type locality of *M. f. piceus* (black phase), Camp Grant, is not included in the Sonoran Desert, as outlined by Shreve and Wiggins. This snake may provide additional evidence for a zoological redefinition of the eastern edge of the Sonoran Desert (Lowe, 1955), but it does not occur as far east as Lowe has placed the boundary.

It is difficult to decide exactly where the zone of intergradation between *testaceus* and *lineatulus* in southwestern New Mexico should be drawn. I examined a series of specimens from Hidalgo and Cochise coun-

ties (three specimens), and three from Chihuahua and Coahuila side by side, and found that if they were arranged in linear order according to snout-vent length the gradation in color pattern was not even. The Mexican specimens showed more characteristics of the subspecies *lineatulus*.

The New Mexico and Arizona specimens showed fewer characteristics of *lineatulus* and more influence from the subspecies *testaceus*. I consider, therefore, that populations of *Masticophis flagellum* from the southwestern portion of New Mexico and extreme eastern Cochise County, Arizona, represent intergrades between *lineatulus* and *testaceus*, albeit much closer to *lineatulus*.

Masticophis flagellum piceus (Cope)

Red Racer, Western Black Racer

Bascanium flagelliforme testaceum: Cope, 1875: 40 (part)

Bascanium flagelliforme piceum Cope, 1875: 40

Bascanion flagelliformis: Duméril and Bocourt, 1886: 704

Zamenis flagelliformis: Boulenger, 1893: 389 (part)

Bascanion flagellum frenatum Stejneger, 1893: 208 (type: USNM 16340, Mountain Spring, Colorado Desert, San Diego County, California)

Bascanion piceum: Van Denburgh, 1896: 1006

Zamenis flagellum flagellum: Cope, 1900: 789 (part)

Zamenis flagellum piceus: Cope, 1900: 804

Bascanium flagellum: Meek, 1906: 15 (part)

Zamenis flagelliformis frenatus: Ditmars, 1907: 288

Zamenis flagelliformis piceus: Ditmars, 1907: 288

Coluber flagellum frenatus: Grinnell and Camp, 1917: 190

Coluber flagellum piceus: Stejneger and Barbour, 1917: 79

Masticophis piceus: Ortenburger, 1923: 2

Masticophis flagellum frenatus: Ortenburger, 1923: 2

Masticophis flagellum frenatum: Klauber, 1926: 144

Masticophis flagellum piceus: Tanner, 1927: 57

Holotype.—USNM 7891. Skin of an adult female (?) from Camp Grant (= Fort Grant), Graham County, Arizona, collected by E. Palmer.

Diagnosis.—A subspecies of *Masticophis flagellum* with two color phases, one black and the other red. The former is completely black dorsally and salmon pink to red posteroventrally. The red phase is pink to red with relatively wide crossbands on the

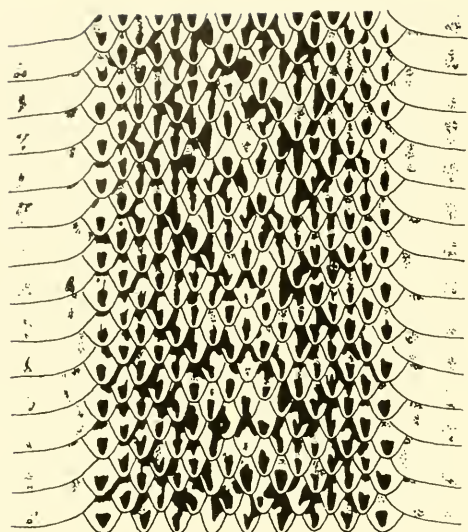


Figure 12. Pattern on the anterior portion of the body of *Masticophis flagellum liucatus* (MSU 4448) from 3 miles E Las Nieves, Durango, Mexico.

neck that range in color from that of the general ground color (in which case the anterior and posterior edges are outlined with darker pigment) to black (Fig. 13).

Range.—Arizona south of the Mogollon and Coconino plateaus, excepting Santa Cruz County and southern and southeastern Cochise County, then north through Mohave County, Arizona, into Washington County, Utah. From there the range extends westward into southern and western Nevada and southern and southeastern California exclusive of the San Joaquin Valley. In Mexico this subspecies occurs only in the Gran Desierto of northwestern Sonora and that part of Baja California del Norte that lies east of the San Pedro Martir Mountains and north of Bahia San Felipe (Figs. 2 and 3).

Description of Holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 9-10, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 8-7; ventrals 194; caudals 106 (tip of tail broken off).

The holotype of *Bascanium piceum* Cope is a representative of the black phase of this subspecies. Inasmuch as the colors of the living animal have been lost or subdued by

its long preservation the following description of a specimen without precise locality data and purchased from a dealer is given. The dorsum is black except for a few small flecks of salmon pink on the frontal and parietals. The venter is black anteriorly becoming increasingly salmon pink. The lateral $\frac{1}{4}$ of each ventral is black. The distal end of the dorsum of the tail is salmon pink with black flecks. The head is black except for a white spot on the upper preocular, the first and fourth infralabials, and a few gulars.

Discussion.—Meristic and mensural data for this subspecies, based on 232 males and 145 females, may be summarized as follows: supralabials 7 to 9, infralabials 9 to 12, preoculars 2 or 3, postoculars 2 or 3, loreal 1 or 2, ventrals in males 183 to 205, ventrals in females 184 to 205, subcaudals in males 97 to 120, subcaudals in females 96 to 115, dorsal scale rows 19-17-12 to 19-17-14. Body length in males of all ages ranges from 294 to 1290 mm, in females 300 to 1154 mm. Total length in males of all ages ranges from 393 to 1668 mm, in females 400 to 1541 mm. Tail length/total length ratios in males range from 0.221 to 0.326, in females 0.233 to 0.298.

The more widespread red phase of the subspecies *piceus* was described by Stejneger as *Bascanium flagellum frenatum*. The scutellation data for its holotype (USNM 16340) is: supralabials 8-8, fourth and fifth entering the orbit; infralabials 11-9, four touching the anterior chin shields, fifth the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 5-6; scale reduction pattern

$$\begin{array}{cc} 19 \frac{3+4(10)}{3+4(11)} & 17 \frac{3+4(110)}{3+4(112)} \\ 15 \frac{7+8(112)}{14 \frac{7+8(128)}{13}} \end{array}$$

ventrals 194; subcaudals 114.

The coloration of the type specimen is faded, and therefore the following description is given of a specimen (LSUMZ 10058) which I collected 9 miles WNW Westmorland, Imperial County, California, on 10 August 1965. The dorsum is reddish orange anteriorly grading to pinkish tan



Figure 13. Red phase of *Masticophis flagellum piceus* from Miramar, San Diego County, California.

posteriorly. The first two neck bands are somewhat more brown than the ground color. The venter is light orange anteriorly grading to bright pink posteriorly. There are a few darker flecks on the ventral surface of the neck. The head is grayish brown dorsally and laterally. There are light markings present on the posterior nasal, loreal, preoculars, postoculars, and temporals. The temporals are tinged with pink. The chin is white with gray flecks.

The most significant aspect of color pattern variation in this subspecies is the sympatric occurrence, in certain parts of the range, of two dimorphic phases, a black and a red one. As can be seen above, these phases were originally described as distinct species and were retained at that level by Ortenburger (1928). He was of the opinion that the black and red phases differed in at least four other characteristics besides color. He stated that the black phase snake "is noticeably a stouter and larger animal than *frenatus*," that the red phase snakes take to the bushes as a means of escape, whereas black phase snakes escape into holes in the ground, that the subcaudals are more numerous in black snakes than in red ones, and, finally, that black snakes have a proportionally longer tail than the red snakes.

Smith (1941) pointed out that *piceus* is "almost beyond question, a mutant form, occurring within the range of '*frenatus*,'" and that the name *frenatus* is not available, because it is a junior secondary homonym of

Coluber frenatus (= *Elaphe frenata*) and thereby permanently rejected.

Klauber (1942), in an excellent paper on the subject, discussed the status of the black whipsnake. In this paper he showed that each of Ortenburger's alleged differences between the black and red phases was untenable. He also pointed to the existence of intermediate specimens as indicative of the conspecificity of the two forms. Furthermore, he stated that this is not the only example of color pattern variation in this subspecies, to wit "coastal San Diego specimens have black necks, while those from the desert side of the mountains and the Imperial Valley are without this dark color or it is only faintly evident."

No one seems seriously to have questioned this interpretation, with the exception of Brattstrom and Warren (1953). In their description of *Masticophis flagellum ruddocki* they stated (p. 179) "because we have described *ruddocki* primarily on the basis of color, we feel that it might be well to clarify our position on the taxonomic status of the black forms of *M. f. piceus* in Baja California and Arizona. No new additions have appeared to challenge Klauber's (1942) conclusions that the black racer (*M. piceus*) is merely a color phase of the red phase (*M. f. frenatum*) (= *M. f. piceus*). We feel that intensive study will support some of Ortenburger's (1928) observations on the distinct ecological separation of these two forms. Ortenburger, however, came to the conclusion that the black racer (*M.*

piceus) deserved specific recognition. We feel that because of the existence of a few specimens which appear to be intergrades, the black racer should only be considered a race of the red racer (*M. f. piceus* and *M. f. frenatum*, respectively). As for the black forms of southern Arizona, it is quite possible that these represent another subspecies whose closest affinities are with the black racers of Baja California. (If so, it would become *M. f. piceus* and the Baja California form named new). Such a disjunct distribution need not cause undue surprise in light of other recent works dealing with the same situation in almost the same area. We refer to the relationship between *Crotalus viridis helleri* and *Crotalus viridis cerberus* (Klauber, 1949) and to the possible relationship of *Lampropeltis zonata* to *L. doliata gentilis* (Zweifel, 1952). These authors seem to have misunderstood Klauber's paper specifically and the subspecies concept generally. Klauber rightly pointed out in his 1942 paper (p. 88) that "since there appears to be no area in which the black form is found alone, it can hardly be considered a valid subspecies." Thus, Brattstrom and Warren's statement that the intermediate specimens support the recognition of the black and red racers as subspecies of the same species is meaningless. The rest of the paragraph also has little pertinence. The situation in the whipsnakes is not at all comparable with that of *Crotalus viridis cerberus* and *C. v. helleri*, or *Lampropeltis zonata* and *L. triangulum*.

The distribution of the black phase of *piceus* (Fig. 14) is confined to south-central Arizona. I have seen specimens from as far north as 15 miles SE Florence, Pinal County, and Klauber (1942) reported a specimen from a little farther north at Florence Junction. I have seen the phase as far west as 25 miles E Gila Bend, Maricopa County, and 5 miles N Park Headquarters, Organ Pipe Cactus National Monument, Pima County; as far south as Sasabe, Pima County, and the Santa Rita Experimental Range, Pima County; and as far east as Fort Grant (= Camp Grant, the type locality of *piceus*), Cochise County.

In order to determine, at least approximately, the density of distribution of the black phase over its range I placed a 10-mile square grid over a standard highway

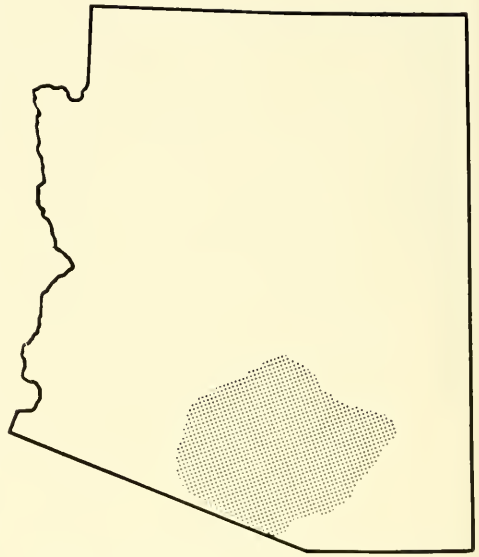


Figure 14. Distribution of the black phase of *Masticophis flagellum piceus* in Arizona.

map of Arizona and recorded the number of specimens that fell within each section of the grid. I also recorded the numbers of specimens of typical red phase *piceus* and those with intermediate coloration. Of the specimens of the black phase examined, 75% were collected within all the squares touching the square occupied by Tucson in Pima County. Beyond this area the percentages become smaller, although more black phase individuals occur west of Tucson than in other directions. The most distant record is about 110 air miles from Tucson, in the Organ Pipe Cactus National Monument (UAZ uncatalogued). Other outlying records lie between 60 and 90 miles from Tucson.

Klauber (1942) stated that black racers outnumber red ones in the vicinity of Tucson. In order to determine whether or not this is the case, I counted the numbers of the red, intermediate, and black snakes within each section of the grid from which specimens were available. My determinations made by this method corroborate those of Klauber. Within all the squares touching the square occupied by Tucson, where the black phase is most common, of the total number of *Masticophis flagellum piceus* examined, 58.9% are of the black phase, 26.3% are of the intermediate phase and

14.8% are of the red phase. It is also interesting that although the black racer inhabits an area encompassing most of Pima and Pinal counties and portions of Maricopa and Graham counties, the snakes intermediate in coloration between the black and red phases are only found within a 30-mile radius of Tucson.

A specimen of this intermediate phase (LSUMZ 10521) from the vicinity of Tucson, Pima County, was given to me by John W. Wright. The neck and forebody of this specimen are black grading to reddish-brown, speckled with black markings on some scales. The middorsal area is more red than the lateral area. The venter is black on the neck grading to pink on the rest of the venter. The head is velvety black dorsally and laterally. The chin is very dark brown with a small amount of white blotching. The eye is gold around the pupil and dark brown around the edge.

Unfortunately I have seen very few living specimens of the red phase of *piceus* and comments on color are taken from the literature. One feature of the color pattern that can be observed on preserved specimens is the difference in coloration of the neck bands. Klauber (1942) stated "coastal San Diego County specimens have black necks, while those from the desert side of the mountains and the Imperial Valley are without this dark color or it is only faintly evident." The degree of variability over the entire range of *piceus* is great. The neck bands may be the same color as the dorsum (outlined anteriorly and posteriorly by a very narrow band of darker pigment) or range from light brown or light gray through grayish brown to black. I have subdivided this continuous variation into five arbitrary categories: A. pink (essentially the same color as the dorsum), B. light gray or light brown, C. brown or gray, D. dark gray or dark brown, E. black. I have excluded those specimens having a coloration intermediate between the black and red phases. By this method a crude estimate can be made of the incidence of occurrence of each band color type in any given area (Table 3). With the exception of coastal southern California, which apparently lacks pink-banded individuals, all the neck band colors occur in every area, although one type may predominate.

Concerning the occurrence of *Masticophis flagellum* in the southwestern portion of Colorado, Maslin (1959) stated "the inclusion of this species [meaning the subspecies *piceus*] in the fauna of the state is based on reports of specimens seen in the vicinity of Mesa Verde National Park. I also saw, but failed to collect, a pale reddish-brown specimen 30 mi. W Cortez, Montezuma County, at the mouth of Yellow Jacket Canyon in June, 1958. It is possible that the form that undoubtedly occurs in this area should be assigned to *M. f. flavigularis*. But biogeographic evidence, based on the distribution of other species of reptiles, indicates that it should be tentatively recognized as *M. f. piceus* until corroboration from actual specimens is possible." Douglas (1966), who spent three years at the Mesa Verde National Park, did not mention this subspecies in his paper on the amphibians and reptiles of the park and, to my knowledge, no specimens have been collected to date. Douglas (pers. comm.) also stated that he had never heard of any red racers being found in this area. It seems unlikely that *piceus* or any subspecies of *flagellum* would occur in this area since no specimens are known from the higher elevations of northeastern Arizona and northwestern New Mexico and, indeed, the distribution of *Masticophis flagellum* seems to be limited by these higher elevations.

Masticophis flagellum ruddocki

Brattstrom and Warren

San Joaquin Whipsnake

Coluber flagellum frenatus: Grinnell and Camp, 1917: 190 (part)

Coluber flagellum piceus: Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part)

Masticophis flagellum frenatus: Ortenburger, 1928: 112 (part)

Masticophis flagellum ruddocki Brattstrom and Warren, 1953: 177; Cunningham, 1955: 218; Conant, *et al.*, 1956: 12; Miller and Stebbins, 1964: 409; Montanucci, 1965: 278; Stebbins, 1966: 150

Masticophis flagellum piceus: Stebbins, 1954: 495 (part)

Holotype.—UCLA 6108 (specimen now in the collection of the Museum of Vertebrate Zoology, University of California at Berkeley), collected $\frac{1}{4}$ mile S of ridge at Wheeler Ridge and $1\frac{1}{2}$ miles W U.S. Hwy. 99, Kern County, California, on 12 April 1953 by James W. Warren.

TABLE 3.
Percentage of specimens of the red phase of *Masticophis flagellum piceus*
exhibiting various colorations of the neck bands.

Area	Color of neck bands				
	Pink	Light gray or light brown	Brown or gray	Dark gray or dark brown	Black
Arizona	30	25	11	9	25
Utah and Nevada	11	20	33	13	23
Desert areas of southern California	15	8	8	15	54
Coastal areas of southern California	0	3	6	8	83

Diagnosis.—A subspecies of *Masticophis flagellum* characterized by a light yellow to olive yellow dorsum with neck bands obsolete or absent (Fig. 15).

Range.—The San Joaquin and Sacramento valleys of central California from Colusa County south to Kern and San Luis Obispo counties (Fig. 2).

Description of the Holotype.—(based on data from original description). Scutellation: supralabials 8-8; infralabials 10-10; preoculars 1-1; postoculars 2-2; ventrals 197; subcaudals 105.

Brattstrom and Warren (1953) gave the following description of the color pattern (presumably in life). "The color varies from spots of Aniline Yellow on the sides of the head and neck to a solid ground color of Buffy Citrine on the sides of the body and Saccardo's Olive dorsally. The ventral color is consistently Straw Yellow (capitals are Ridgway's Color Standards, 1912), with Aniline Yellow or black on the lateral edges. The top of the head is light brown with two dark spots on the supraoculars. There is a small postocular brown stripe on the edge of the postocular and anterior temporals. The labials each have a dark spot and the anterior ventrals have Aniline Yellow spots on them. There are two faint lateral light stripes on the anterior one-third of the body. This is caused by the first scale row being yellow-tipped at its dorsal and ventral corners. There is no evidence of any neck banding."

Discussion.—Meristic and mensural data for this subspecies, based on 10 males and 6 females, may be summarized as follows: supralabials 8 or 9, infralabials 9 to 11, preoculars 2 to 4, postoculars 2, loreal 0 or 1,

ventrals in males 188 to 198, ventrals in females 191 to 198, subcaudals in males 101 to 112, subcaudals in females 102 to 108, dorsal scale rows 19-17-13. Body length in males of all ages ranges from 764 to 970 mm, in females 987 mm. Total length in males of all ages ranges from 1015 to 1323 mm, in females 1329 mm. Tail length/total length ratios in males range from 0.247 to 0.267, in females 0.257.

I have seen only 17 specimens of *rud-docki*, excluding the holotype, the identity of which is made unquestionably clear by Brattstrom and Warren (1953).

This subspecies, in common with *M. f. lineatulus*, exhibits none of the types of color pattern variation seen in the other subspecies and it has only one basic pattern. All of the specimens I have examined exhibit the coloration described for the subspecies by Brattstrom and Warren (1953), but there does seem to be some slight color variation. The dorsum ranges from yellowish tan to light olive yellow. Most specimens have at least some evidence of banding on the neck, but the bands are reduced in number, in comparison with *M. f. piceus*, or are indistinct and, in general, the same color as the dorsum. Some specimens are light tan ventrolaterally (to the level of scale row 5 or 6) and light olive yellow on the more dorsal rows. Several specimens examined have a distinct orange tinge on the neck region, both dorsally and ventrally.

The single specimen (SDSNH 26084) I have seen from the northern portion of the range (actually in the Sacramento Valley) is somewhat peculiar in having each dorsal scale with a darker central area giving the impression of a vague stripe on each dorsal scale row.

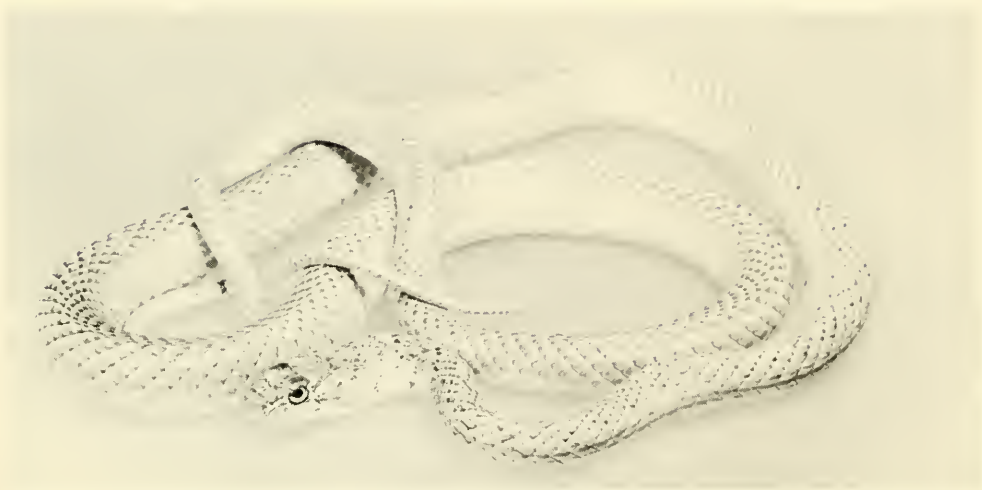


Figure 15. *Masticophis flagellum ruddocki* (UMMZ 78242) from 50 miles W Maricopa, Santa Barbara County, California.

Apparently there is some color variation in this subspecies which reflects the influence of *M. f. piceus*. Joseph F. Copp (*in litt.*) stated that "... a DOR adult that was partly picked clean by birds was noted on California 166, 14.6 mi. W of New Cuyama, and was red rather than yellow as *M. f. ruddocki* is supposed to be. When they were fresh, the two specimens in my collection from that valley [JFC 62-62 and 63-55] were also red, and the black banding on the neck is moderately evident." Stebbins (1966, pl. 30) illustrated a specimen of a coachwhip from Santa Cruz County, California, which is red. The specimen shows some neck banding but of a kind atypical for either *ruddocki* or *piceus*. The illustration closely resembles the pink phase of *M. f. testaceus*.

Intergradation with *Masticophis f. piceus* takes place in low passes through the mountains surrounding the southern end of the San Joaquin Valley. *M. f. piceus* occurs in Mohave, Great Basin, and Sonoran Desert vegetation in southern and southeastern California, extending as far north into chaparral as Los Angeles County to the west and Inyo County to the east. Intergradation may be expected anywhere along the southern end of the valley where there are areas in the mountains of sufficiently low elevation to allow contact between the two subspecies. I have seen an intergrade from 15.9 miles

W New Cuyama, Cuyama Valley, San Luis Obispo County (JFC 63-55). Another specimen (LACM 2239) from 5 miles W Arwin cutoff, 3 miles S Bina Siding, Hwy. 466, Kern County, only about 20 miles from the type locality and within the valley, shows influence of *piceus*. It is yellowish tan above with gray neck bands, which are better developed than in *ruddocki*. Five specimens were considered by Brattstrom and Warren (1953) to be intergrades between *ruddocki* and *piceus*, and the localities for them are as follows: Kern River at Bodfish (MVZ 2792), 6 mi. SSE Weldon (MVZ 56717), Weldon (MVZ 2793), Isabella (MVZ 2794), 1 mile E Onyx (UCLA 6106 = LACM 19258), and Monolith (LMK 27422 = SDSNH 27422). All localities are in Kern County, four in the Kern River-Walker Pass area (5245 ft elevation), and one in the Tehachapi Pass area (3793 ft elevation). I have seen two of these specimens (LACM 19258 and SDSNH 27422) and consider both of them to be *piceus* with no evidence of the influence of *ruddocki*. Thus, the zone of intergradation between *piceus* and *ruddocki* as pictured in Fig. 2 is largely conjectural and roughly corresponds with the location of the mountains at the southern end of the San Joaquin Valley.

The areas of intergradation between *ruddocki* and *piceus* need to be determined and

the distribution of *ruddocki* within the valley needs to be better documented.

Masticophis flagellum cingulum

Lowe and Woodin

Banded Red Racer

Bascanion flagellum frenatum: Van Denburgh, 1897: 463

Coluber flagellum piceus: Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part); Bogert and Oliver, 1945: 363

Masticophis flagellum frenatus: Ortenburger, 1928: 112 (part)

Masticophis piceus: Allen, 1933: 11; Taylor, 1936: 490

Masticophis flagellum frenatum: Taylor, 1936: 490

Masticophis flagellum frenatum × *flavigularis*: Gloyd, 1937: 117

Masticophis flagellum piceus: Smith, 1941: 397 (part); Smith and Taylor, 1945: 95 (part); Langebartel and Smith, 1954: 134; Zweifel and Norris, 1955: 252; Stebbins, 1966: 150 (part)

Masticophis flagellum cingulum Lowe and Woodin, 1954: 247; Conant, *et al.*, 1956: 12; Fowlie, 1965: 69; Stebbins, 1966: 150

Holotype.—UAZ 672 collected at Moctezuma, Sonora, Mexico, about 2000 ft elevation, in 1951 by A. W. Ruff.

Diagnosis.—A subspecies of *Masticophis flagellum* with a highly variable color pattern. The dorsal coloration ranges from a series of wide reddish brown bands separated by narrower, paired light bands to uniform reddish brown or uniform black.

Range.—Arizona, from about midway between Tucson and Nogales, east to Douglas, and west to the region of Arivaca, thence southward to southern Sonora, including most of that state except for the Gran Desierto and the mountainous eastern portion (Figs. 2 and 3).

Description of the holotype.—Scutellation: supralabials 8-8, fourth and fifth entering the orbit; infralabials 11-12, four touching the anterior chin shields on the left and five on the right, fifth on the left and sixth on the right the largest; loreal 1-1; preoculars 2-2; postoculars 2-2; temporals 7-7; scale reduction pattern

$$19 \frac{4+5 (11)}{3+4 (14)} \quad 17 \frac{8+9 (113)}{13} \\ 16 \frac{3+4 (117)}{3+4 (117)} \quad 14 \frac{7+8 (138)}{13};$$

ventrals 191; tail incomplete. Body length is 1023 mm, tail incomplete.

Lowe and Woodin (1954) described the color pattern (in life) as follows: "Mid-dorsally the dark brown ground color tends to be blackish brown, grading to dark reddish brown (near Pl. 7, J 12)¹ dorso-laterally and to lighter reddish brown (near Pl. 7, J 7) laterally. Each dorsal scale tends to be darker on its posterior portion. On the anterior body, only a few scales are edged with pink (on the anterior portion of the scale); there is a progressive increase posteriorly in amount of pink per scale. Thus pink predominates on the posterior body and tail and the darker brown is there restricted to the posterior edge of each scale.

"The upper surfaces of the head are reddish brown, distinctly darker on the supraoculars and with faint light edges to the scales. There are conspicuous pink, (Pl. 2, J 9) marks (light areas) on the labials, postoculars, preoculars, nasals, and loreal. The pink of the postnasal, loreal, and preocular is continuous and forms a 'loreal stripe' from orbit to naris. Under surfaces of the head are variously colored cream and pink with small dark brown and black spots and blotches.

"The ventral surface of the neck is dark pink (Pl. 2, J 9) being approximately the same color as the undersurface of the tail and of the gular area. The ventral surface at mid-body is a lighter pink (Pl. 2, G 8) than the neck and tail venters. The dark pink venter of the tail is near Pl. 2, J 8. The entire ventral surface is patterned by bold brown transverse cross lines adhering to the posterior margins of the ventral scutes and extending completely across them. These are commonly associated with brown blotches on the lateral margins of the scutes. In addition to the dark transverse lines on the neck, there are the commonly observed (in *M. flagellum*) bilateral row of dark blotches and spots on neck and gular region gradually fading away posteriorly.

"On the upper surfaces, there is a series of conspicuous light-colored transverse, narrow bands or cross-bars which extend completely across the lateral and dorsal surfaces of the neck and body. Their effect is to

¹ Their color terminology based on Maerz and Paul (1950).

break up the dark ground color of the upper surfaces into several large, longitudinally oblong sections. The first of these bands is approximately four scales posterior to the parietal head plates (counting scales along the vertebral line). This anterior-most band is the narrowest and most sharply defined and is approximately one and a half scales in width. The second pink band is somewhat wider, being approximately two scales in width, and, like the remainder, is less sharply delimited along its edges than is the first. The second band is approximately 12 scales posterior to the first. The third, fourth, and fifth bands are simple single transverse bands approximately like the second. The next and last three bands or band areas (sixth, seventh, and eighth) are actually narrow double bands of pink separated by a similar narrow band of dark brown ground color. The sixth band area (double band of pink) begins approximately 75 scales posterior to the head (parietals). It is separated from the seventh band area by approximately 18 scales; the seventh is similarly separated from the eighth by approximately 17 scales. There appears to be a faint trace of a ninth band area on the posterior body half where the ground color gradually becomes the uniform braided pattern of the tail.

"There is a faint, barely perceptible trace of a light longitudinal . . . line (pink) on the anterior body involving the first two scale rows. On the posterior body area, the lower scale row gradually becomes predominately pink, taking on the color of the adjacent scutes. This is concomitant with the graduation posteriorly into a 'uniform' braided whiplike pattern of light pink and brown. On the neck are traces of additional pink 'bands' which give a clue to a probably more banded neck in hatchlings and juveniles as is commonly seen in members of the *flagellum* complex."

Discussion.—Meristic and mensural data for this subspecies, based on 84 males and 41 females, may be summarized as follows: supralabials 7 to 9, infralabials 9 to 12, preoculars 1 to 3, postoculars 2, loreal 0 or 1, ventrals in males 189 to 203, ventrals in females 188 to 201, subcaudals in males 97 to 121, subcaudals in females 97 to 111, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from

303 to 1410 mm, in females 282 to 1186 mm. Total length in males of all ages ranges from 408 to 1850 mm, in females 371 to 1541 mm. Tail length/total length ratios in males range from 0.223 to 0.269, in females 0.226 to 0.280.

This subspecies was envisioned by its describers as ranging from Moctezuma, Sonora (the type locality), northward to Amado, Santa Cruz County, Arizona. They stated, however, that the southern, eastern, and western limits were unknown at that time. The subspecies was diagnosed as follows: "characterized by adult dark red-brown ground color on upper surfaces periodically broken by complete transverse, narrow, light-colored (pink) cross-bands which break the ground color into large, dark, longitudinally oblong sections; a single outstanding light band crossing the nape." The approximate distribution of whipsnakes that fit this concept of the subspecies *cingulum* is indicated by Stebbins (1966, map 132).

An examination of a large amount of material from Arizona and Sonora indicates a considerably more complex situation than was formerly recognized and requires a redefinition of this form. This new information reveals that *M. f. cingulum* is distributed from Moctezuma in eastern Sonora to, and including, Isla Tiburón to the west. It extends northward to intergrade with *M. f. picens* and *M. f. lineatulus* in Pima and Cochise counties in Arizona. It occurs at least as far south as the Sonora-Sinaloa border. The situation in northern Sinaloa is discussed in another section.

Masticophis flagellum cingulum exhibits more pattern variation than any other race of *flagellum*. This has been the primary reason for the confusion concerning *Masticophis flagellum* in Sonora. Bogert and Oliver (1945) discussed the problem in part. They stated that their material from Alamos and Guirocoba might be referable to any one of three subspecies, *picens*, *testaceus*, or *lineatulus*, and they noted that this being the case, "it becomes increasingly difficult to allot specimens from critical areas, and for the most part, identifications are not based on characters but on geographical data." Taylor (1936) and Zweifel and Norris (1955) noted the considerable variability of color pattern in the material they ex-

aminated, while continuing to use the name *piceus*.

I suggest the following explanation for this situation. *Masticophis flagellum cingulum* exhibits an unusual amount of variation in color pattern including a red phase (the phase originally described), a black phase (as in *M. f. piceus* and the Baja California form), a patternless phase (the phase discussed by Bogert and Oliver, 1945, p. 363, and thought to resemble *M. f. testaceus*), and intermediate patterns between these three phases. For purposes of discussion I have divided the wide spectrum of color pattern variation into seven pattern classes labelled as follows:

- A. Pattern of wide, dark red bands separated by light pink interspaces;
- B. As in A but with a reduced number of light bands;
- C. As in A but with only the nuchal band present;
- D. Uniform pink or tan dorsal coloration with no evidence of pattern;
- E. As in A but with a few black scales distributed on the anterior portion of the body;
- F. Anterior 1/3 to 1/2 of the body black, posterior 2/3 to 1/2 red;
- G. Solid black dorsal coloration.

The distribution of these color pattern classes is illustrated in Fig. 16. It will be noted that the individuals constituting the pattern A class tend to be concentrated in the northern and northeastern portions of the range. The patternless D class tends to be concentrated in southern Sonora, and the predominately black F and G classes are concentrated in central and western Sonora. The intermediate classes are rather indiscriminately distributed throughout the range.

Figure 16 only approximates the actual distribution. The phases A, D, F, and G tend to predominate and there are a lesser number of the intermediate phases B, C, and E. In the samples examined, the incidence of the seven color pattern classes is as follows: A—35.6%; B—5.9%; C—2.5%; D—12.7%; E—12.7%; F—23.7%; G—6.8%. Also, as mentioned above, classes A, D, F, and G tend to be concentrated in certain areas and also to predominate in those areas. In Santa Cruz County, Arizona, 84% are of pattern class A and 16% are of pat-

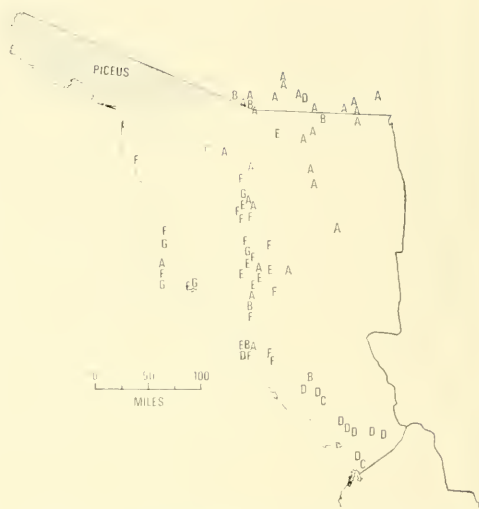


Figure 16. Distribution of the color pattern classes of *Masticophis flagellum cingulum* in Sonora.

tern class B. In Cochise County, Arizona, 89% are of pattern class A and 11% of pattern class D. From Naco, Sonora, south to Moctezuma, and west to Arizipe, 89% are of pattern class A and 11% of pattern class B. In the area from Imuris and Santa Ana south to Hermosillo, east to Mazatán and west to Pitiquito the following percentages obtain: A—18%, B—5%, C—3%, D—0%, E—26%, F—38%, G—10%. From Desemboque south along the coast to Empalme, including Isla Tiburón, the frequency of occurrence of the various pattern classes is as follows: A—8%, B—4%, C—0%, D—12%, E—15%, F—46%, G—15%. Finally, in the area between Ciudad Obregón, Alamos, and the Sonora-Sinaloa state border, 77% are of pattern class D, 15% are of pattern class C, and 8% are of pattern class B.

Thus, it may be seen that the percentage of pattern class A is highest in the region from Santa Cruz and Cochise counties south to Moctezuma (90% of the total number of pattern class A). Percentages of pattern classes F and G are highest in the area from Santa Ana and Imuris south to Hermosillo and west to Guaymas and Desemboque (100% of the total number of pattern F and G classes). Finally, percentages of pattern class D are highest in the area from Obregón south to the Sonora-Sinaloa border

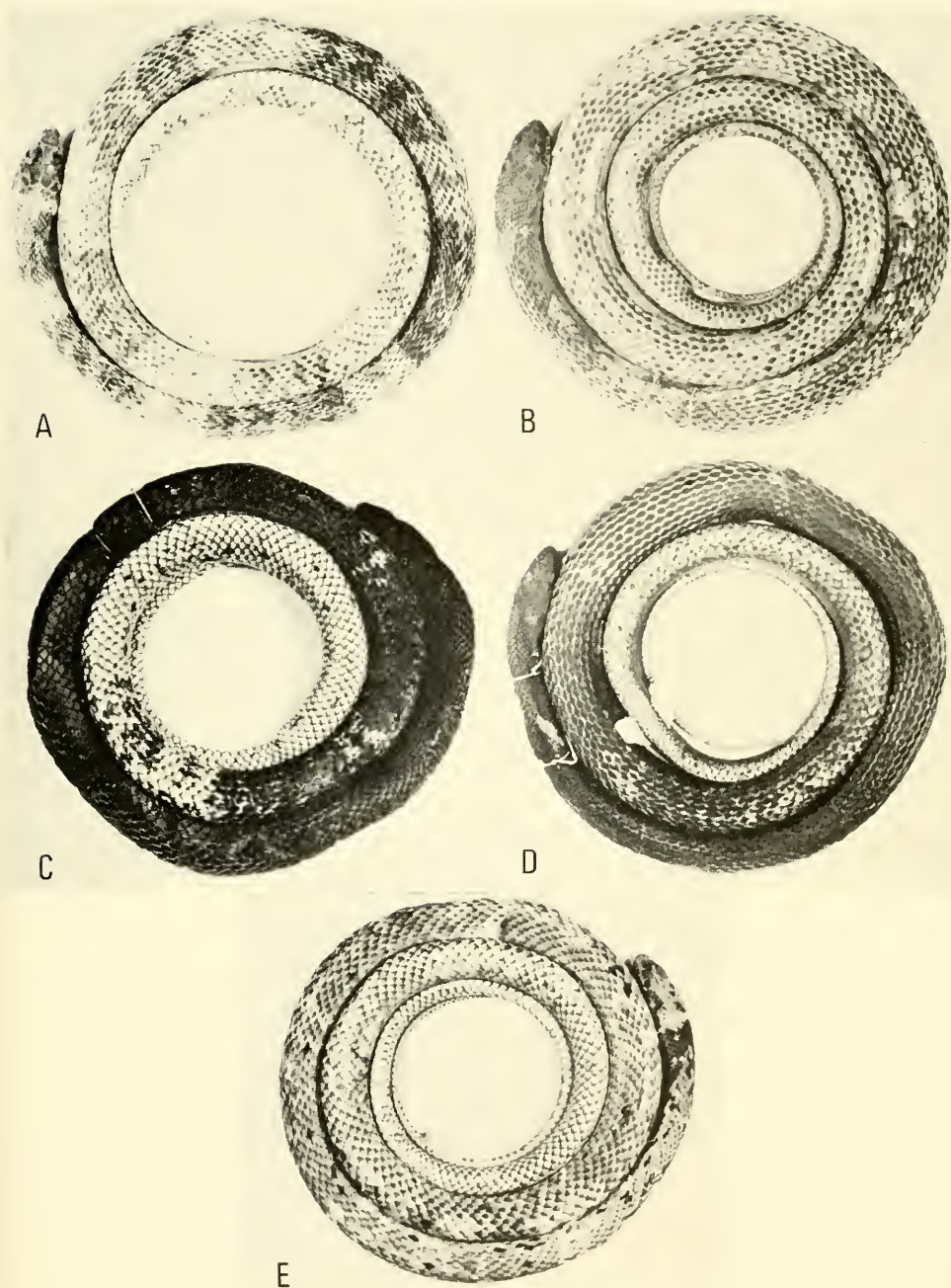


Figure 17. Pattern variation in *Masticophis flagellum cingulum*. A. *M. f. cingulum* (LSUMZ 10520) from Douglas, Cochise County, Arizona (Pattern A). B. *M. f. cingulum* (LACM 6996) from Terreros, Sinaloa, Mexico (Pattern D). C. *M. f. cingulum* (AMNH 99370) from 0.5 miles S San Miguel de Horcasitas, Sonora, Mexico (Pattern F). D. *M. f. cingulum* (LACM 25922) from 25 miles N Hermosillo, Sonora, Mexico (Pattern G). E. *M. f. cingulum* (KU 78957) from 7 kilometers W Kino, Sonora, Mexico.

(77% of the total number of pattern D class).

There is variability in each of the above color pattern classes and, in reality, there is a complete continuum from the A pattern to the D pattern and from the A pattern to the G pattern. The basic coloration of pattern A is given in the following description (based on color notes taken in life on LSUMZ 10520 from Douglas, Cochise County, Arizona; Fig. 17A). The dorsum has long, dark mahogany-red blotches separated by narrower interspaces that are composed of scales that are light at the base and dark brownish red at the tip. Within each light interspace is a band that is somewhat browner than the long bands. There are 10 or 11 dark red bands. These bands range from about 11 to 14 scales long. The light pink interspaces are 5 to 6 scales long and the dark band within these interspaces is about 2 scales long. Posteriorly, the long bands become less prominent and on the tail the color is like that of the interspaces on the more anterior portion of the body. Three scales behind the parietal there is a narrow (one scale long) band that is colored like the interspaces. The venter is dark pink with a slight orange cast. On the neck and forebody there is a double row of faint spots. The top of the head is dark red with the scales lightly outlined with white. The temporal scales are dark red. Most of the rostral is dirty white. The chin is white, blotched with tan and speckled with dark brown. The iris is golden orange and dark brown.

The long dark bands vary from 5 to 16 scales in length and the light interspaces from 2 to 6. The number of dark bands on the body varies from 9-12. Frequently there is a narrow light band in the center of the dark band and occasionally two of these are present.

I have seen no living material of pattern class B animals but the pattern, and probably the color, is similar to that of pattern class A animals except that the long bands are reduced in number.

Specimens that have a class C pattern are uniform pinkish tan, and the narrow light nuchal band is the only vestige of the class A pattern that remains.

I also have seen no living specimens of pattern class D, but Bogert and Oliver

(1945) described a specimen from Alamos as "uniform brownish olive above and essentially devoid of markings, although each of the lateral scales has a lighter area in the anterior median part. This specimen is similar in coloration to specimens of *Coluber flagellum testaceus* from Texas, although its coloration is somewhat darker than any specimens at hand. The sides of the head, including the lips are almost uniformly brownish and bear no trace of pattern found commonly on *piceus*." These authors did not state whether the color description was based on a living specimen. Joseph F. Copp has informed me (*in litt.*) that "the species [*Masticophis flagellum*] is also common on the same highway [Mexico 15] south of Navajoa where nearly uniformly red individuals seem to be the rule." Preserved specimens are uniform tan to light velvety brown without any trace of bands (Fig. 17B). The venter is cream with a double row of light-centered spots on the neck and forebody. The top and sides of the head are the same color as the dorsum of the body. The lower portion of the supralabials is cream and they are often blotched with dark brown. The chin is cream, mottled with brown.

The animals of pattern class D do, indeed, appear similar to some specimens of *Masticophis flagellum testaceus*, especially the pattern variety that is devoid of any dorsal markings. The most common pattern variant of *testaceus* is tan on the dorsum with narrow brown to dark brown bands on the neck, but the uniformly colored Sonoran specimens may be easily distinguished from this variety as well as from the wide-banded variety of *testaceus* discussed in the account of that subspecies. Separating nonpatterned *cingulum* and nonpatterned *testaceus* involves rather subtle distinctions, and, were it not for the fact that a continuum can be demonstrated from pattern A to D, it would be tempting to consider the convenient but zoogeographically untenable idea that nonpatterned *cingulum* are *testaceus*. The velvety appearance of the dorsal coloration in nonpatterned *cingulum* is something that I have not seen in *testaceus*. Also the dorsal color seems to be darker in *cingulum* than in *testaceus*. Any attempt to delineate these differences in a key would be fruitless, and identification should be made on the basis of geographic probability.

From the above it is obvious that a gradual obliteration of the banded pattern of class A animals occurs through classes B and C to pattern class D animals. This change is also indicated in the clinal shifting of the relative percentages of pattern A animals and pattern D animals from the northern portion of the range of *cingulum* to the southern portion. This same trend is also indicated to a lesser extent (due, perhaps, to lack of sufficient material) by the intermediate patterns B and C.

Pattern E animals exhibit considerable variation and grade almost imperceptibly from the typical A pattern to the F pattern. At one end of the spectrum are animals similar to pattern class A animals but with 3 or 4 dark scales on the neck and some dark markings on the side of the head (KU 48921, JFC 63-117). Others have a few more black scales on the neck (LACM 9136, 25166; AMNH 75129, 84979-80; UAZ 9336; KU 78957, 78959; see Fig. 17E). Others have aggregations of black or very dark brown scales on the neck (JFC 64-200) and farther posteriorly along the body (KU 78956, JFC 64-202, UIMNH 23917). This pattern type occurs primarily between Imuris and Guaymas.

Pattern F animals also exhibit variability in the amount of the body covered by black (Fig. 17C). This black coloration is present on about 1/3 to 3/4 of the anterior portion of the body. The remaining 2/3 to 1/4 of the body is colored with a variegated mixture of red and black that, in many specimens, takes a banded form. These bands are very similar, and in some specimens identical, to the bands of pattern A animals except that the dark red pigment is replaced by black. This type of banding is well evidenced in UNM 13705, MSU 7875, JFC 64-201, OSU 2029, and several uncatalogued specimens in the collection of the University of Arizona. More commonly, however, the black coloration is broken into long bands by lighter interspaces that are not bisected by a narrow black band. In these specimens the number of light bands varies from 2 to 7.

Pattern G animals are solid black dorsally (Fig. 17D), although certain specimens have some dark brown pigment on the posterior portion of the body. One specimen (LACM 25922; Fig. 17D), which is black

on the anterior 3/4 of the body grading to dark brown posteriorly with remnants of 3 lighter bands, is intermediate in coloration between those specimens that are classed as belonging to patterns F and G. The following description is of a living specimen of pattern class G (JFC 65-217). The dorsum is black except for the extreme tip of the tail which is blotched with pink. The venter is black on the anterior half of the body grading into pink on the posterior 1/4. The tail is dark pink ventrally. The head is very dark brown dorsally and laterally, except for a pink blotch on the loreal and upper preocular. The chin is very dark brown with fine white stippling on the anterior infralabials. The eye is golden orange around the pupil and dark brown around the edge.

The pattern described above is identical with the pattern exhibited by black *piceus* from the region of Tucson. The two forms do not come into contact, however, and each is connected, through a pattern gradient, with the more easily identified individuals of the subspecies *cingulum* and *piceus*. As is the case among the patternless phases of *cingulum* and *testaceus*, subspecific allocation must be made on the basis of geographic probability.

Masticophis flagellum fuliginosus (Cope),
new combination

Baja California Whipsnake

Bascanion flagelliforme testaceum: Yarrow, 1883: 112 (part)

Bascanion flagelliforme testaceum: Belding, 1887: 98

Bascanion laterale: Cope, 1890: 147

Zamenis lateralis fuliginosus Cope, 1895: 679

Bascanion flagellum frenatum: Van Denburgh, 1895: 148

Zamenis flagellum frenata: Mocquard, 1899: 323

Bascanion laterale fuliginosum: Van Denburgh, 1905: 26; Van Denburgh and Slevin, 1914: 145

Bascanion flagellum: Meek, 1906: 15 (part)

Coluber flagellum piceus: Van Denburgh and Slevin, 1921: 64; Schmidt, 1922: 683; Van Denburgh, 1922: 664 (part); Klauber, 1942: 88 (part)

Masticophis piceus: Ortenburger, 1928: 125 (part); Linsdale, 1932: 375

Masticophis flagellum frenatus: Ortenburger, 1928: 112

Masticophis flagellum frenatum: Linsdale, 1932: 375

Coluber flagellum frenatum: Mosauer, 1936: 16



Figure 18. Pale phase of *Masticophis flagellum fuliginosus* from 7 miles N San Pedro, Baja California del Sur, Mexico.

Masticophis flagellum piceus: Brattstrom and Warren, 1953: 179 (part); Cliff, 1954: 77; Murray, 1955: 45; Leviton and Banta, 1964: 150; Stebbins, 1966: 150 (part)

Syntypes.—USNM 15135-15136, collected on Santa Margarita Island, Baja California del Sur, Mexico, on 2 May 1888 by the crew of the U. S. Fish Commission vessel *Albatross*.

Diagnosis.—A subspecies of *Masticophis flagellum* with two color phases, one having a yellow or light gray dorsum with a zigzag pattern of black bands along the body and wider dark brown bands on the neck (Fig. 18), and the other having a dark grayish brown dorsum with a lineate pattern of variable length on the lateral portion of the dorsum, and a variable amount of cream coloration on the venter.

Range.—All of the peninsula of Baja California except for the portion east of the San Pedro Martir Mountains and north of Bahía San Felipe. The dark phase extends into the southern portion of San Diego County, California (Figs. 2 and 3).

Description of the Syntypes.—Scutellation (the first set of numbers applies to USNM 15135, the second to USNM 15136): supralabials 8-8, 8-8, the fourth and fifth entering the orbit in both; infralabials 10-10, 10-10, four touching the anterior chin shields and the fifth the largest in both; loreal 1-1, 1-1; preoculars 2-2, 2-2; postoculars 2-2, 2-2; temporals 8-8, 7-7; scale reduction pattern (of USNM 15135)

$$19 \frac{3+4(7)}{3+4(8)} \quad 17 \frac{3+4(108)}{3+4(112)}$$

$$15 \frac{\quad}{6+7(118)} \quad 14 \frac{\quad}{6+7(124)} \quad 13;$$

ventrals 192 (Cope gave an incorrect count of 201), 190 (Cope's count is 205); tail incomplete in both. Body lengths are 809 mm and 670 mm, respectively, tail incomplete in both.

Cope (1895) described the color pattern as follows: "Color above blackish-brown anteriorly, becoming lighter posteriorly to the end of the tail. The dark color extends on each end of the gastrosteges to the angulation throughout the length, and in the younger specimen [USNM 15136], fading out beyond the middle of the length. Ground color of belly yellow. In the larger specimen [USNM 15135] the black-brown predominates on the inferior surfaces, yielding gradually to the ground color, which predominates on the inferior surface of the tail. A yellow spot on the preocular; and in the younger specimen on the postoculars and labial plates. Gular and genial plates yellow spotted in the younger specimen, nearly uniform dark brown in the older. On the anterior part of the body of the younger specimen the lateral scales to the third and fourth row have brown shades, with an obscure trace of cross-banding. On the same specimen near the middle of the body, there are two pale half-cross-bands near together.

In the same, the center of each parietal plate is brown."

To this description I can add that both specimens show a light flecking throughout the length of the body and on the side of the neck, this being better developed in the smaller of the two specimens.

Discussion.—Meristic and mensural data for this subspecies based on 92 males and 70 females may be summarized as follows: supralabials 7 to 9, infralabials 8 to 11, preoculars 1 or 2, postoculars 1 to 3, loreal 1 or 2, ventrals in males 175 to 204, ventrals in females 176 to 205, subcaudals in males 100 to 129, subcaudals in females 99 to 123, dorsal scale rows 19-17-12 to 19-17-13. Body length in males of all ages ranges from 239 to 1320 mm, in females 237 to 1242 mm. Total length in males of all ages ranges from 317 to 1729 mm, in females 311 to 1676 mm. Tail length/total length ratios in males range from 0.209 to 0.288, in females 0.224 to 0.295.

Because of demonstrable and consistent differences in coloration and pattern, I recognize the populations of *Masticophis flagellum* inhabiting the greater part of the peninsula of Baja California as distinct, and, therefore, resurrect the name *fuliginosus* for this subspecies. The race was described by Cope (1895) from the Isla Santa Margarita, but he assigned it to the species *lateralis*. It was placed in the synonymy of *Coluber flagellum piceus* (= *Masticophis flagellum piceus*) by Schmidt (1922), who noted the resemblance of Cope's specimens to snakes from the mainland of Baja California. The name *Zamenis lateralis fuliginosus* has remained in the synonymy of *M. f. piceus* to this date.

This subspecies may be distinguished from *M. f. piceus* and all other races of *Masticophis flagellum* by the following characters: The dorsal coloration of the pale phase is some shade of yellow (usually bright yellow) or light gray (pink to red in *piceus*); the dorsal pattern consists of a series of transverse zig-zag bands, between which the ground color is uniformly pale (in *piceus* there is an alternating series of red and cream bands between the dark bands); and the dark bands in *fuliginosus* are formed by dark markings at the apex and anterolateral edges of each scale. Thus, since the scales of each dorsal scale row al-

ternate in position with those above and below, the placement of this pigment produces a zig-zag pattern.

The dark phase of *fuliginosus* may be distinguished from the dark phases of both *piceus* and *cingulum* by the following characters: The dorsal coloration is dark grayish brown; the scales of the anterolateral portion of the dorsum have pale lateral edges that give the impression of a pale, narrow line along the junction of each scale row with that above and below; this coloration extends for a variable length along the body; the head is usually brown, a little paler in coloration than the dorsum; a varying portion of the venter is cream to yellowish cream. In contrast, the dark phases of *cingulum* and *piceus* are solid black above and the posterior portion of the venter is salmon pink to salmon red; in these forms the head is the same color as the dorsum.

The following description of the color pattern of a specimen from Isla Carmen, Gulf of California (JFC 65-204), is characteristic of the pale phase of this subspecies. The greater part of the dorsum is yellowish tan. The ground color of the neck, however, is olive green and the scales are heavily speckled with black. There is an orange suffusion on the first dorsal scale row and to some extent on the second. The venter is pale yellow anteriorly and lemon yellow posteriorly. There is a double row of irregularly shaped cinammon blotches on the neck. The head is grayish brown dorsally. The lateral area of the head is similar with white blotches on the loreal, upper preocular, and supralabials. The chin is white with brown blotching.

The following description is of a dark phase *fuliginosus* from 21 to 22 miles S La Paz (LSUMZ 12630). The dorsum is dark brown grading to brown on the extreme posterior portion of the body and tail. The first dorsal scale row is a shade paler. The venter is dark brown on the throat grading to creamy white posteriorly. The head is dark brown above, brown laterally, with a white blotch on the sixth supralabial. The chin is brown with cream blotching, which extends to the posteroventral edge of the last supralabial.

Although there is some degree of variability in the intensity of the color pattern at any one stage in a snake's life, there is

a definite ontogenetic darkening of the pattern from juvenile to adult. This change is illustrated by the following description of a series of dark phase *fuliginosus* from various localities in Baja California del Norte in the collection of Mr. Joseph F. Copp.

New-born specimens have essentially the same color pattern as do the young of "red phase" *piceus*, but the color is much darker. There are dark brown bands on the neck separated by cream bars. The rest of the dorsum is covered with a mottling of dark and light brown. The venter is cream with dark brown spotting on the neck. The head is brown with cream blotching on the side. The chin is cream with brown mottling.

As a snake grows larger (as exemplified by JFC 441 from 2.2 miles S Colnett, Baja California del Norte, snout-vent length 472 mm) the entire dorsum begins to darken. The mottling is less evident and the pale interspaces between the neck bands are restricted to the side of the neck. Cream blotching on the side of the head is less extensive. The venter is much the same at this stage as in new-born animals.

At a snout-vent length of 967 mm (JFC 60-94 from 4.2 miles S Rosarito, Baja California del Norte), a snake is much darker. The dorsum is very dark brown from scale rows five or six to the middorsal row. Rows one to five or six have a lineate pattern that is more diffuse posteriorly. The cream interspaces on the neck are still visible although almost obscured by the lineate pattern. The venter is cream with a double row of light-centered brown spots. The head is darker and the brown blotching on the side of the head and chin is darker and more extensive.

As a snout-vent length of 1029 mm (JFC 60-100 from 2 miles N Arroyo San Telmo, Baja California del Norte) the dark coloration of the dorsum is more extensive, tending to obscure the lineate pattern on the side of the neck. Spotting on the venter is more prominent and the spots on the neck show indications of fusing together. The brown coloration on the side of the head and chin is more extensive.

At a snout-vent length of 1044 mm (JFC 398 from the San Telmo Valley, 3 miles E San Telmo, Baja California del Norte) the cream blotching on the side of the head has almost disappeared and the chin and

throat are heavily blotched with grayish brown.

At a snout-vent length of 1068 mm (JFC 59-73 from Punta Cabras, Baja California del Norte) the lineate pattern on the side of the neck has virtually vanished, and there is only a slight indication of it on scale row one.

At a snout-vent length of 1267 mm (JFC 60-110 from the north base of Punta Banda, Baja California del Norte) the side of the head and chin have very little cream blotching.

In summary, as a juvenile snake of the dark phase of *fuliginosus* attains adulthood, there is a progressive darkening of the dorsum, head, throat, and chin, and an intensification of the spotting on the venter.

The dorsum of the light phase of *fuliginosus* is either pale to dark yellow, pale tan to tan, or pale gray. Some specimens that have been long preserved are ivory-white in coloration; this may be the result of fading from an original pale gray coloration.

In a series of 14 specimens from Miraflores, 6 are yellow, 2 pale gray to grayish tan, and 6 are ivory-white. The number of specimens of each color type that I have examined from several localities in Baja California are as follows: La Paz—yellow (2), tan (1), pale gray to dark gray (3); Agua Caliente—yellow (1), tan (2); San José del Cabo—yellow (2), tan to grayish tan (3); Cabo San Lucas—yellow (3), tan (10), pale gray (2); Santa Anita—yellow (1), tan (3). That this difference in coloration is not due to variations in methods of preservation or storage of specimens is evident from the presence of both yellow and pale gray specimens in series collected at the same time. There is also variability in the amount of dark pigment on the body (Fig. 19).

Distribution of the dark and pale phases of the subspecies is shown in Figure 20, in which it is obvious that the black phase is more common in the northern portion of the peninsula. A single specimen of pale-phase *fuliginosus* (USNM 37551) is available from that portion of the peninsula. It was collected in Trinidad Valley at the northwest base of the San Pedro Mártir Mountains by Nelson and Goldman. On the other hand, the pale phase is the more abundant form in the southern part of the pe-

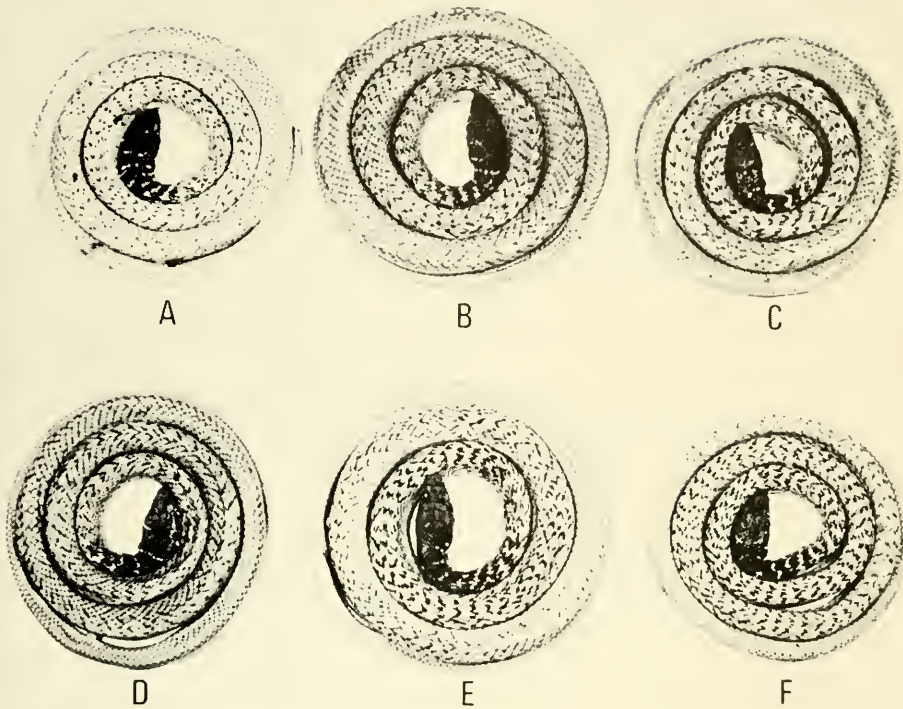


Figure 19. Dorsal view of six specimens of *Masticophis flagellum fuliginosus* showing the extent of variation in the amount of dark pigment in the dorsal pattern in the pale phase. The numbers for the specimens in the upper row, from left to right, are as follows: CAS 71150, 71151, 71147. For the bottom row, from left to right, the numbers for the specimens are as follows: CAS 71141, 71142, 71148. All specimens are from Cabo San Lucas, Baja California del Sur, Mexico.

ninsula. Of 81 adult specimens examined from Baja California del Sur, 66 are of the pale phase.

Only one phase has been found at most localities. There are, however, a few mainland localities where both have been collected. These localities, all in the southern part of the peninsula, are San Bartolo, San Pedro, Scammon's Lagoon, La Paz, San Antonio, and San Ignacio. Because the samples from each of these localities are small, it is useless to speculate which phase is more abundant in areas of sympatry.

Masticophis flagellum fuliginosus is known from many of the islands off both coasts of Baja California, but not from the islands adjacent to the northern portion of the peninsula. I have seen specimens from Isla

Magdalena and Isla Margarita (the type locality) on the Pacific side, and from Islas Coronados, Carmen, Monserrat, San José, Espíritu Santo, and Cerralvo in the Gulf of California. In addition this subspecies has been reported from Isla San Ildefonso (Klauber, 1942; Cliff, 1954).

Previously, each island was thought to be inhabited by only a single color phase (Klauber, 1942; Cliff, 1954). Whereas this is true of most of the islands, there are exceptions. Islas Carmen and San José have only the pale phase, and Islas San Ildefonso, Coronados, Espíritu Santo, Margarita, and Cerralvo have only the dark phase. Isla Monserrat has both phases, however, as does Isla Magdalena.

Though obviously related to the mainland

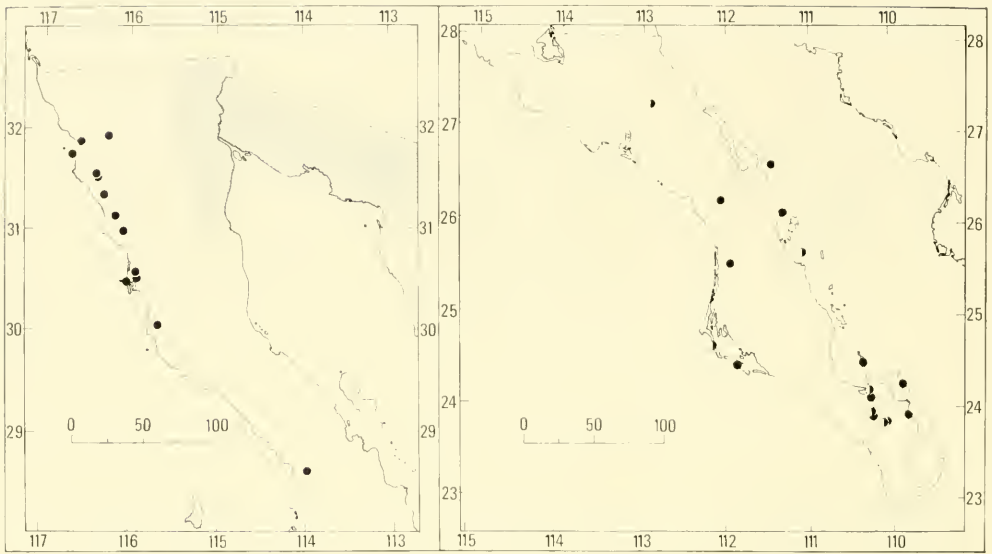


Figure 20. Distribution of the pale and dark phases of *Masticophis flagellum fuliginosus* in Baja California, Mexico. Black dots represent localities for the dark phase, open dots localities for the light phase, and half-filled dots localities for both. The stippled area indicates the range of *M. f. picus*.

populations, the snakes from the islands show a considerable amount of interisland variation in color pattern (Figs. 21A and B). The population of dark phase snakes on Isla Coronados is very similar to the mainland populations. I have seen two specimens (SDSNH 30378, 30379) from this island. The larger of the two (snout-vent length 1309 mm) is very dark grayish brown on the anterior portion of the body, grading to dark brown posteriorly. There is some pale flecking laterally. The venter is largely cream (dorsal coloration extends onto the lateral edges of the ventrals) with a dark brown suffusion on the neck. The head is brown dorsally and laterally with cream spotting. The chin is cream with heavy brown blotching. The smaller specimen (snout-vent length 1112 mm) generally conforms to this description, but its dorsal

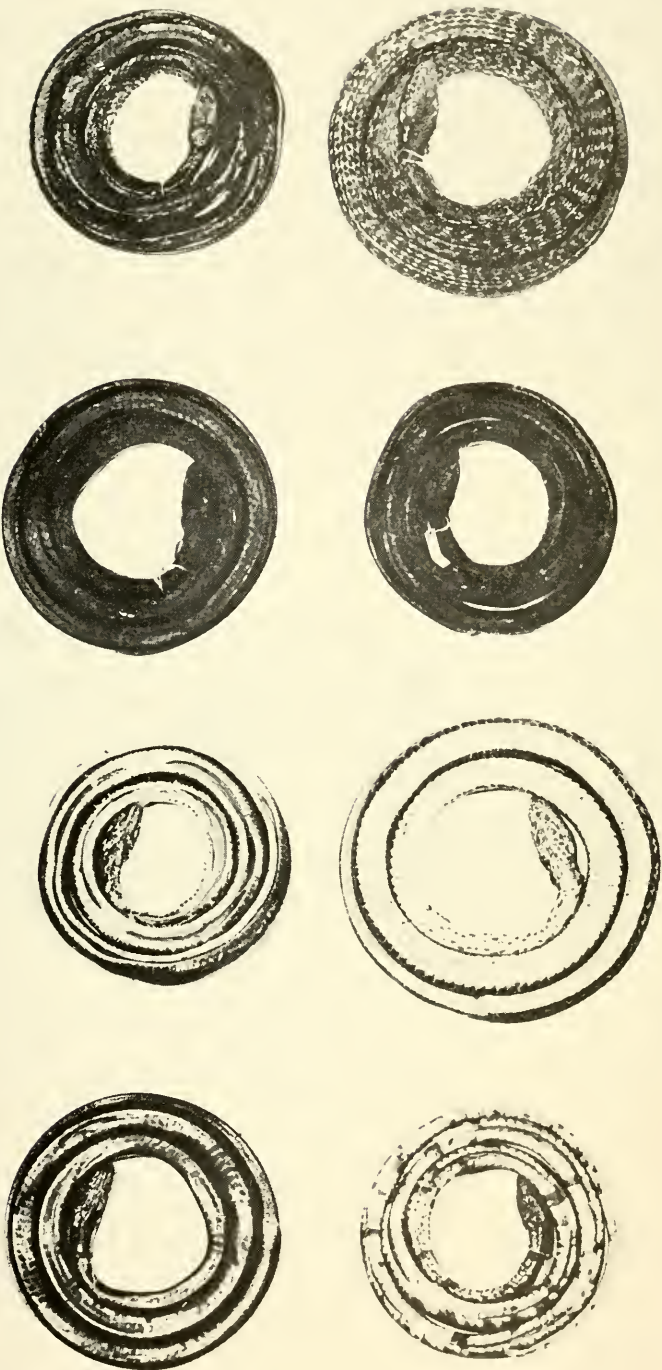
coloration is much paler. This description agrees well with the description given by Cliff (1954) for thirteen specimens from the same island.

The specimens I have seen from Isla Cerralvo (SDSNH 44373-74, 44481, 52708; UCM 26384-85; LACM 25070) are similar to one another in having the dorsum very dark brown, grading to dark brown posteriorly. The head is more or less uniformly dark brown dorsally and laterally. The venter is cream with the dark dorsal color extending onto it in patches, thus producing a checkerboard pattern. The lateral flecking is reduced or absent. Again there is agreement with the description given by Cliff (1954).

I have seen four specimens from Isla Espíritu Santo, three of which (SDSNH 44385, 3820, 44637) are similar to one

Figure 21. Interisland variation in the dark phase of *M. f. fuliginosus*. A. Dorsal view of four specimens from the islands in the Gulf of California. The numbers and localities for the specimens illustrated are as follows: upper left, SDSNH 30379, from Isla Coronados; upper right, SDSNH 44639, from Isla Monserrat; lower left, SDSNH 44637, from Isla Espíritu Santo; lower right, SDSNH 44373, from Isla Cerralvo. B. Ventral view of four specimens in the same order as in A.

A



another in color pattern. The other specimen (SDSNH 3821), however, resembles specimens from Monserrat. Although of different sizes, the first three specimens agree in having the total ventral surface heavily suffused with dark brown pigment. The largest specimen (SDSNH 44637) has a completely dark brown venter, except for some cream flecking in the region of the vent and along the midventral line of the tail. Dorsally this specimen is very dark brown with no lateral flecking except at the angle of the jaw. The smaller specimens show an intermediate stage in development of the adult pattern and are similar, except for the ventral coloration, to representatives of the mainland population. One specimen (SDSNH 3821) differs from the rest in having a cream venter which is only lightly suffused with dark brown pigment. It is identical to dark phase specimens from Monserrat, hence the locality data for this specimen may be in error.

The specimens of the dark phase from Monserrat (SDSNH 44375, 44480, 44639-40) are very dark grayish brown dorsally, grading to dark brown posteriorly. The venter is cream with a double row of brown spots on the neck and the forebody. They appear to differ from specimens from the other gulf islands in retaining dorsal flecking to a greater body length and in having the brown pigment of the venter more clearly arranged into a double row of spots. There is essential agreement with the description given by Cliff (1954) for specimens from Monserrat.

From Isla Santa Margarita I have seen only the two syntypes of *Zamenis lateralis fuliginosus*. They have been described above and they agree with the mainland population in color pattern. Two specimens (CAS 56048-49) examined by Klauber (1942), but not by me, are also of the dark phase.

Seven specimens have been examined from Isla Santa Magdalena (CAS 55887-91; SDSNH 3824, 10546). Both phases are present as well as specimens that are intermediate in coloration between the two (Fig. 22). The dark phase individuals agree well with those from the mainland. The dorsum is dark grayish brown with lateral flecking; the venter is creamy yellow with grayish brown spots on the neck and forebody, which break up into flecks posteriorly. One

specimen (CAS 55890) is intermediate in coloration. It has a snout-vent length of 1440 mm but is much paler than CAS 55888, which has a snout-vent length of 1365 mm.

The pale whipsnakes I have seen from the islands all have a yellowish ground color. The animals from Isla San José (UCM 26137; SDSNH 6872, 44638, 44641-43) and Isla Carmen (JFC 65-204, UCM 27269-70, SDSNH 3824) are more or less similar to one another and to the pale phase snakes from the mainland. A single specimen (SDSNH 44375) from Isla Monserrat is much more heavily speckled with dark pigment dorsally than are those from San José and Carmen. A pale phase snake from Isla Magdalena (SDSNH 10546) is also similar to animals from the above-mentioned islands and to the animals from the mainland.

In summary, specimens of *M. f. fuliginosus* from the islands off both coasts of Baja California del Sur show varying degrees of affinity to the snakes of the mainland populations and tend to be more stable in color pattern than those from mainland populations. Consistent interisland differences in color pattern appear to have become established. There is more color pattern variability in the dark phase than in the pale phase snakes. The level of divergence of color pattern between the island snakes, especially those of the gulf islands, and the mainland snakes might prompt some workers to describe new subspecies. It appears to me, however, that this would only obscure the situation by de-emphasizing the close relationships of the island populations to those of the mainland, with which their affinities obviously lie.

Dark specimens are also known from San Diego County, California. I have examined specimens of the pale phase from San Diego County that either were red (if freshly preserved) or, probably, would have been red in life. This information corroborates Klauber's statement that San Diego County specimens are predominantly red. They also agree in general pattern with snakes of this phase found farther north and east, and I have no hesitation in referring them to the subspecies *piceus*. On the other hand, the San Diego County specimens of black phase *fuliginosus* that I have examined (SDSNH 2144, 7579, 13710,

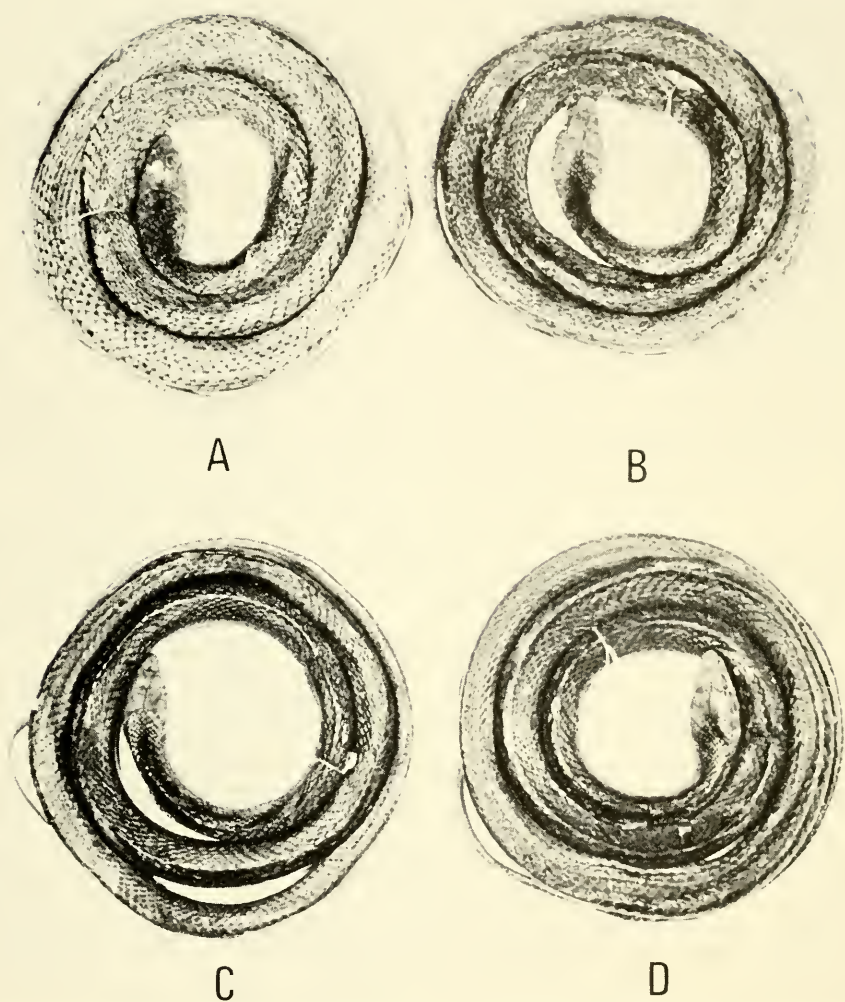


Figure 22. Dorsal view of four specimens of *Masticophis flagellum fuliginosus* from Isla Santa Magdalena, Baja California del Sur, Mexico. The numbers for the specimens illustrated are as follows: (A) CAS 55890; (B) CAS 55889; (C) CAS 55887; (D) CAS 55888.

25600, 44341) agree in every respect with black *fuliginosus* from farther south in the peninsula of Baja California and are distinct from black *piceus*. It appears that the red phase of *piceus* and the black phase of *fuliginosus* are not sympatric within San Diego County; *fuliginosus* occurs in the extreme southern portion of the county and *piceus* occurs in other areas. I have seen no intermediate specimens but such are to be

expected in areas of contact. Interpretation of intergradation between these two subspecies may be difficult inasmuch as it is the pale phase of *piceus* and the dark phase of *fuliginosus* that occur in San Diego County.

Populations of Questionable Status

There remains a problem regarding the status of the populations of *Masticophis*



Figure 23. Dorsal view of a specimen of *Masticophis flagellum* from El Dorado, Sinaloa, Mexico (AMNH 90730).

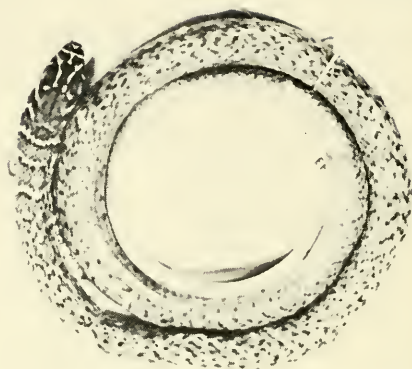


Figure 24. Dorsal view of a juvenile specimen of *Masticophis flagellum* from Hacienda Simón, 7.6 miles N Culiacán, Sinaloa, Mexico (UMMZ 120233).

flagellum in northern Sinaloa. I had been under the impression that the specimens from this area were all of the pattern D type of *M. f. cingulum*, i.e., unicolorous. However, during the final stages of this study I received several specimens that did not fit my concept of *cingulum*. This material includes individuals of all size groups.

As previously noted, southern populations of *cingulum* lack the banded pattern that is typical farther north, and adults are uniformly tan or brown dorsum (in preserved material). I have seen no living specimens from southern Sonora, but Joseph F. Copp has reported that specimens from the area are nearly uniform red.

In Sinaloa the large adults are nearly uniform tan in color (in preservative), but have some small gray or black spots on many of the dorsal scales (LACM 6995-96). Subadult specimens (AMNH 90728-32; KU 67688) usually have more pronounced spotting and, in addition, they retain the typical juvenile head pattern of the *piceus* group until they attain a greater body size than is the case in either *cingulum* or *piceus* (Fig. 23). The dorsal head pattern is much more pronounced than in juvenile *cingulum*. The border of each dorsal head scale is outlined with white or cream. The area immediately within the cream area is dark brown and the middle portion of the scale is pale

brown. The juveniles, although they have the typical *piceus* group juvenile pattern, have brighter head markings and a more spotted dorsum.

The following description is of the head pattern of UMMZ 120233, a juvenile from Hacienda Simón, 7.6 miles N Culiacán, Sinaloa (Fig. 24). The internasals and prefrontals have wide cream borders anteriorly and medially. The greater part of each scale is dark brown; the posterior edge is tan. The frontal is edged with cream anteriorly and tan laterally. Inside this area there is another narrow region of dark brown. The middle of the frontal is pale brown. The supraoculars are edged with cream anteriorly and laterally and tan posteriorly. Most of the rest of the scale is dark brown except for the median and outer lateral portions, which are light brown. The parietals have a cream spot anteriorly and a continuation of the cream stripe on the upper postocular onto the anterolateral area. The lateral edge of the parietal is edged with dark brown. The ventral portion of the rostral is cream. The upper half is brown with a central light brown blotch. The anterior nasal is mostly brown except for the anterior edge, which is cream. The posterior nasal is dark brown dorsally and ventrally with a central cream area. The loreal is dark brown with an anteromedial cream blotch.

The upper preocular is dark brown along, and dorsal to, the canthus rostralis; the ventral portion is cream. The lower preocular is cream anteriorly, dark brown posteriorly. The upper postocular is dark brown with a central cream stripe. The supralabials are cream with dark brown blotching. The temporals are cream with dark brown blotching.

These specimens differ from *M. f. cingulum* in having, as adults, a patternless dorsum, except for some small spots on the dorsal scales, and in having the juvenile head pattern accentuated and retained in larger individuals. Subadult specimens from Sinaloa are patternless, whereas adult *piceus* are banded. In addition, juveniles from Sinaloa are much more brightly marked than juvenile *piceus* and the dorsum is more spotted.

These specimens from Sinaloa may represent a distinct pattern form that deserves subspecific recognition. I have seen insufficient material, however, to make such a decision at this time.

KEY TO THE SUBSPECIES OF ADULT

Masticophis flagellum

This key is designed so that all pattern phases of the subspecies of *Masticophis flagellum* may be identified.

1. Each dorsal scale (at least on the anterior portion of the body) with a dark brown to black medial line; mid-portion of venter bright yellow; subcaudals and posterior portion of venter with a salmon pink to red posterior border which does not fade in preservative *Masticophis flagellum lineatulus*
Pattern not as above 2
2. Anterior 1/3 to 1/2 of dorsum dark to very dark brown (some specimens nearly black), posterior 2/3 to 1/2 brown to tan (in black specimens, the posterior portion of the venter and underside of tail are cream as opposed to the pink coloration (in life) of this area in black *M. f. piceus* and *M. f. cingulum*)
Masticophis flagellum flagellum
Color pattern not as above 3
3. Some portion of dorsum red or pink in life (tan or light brown in preservative) 4
Dorsum not red or pink 10
4. Anterior portion of dorsum solid black, posterior portion red 5
Pattern not as above 6
5. Posterior 1/3 to 1/2 of body with a pattern of black bands separated by

light red (tan in preservative) interspaces; sometimes a narrower, black band bisects the light interspaces

..... *Masticophis flagellum cingulum*
(pattern F)

Posterior 1/3 to 1/2 of body with a variegated pattern of red and black scales with no division into dark bands and narrow, light interspaces

..... *Masticophis flagellum piceus*
(intermediate phase)

6. Dorsum dark red to dark reddish-brown, this coloration being broken into long bands (11 to 14 scales long) by light (pink in life) interspaces 5 to 6 scales in length. A dark narrow band usually bisects each light interspace. This type of pattern usually extends the length of the body (pattern class A) but some specimens have this banding reduced and confined to a variable amount of the anterior portion of the body (pattern class B) 7
Dorsal banding, if present, confined to neck 8
7. Some black scales on neck
..... *Masticophis flagellum cingulum*
(pattern type E)
No black scales on neck
..... *Masticophis flagellum cingulum*
(pattern classes A and B)
8. A single light band across nape 7
..... *Masticophis flagellum cingulum*
(pattern C)
Pattern not as above 9
9. Dorsum with relatively long (3 to 4 scales long) black, gray, or brown (also sometimes the same color as the dorsum, outlined anteriorly and posteriorly with darkened pigment) bands on neck and a light, dark-bordered stripe through loreal 9
..... *Masticophis flagellum piceus*
(red phase)
Dorsum uniformly pink or salmon pink with slight banding on neck (bands, when present, narrow, about 1 scale long); no light, dark-bordered stripe through loreal
..... *Masticophis flagellum testaceus*
(pink phase)
10. Dorsum tan to light brown, yellow or light gray, or light yellow to light olive yellow 11
Dorsum dark grayish-brown to black 17
11. Dorsum tan to light brown 12
Dorsum yellow, light gray, or light yellow to light olive yellow 16
12. Remnants of juvenile pattern present; dark juvenile head markings of *flagellum* group present on dorsal head scales; bands on neck dark brown and well defined
..... *Masticophis flagellum flagellum*
(pale phase)
Dorsal pattern not as above 13
13. Dorsum uniform tan to light brown (at least in preservative) with no pattern

- Masticophis flagellum testaceus* (patternless phase), *Masticophis flagellum cingulum* (patternless phase), and Sinaloan specimens
Dorsum tan with some type of pattern 14
14. Dorsum uniform tan to light brown with a narrow, light band across nape of neck ... *Masticophis flagellum cingulum* (pattern C)
Dorsal pattern not as above 15
15. Dorsum with narrow (usually 1 and sometimes 2 scales long) brown to dark brown bands on neck and forebody; dorsum of head more or less uniform in coloration
..... *Masticophis flagellum testaceus* (narrow-banded phase)
Dorsum tan with wide, brown bands separated by narrower, lighter interspaces; wide bands sometimes composed of a series of dark brown narrow bands which are separated by a much lighter, shorter series of narrow bands
..... *Masticophis flagellum testaceus* (wide-banded phase)
16. Dorsum yellow or light gray with narrow, zig-zag black bands on dorsum, and with wider dark brown bands on neck; a double row of brown to dark brown spots on anterior portion of venter
..... *Masticophis flagellum fuliginosus* (pale phase)
Dorsum light yellow to light olive yellow; pattern absent or with obsolete bands on neck more or less the same color as the ground color; no spotting on anterior portion of venter
..... *Masticophis flagellum ruddocki*
17. Dorsum and head completely black; posterior portion of venter and underside of tail salmon pink to red
..... *Masticophis flagellum piceus* (black phase) and *Masticophis flagellum cingulum* (black phase)
Dorsum dark grayish-brown with indication of light lines on a variable amount of the lateral area of the dorsal scales; head usually somewhat lighter than rest of dorsum; venter usually completely cream with a double row of dark spots on anterior portion (specimens with a variable amount of dark pigment on anterior portion of venter still have cream coloration on posterior portion of the body) *Masticophis flagellum fuliginosus* (dark phase)

SIGNIFICANCE AND EVOLUTION OF COLOR PATTERN

Masticophis flagellum is one of the most variable snakes in North America. Not only is the species divisible into geographic races, but almost all the subspecies exhibit pattern

variations. Only two, *M. f. lineatulus* and *M. f. ruddocki*, do not. Also, most of the subspecies exhibit an ontogenetic change in color pattern. Only *M. f. testaceus*, of the *testaceus* group, and the red phase of *M. f. piceus* and the pale phase of *M. f. fuliginosus*, both of the *piceus* group, show very little change in color pattern from juvenile to adult.

The types of variation in adult pattern within the subspecies of *Masticophis flagellum* fall into four categories. These are: (1) clinal variation, (2) random variation, (3) non-clinal geographic variation, and (4) polymorphic variation. Clinal variation in color pattern is exhibited by *M. f. flagellum* and *M. f. cingulum*. In *M. f. flagellum* the color pattern is paler (has less dark brown pigment on the anterior portion of the body) in the southeastern portion of its range and is darker in the northwestern portion of its range. In *M. f. cingulum* there are two, more or less parallel clines within the range. First, there is a clinal trend toward loss of the banded pattern (pattern A), found most commonly in the northern and northeastern portions of the range, to the unicolor pattern (pattern D), found most commonly in the southern portion of the range. Second, there is another clinal trend toward progressive melanization of the banded pattern (pattern A) of the northern and northeastern portion of the range to produce the black pattern (pattern G), found in the central and eastern portions of the range. This deposition of black pigment takes place from anterior to posterior, and some specimens are totally black dorsally, thus paralleling the type of pattern seen in the black phase of *M. f. piceus*.

Random variation is seen in all subspecies, but it is most conspicuous in *M. f. testaceus*, in which the variation in color pattern is discontinuous, *i.e.*, there are three distinct patterns found in varying proportions throughout the range.

Geographic variation within subspecies limits is seen in *M. f. flagellum* and *M. f. testaceus*. In *M. f. flagellum* there is a pale tan phase centered in Florida, the adult pattern of which closely resembles the pattern of all juveniles of the *testaceus* group generally, and the pattern of juvenile *flagellum* particularly. This phase has a clearly defined, albeit discontinuous, range in portions

of Florida and Georgia (a single comparable specimen from North Carolina was also seen). In *M. f. testaceus* there is a pink phase, which differs from the more common and widespread tan form. This phase inhabits three disjunct areas in Trans-Pecos Texas, eastern New Mexico, and eastern Colorado.

Polymorphism is seen in *M. f. piceus* and *M. f. fuliginosus*. Both subspecies have a pale (red in *piceus*, yellow, tan, or light gray in *fuliginosus*) and a dark phase (black in *piceus*, dark grayish-brown in *fuliginosus*). Intermediate specimens are more common in the case of *piceus*, less so in *fuliginosus*. There is a dearth of information on the basis for this polymorphism. It is not known whether dark phase adults always give birth to dark phase young and light phase adults to light phase young, or whether both might appear in a single brood of either phase as is the case in *Lampropeltis getulus californiae* (Klauber, 1944). There is no information, other than that which I have presented in discussing color pattern variation, on the relative frequency of each color pattern in any given population. It is known that the range of the black phase of *M. f. piceus* is centered around Tucson, and that radiating from that central point the phase becomes less frequent in occurrence. It is also known that within its range the black phase is most common, the intermediate phase next, and the pale phase least common.

Within the subspecies *fuliginosus* the picture is less clear, largely because of insufficient material. Are there areas where only the pale phase occurs, as is suggested by the specimens available from the extreme southern cape region of the peninsula of Baja California and some of the gulf islands? Are there areas where only the dark phase occurs, as is suggested by material from the northwest coast of Baja California del Norte and others of the gulf islands? If so, why is this the case and why is it that both phases occur in some areas? What is the genetic basis of this pattern dimorphism? It would appear that neither in the case of *piceus* nor that of *fuliginosus* is it based on a single pair of alleles, for intermediate specimens do exist, which suggest the action of modifier genes in producing the adult pattern. Mayr (1963, p. 151)

stated "the genes involved in polymorphism have, in general, conspicuous discontinuous effects, and different genotypes (except some heterozygotes) can be distinguished phenotypically." If the intermediate is considered a heterozygote, resulting from the crossing of a homozygous pale phase snake with a homozygous black phase snake, then the situation cannot be designated as balanced polymorphism, which is maintained by "overdominance" of the heterozygote (Mayr, 1963, p. 221). In fact, the intermediates appear with a much lower frequency than either the pure dark or pale phases, at least in the peninsula of Baja California. Thus the usual solution to the problem of the maintenance of polymorphism does not seem to apply here.

This situation is similar to that described for the screech owl (*Otus asio*) by Owen (1963). Two phases of the screech owl, a gray one and a rufous one, exist over the portion of eastern United States lying east of meridian 104° W. Intermediate specimens also occur, as is the case among the whip snakes. The relative frequency of rufous screech owls varies geographically, as does the relative frequency of intermediate birds. Owen suggested that this type of polymorphism, which he preferred to call bimodal variation, is the result of a balance of selective forces acting on each phase and that the presence and maintenance of these two phases "represent balanced adaptations of the forms to varying environmental conditions." He goes on to say that "the existence of two distinct forms with few intermediates throughout much of the range of the screech owl in eastern North America is indicative of selection for bimodal variation. In most areas, selection must be continually operating against intermediates, but in Florida, where intermediates are frequent . . . , there is presumably a relaxation of selection pressure. The result of this is that while all six color categories [a pattern classification used by Owen to determine the frequencies of intermediates] occur in Florida, the population is extremely variable, but not polymorphic. Hence in the screech owl the unusual situation exists in which polymorphism for color and pattern is maintained over a large geographical area (eastern North America), while in a much smaller area (Florida) the complete range

of phenotypes occur, but the population is not polymorphic." West of the 104th meridian all the birds are gray.

Although the characteristics of the polymorphism exhibited by the subspecies *piceus* and *fuliginosus* are less well documented, there appear to be some differences from the review presented by Owen for the screech owl. Some of these are due to the smaller range inhabited by the black phase whipsnakes and to the smaller number of specimens available for study. In *fuliginosus*, however, it appears that intermediates are few in number, thus presenting a condition approaching bimodal variation. In *piceus*, on the other hand, intermediate specimens are of rather frequent occurrence and there would seem to be little selective pressures acting against the maintenance of this type of pattern. Also, in the area where the black phase of *piceus* occurs, it is the most common phase, and the light phase is the least common. Thus, at least in the case of *piceus*, there would appear to be little selection for bimodal variation.

In any event, to place a name on the type of variation exhibited by *piceus* and *fuliginosus* would be no solution to the problem of why, in certain areas, a polymorphic phase is maintained. If there are subtle differences in niche preference, it is not presently known what they might be. There is, in fact, very little information on any aspect of the ecology of *Masticophis flagellum*.

It is evident from a study of juvenile pattern, that there are two main evolutionary lines within the species *flagellum*. One, an eastern group of three subspecies (*flagellum*, *testaceus*, and *lineatulus*), is characterized by having a juvenile pattern composed of a tan dorsum with narrow, dark crossbands (usually 1 scale long, sometimes 2) separated by wider interspaces (Fig. 25). The other, a western group of four subspecies (*piceus*, *cingulum*, *ruddocki*, and *fuliginosus*), differs from the eastern group in having relatively long neck bands (3 to 4 scales in length) and narrow (1 scale in length) interspaces (Fig. 25). The members of this western group also have a pale streak through the nasal and loreal scales. This streak usually is straight-edged and longitudinal, and usually extends completely through the loreal, joining with

a pale blotch on the upper preocular. In contrast, in the eastern group, the pale spots on the nasal and loreal scales are not in contact but are separated by a thin stripe of brown pigment along the posterior edge of the posterior nasal. Also, the pale spots on the nasal and loreal are not oriented longitudinally, and the spot on the loreal is not in contact with the spot on the upper preocular. There is considerable irregular cream blotching on the temporals of the western group, which is less evident or absent in the eastern group.

In both groups there is a subspecies that retains the juvenile pattern essentially unchanged to the adult stage. In the eastern (*testaceus*) group it is the subspecies *testaceus*, and in the western (*piceus*) group it is the subspecies *piceus*. The other subspecies of each group have departed in varying degrees from this pattern, at least in the adult color pattern.

Thus, the division of the species *flagellum* into two stocks appears to have taken place at an early time, inasmuch as the basic patterns of the *piceus* and *testaceus* groups are markedly different. None of the juvenile patterns of the subspecies in either group shows any approach in basic pattern to juveniles of the subspecies of the other group.

Within the *testaceus* group, the subspecies *testaceus* is the central form from which the other two subspecies, *flagellum* and *lineatulus*, have diverged. *M. f. flagellum* has invaded the eastern United States and become adapted to the Austroriparian type of vegetation. *M. f. lineatulus* has invaded the Chihuahuan Desert of the northern portion of the Mexican Plateau. These two subspecies have diverged from more or less opposite ends of the range of the *testaceus*-like ancestor and have little in common with each other, *flagellum* having developed a dark brown anterior body color and *lineatulus* a lineate dorsum and a salmon-red venter.

Within the *piceus* group the subspecies *piceus*, or its ancestor, is the central stock from which the other subspecies have diverged. One subspecies has invaded Mexico west of the Sierra Madre Occidental and evolved a different type of banded pattern from that seen in *piceus*. This is the subspecies *cingulum*. The subspecies *ruddocki*

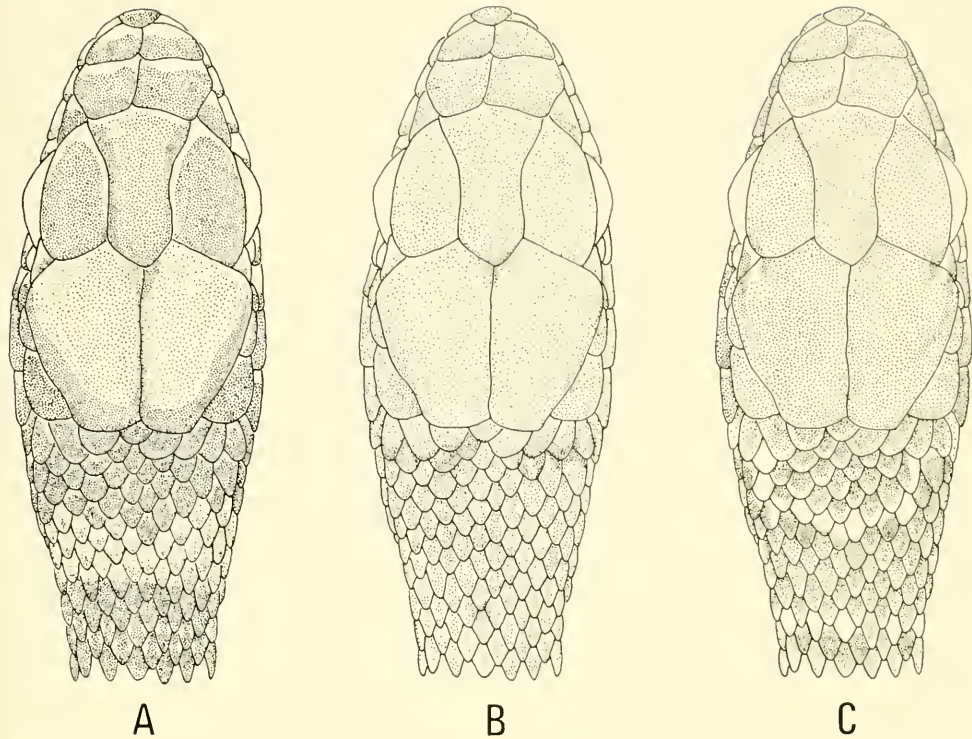


Figure 25. Dorsal view of the head of juvenile *Masticophis flagellum flagellum* (A), *M. f. tescatus* (B), and *M. f. piceus* (C).

has invaded the central valley of California and developed a pattern lacking the type of neck banding seen in *piceus* and having a different ground color. The subspecies *fuliginosus* has invaded the peninsula of Baja California and developed a basically different ground color and a slightly different type of banding on the dorsum.

VARIATION IN SCUTELLATION
AND PROPORTIONS
Head Scutellation

Supralabials.—The number of supralabials is normally 8, the fourth and fifth entering the orbit. Variation from this number is infrequent. Only 7.9% of the specimens examined has a count other than 8-8. Departures from the usual 8-8 condition involve the fusion or division of scales. Increase in the number of supralabials most often involves the division of the third supralabial (82.1%), but may also involve the division of the fourth (10.7%), second

(3.6%), eighth (2.4%), or fifth (1.2%). Decrease in the number of supralabials most often involves the fusion of the second and third supralabials (52.0%), but may also involve the fusion of the seventh and eighth (36.0%), or the fourth and fifth (12.0%). One specimen (TNHC 29117) has the second and third supralabials fused and the seventh divided giving the normal count of eight. The third and seventh supralabials are divided in JFC 63-150. In TNHC 7341 only the fifth supralabial enters the orbit. What apparently has taken place is that one of the anteocular supralabials is divided (probably the third) and the fourth and fifth are fused. In UCM 31533 the fourth supralabial does not enter the eye on the left side and is not present on the right. NTSU 193 has the seventh supralabial fused with one of the temporals. Variation in these scales is shown in Tables 4 and 5.

Infralabials.—The number of infralabials is most often 10 on each side of the head

TABLE 4.
Variation in number of supralabials in *Masticophis flagellum*.

Subspecies	7-7	7-8	8-8	8-9	9-9	Total
<i>flagellum</i>	—	3	321	16	2	342
<i>testaceus</i>	4	10	499	27	5	545
<i>lineatulus</i>	—	—	29	4	1	34
<i>piceus</i>	—	1	238	12	—	251
<i>cingulum</i>	—	1	74	2	1	78
<i>ruddocki</i>	—	—	9	3	—	12
<i>fuliginosus</i>	2	2	49	9	—	62
TOTAL	6	17	1219	73	9	1324

TABLE 5.
Variation in number of supralabials entering orbit in *Masticophis flagellum*.

Subspecies	3+4	3+4	4+5	4+5	5+6	4	5	4	Total
	3+4	4+5	4+5	5+6	5+6	4+5	5	4	
<i>flagellum</i>	—	3	321	16	2	—	—	—	342
<i>testaceus</i>	1	5	491	27	3	2	2	1	532
<i>lineatulus</i>	—	—	29	4	1	—	—	—	34
<i>piceus</i>	—	1	238	11	—	—	—	—	250
<i>cingulum</i>	—	—	75	4	1	—	—	—	80
<i>ruddocki</i>	—	—	9	3	1	—	—	—	13
<i>fuliginosus</i>	1	3	50	9	—	—	—	—	63
TOTAL	2	11	1213	74	8	2	2	1	1313

TABLE 6.
Variation in number of infralabials in *Masticophis flagellum*.

Subspecies	8-10	9-9	9-10	9-11	10-10	10-11	10-12	11-11	11-12	12-12	11-13	8-9	8-11	Total
<i>flagellum</i>	1	2	22	1	159	80	8	35	8	1	1	—	—	318
<i>testaceus</i>	1	17	54	8	248	121	3	29	6	1	—	1	1	490
<i>lineatulus</i>	—	—	6	1	14	5	1	—	—	—	—	—	—	27
<i>piceus</i>	—	1	12	4	101	74	5	39	5	—	—	—	—	241
<i>cingulum</i>	—	—	4	—	31	20	3	11	2	—	—	—	—	71
<i>ruddocki</i>	—	—	1	—	3	3	1	2	—	—	—	—	—	10
<i>fuliginosus</i>	—	6	8	—	36	9	—	2	—	—	—	1	—	62
TOTAL	2	26	107	14	592	312	21	118	21	2	1	2	1	1219

TABLE 7.
Variation in number of infralabials contacting anterior chin shields in *Masticophis flagellum*.

Subspecies	3-3	3-4	4-4	4-5	5-5	Total
<i>flagellum</i>	1	—	283	26	4	314
<i>testaceus</i>	—	4	460	17	1	482
<i>lineatulus</i>	—	—	23	3	1	27
<i>piceus</i>	1	—	230	8	2	241
<i>cingulum</i>	—	1	68	3	—	73
<i>ruddocki</i>	—	—	6	6	—	12
<i>fuliginosus</i>	7	2	53	—	—	72
TOTAL	9	7	1123	63	8	1210

TABLE 8.
Variation in number of loreals in *Masticophis flagellum*.

Subspecies	0-1	1-1	1-2	2-2	2-3	Total
<i>flagellum</i>	3	341	3	5	1	353
<i>testaceus</i>	—	515	15	4	—	534
<i>lineatulus</i>	1	32	—	—	1	34
<i>piceus</i>	—	253	1	—	—	254
<i>cingulum</i>	1	78	—	—	—	79
<i>ruddocki</i>	1	11	—	—	—	12
<i>fuliginosus</i>	—	69	1	—	—	70
TOTAL	6	1399	20	9	2	1436

(48.6%), 4 infralabials being in contact with the anterior chin shields, the fifth the largest. Deviations from this number, however, are manifold (Tables 6 and 7). The first to the fifth infralabials are relatively stable and most variation takes place behind this area. The variation in number of infralabials posterior to the fifth is more erratic and involves the addition, deletion, fusion, and division of small scales. Thus, the pattern is not clear. Division and fusion, however, do take place within this relatively stable anterior zone. Increase in the number of infralabials in this area most commonly involves the division of the third infralabial (82.4%), but also may involve the division of the fourth (11.8%) or second (5.8%) infralabials. Decrease in the number of infralabials in this area most often involves the fusion of the third and fourth infralabials (71.4%), but also may involve the fusion of the second and third infralabials (28.6%). Variation in these scales is shown in Tables 6 and 7.

Nasal.—The nasal scale is always divided vertically. A few specimens, however, have the postnasal section divided horizontally.

Loreal.—The loreal usually is single on both sides of the head (97.4%). Increase in the number of loreals involves the hori-

zontal division of the existing loreal into two parts on one or both sides of the head and the addition of one or more smaller scales, usually between the loreal and the supralabials. Decrease in the number of loreals involves the fusion of this scale either with the prefrontal (50.0%) or with the posterior nasal (50.0%). Variation in this scale is shown in Table 8.

Preoculars.—The number of preoculars usually is 2 (98.9%). Increase in the number of preoculars involves either the formation of a suture at the junction of the canthal ridge on this scale and the flat vertical portion (28.6%), the formation of a suture farther down on the vertical portion of this scale (28.6%), or the splitting off of a scale from the fourth supralabial to form a third preocular-like scale (42.8%). Decrease in the number of preoculars is an uncommon event, but when it occurs it involves the fusion of the lower preocular with the third infralabial. Variation in these scales is shown in Table 9.

Postoculars.—The numbers of postoculars predominantly is 2 (98.0%). Increase in the number of postoculars involves the formation of a suture either in the middle of the lower postocular or in the middle of the upper postocular, or involves the fusion

TABLE 9.
Variation in numbers of preoculars in *Masticophis flagellum*.

Subspecies	1-1	1-2	2-2	2-3	3-3	3-4	Total
<i>flagellum</i>	—	—	342	1	—	—	343
<i>testaceus</i>	—	—	528	4	1	—	533
<i>lineatulus</i>	—	—	33	—	—	—	33
<i>piceus</i>	—	—	246	3	2	—	251
<i>cingulum</i>	1	—	77	1	—	—	79
<i>ruddocki</i>	—	—	11	—	—	1	12
<i>fuliginosus</i>	—	1	70	—	—	—	71
TOTAL	1	1	1307	9	3	1	1322

TABLE 10.
Variation in number of postoculars in *Masticophis flagellum*.

Subspecies	1-1	1-2	2-2	2-3	3-3	Total
<i>flagellum</i>	1	1	337	2	1	342
<i>testaceus</i>	5	5	516	3	1	530
<i>lineatulus</i>	—	—	33	—	—	33
<i>piceus</i>	—	—	255	1	—	256
<i>cingulum</i>	—	—	79	—	—	79
<i>ruddocki</i>	—	—	12	—	—	12
<i>fuliginosus</i>	1	—	69	2	4	76
TOTAL	7	6	1301	8	6	1328

of the two normal postoculars and the splitting off of two scales from the fifth supralabial. Decrease in the number of postoculars involves either the fusion of the upper postocular with the parietal, the fusion of the two postoculars into one scale, or the fusion of the lower postocular with the fifth supralabial. Variation in these scales is shown in Table 10.

Frontal.—The frontal normally is bell shaped. The only anomaly observed in this scale is the presence, in two specimens, of a suture through the middle of the scale dividing it into anterior and posterior portions.

Internasals.—These scales normally are paired. One specimen (NCSM 5886), however, has the right internasal split into right and left halves and the left internasal fused with the anterior nasal.

Prefrontals.—These scales are normally paired. One specimen, however, has the prefrontal area divided into three scales.

Body Scutellation

Ventrals.—The number of ventrals ranges from 173 (in *M. f. testaceus*) to 212 (in *M. f. flagellum*). Ranges for the various subspecies are listed in the appropriate subspecies account. The means of the populations east of the Mississippi River are relatively constant. All means fall within the range of 201.0 to 203.7 for males and 196.0 to 201.8 for females. The highest means are in Florida, southern Georgia, Alabama, Mississippi, and western South Carolina (Fig. 26). West of the Mississippi River the mean number of ventrals drops sharply and continues to decrease more gradually through central and southern Texas (Fig. 27). In western Texas the means again be-

gin to rise, abruptly so in eastern New Mexico. The mean continues to rise through western New Mexico but again begins to decrease in Arizona, Nevada, Utah, and portions of southern California. Both to the north and the south of Los Angeles, San Bernardino, and Riverside counties, California, the mean number of ventrals again increases. Immediately to the south of San Diego and Imperial counties, California, the ventral number decreases, but farther down the peninsula of Baja California the mean number increases, until in the cape region the mean number of ventrals approaches some means for southeastern United States, the area which has the highest mean number of ventrals (Fig. 28). In Sonora the mean number of ventrals increases from north to south, but this cline reverses itself in northern Sinaloa. To the east of the Sierra Madre Occidental, in Chihuahua, the mean number of ventrals is much lower than to the west and most closely resembles means for central Texas. To the south, in Durango and Zacatecas, the mean is similar to that in Chihuahua but is slightly less than the mean of populations to the east in San Luis Potosí and Tamaulipas. There is a minor amount of sexual dimorphism in ventral number but females often have slightly fewer than males.

Anal Plate.—The anal plate is normally divided in this species and only two of the specimens examined have the two halves fused.

Subcaudals.—The variational trends in subcaudals are less clear than for the ventrals primarily because only about 48% of the specimens examined have complete tails. The number of subcaudals ranges from 91 (in *M. f. flagellum*) to 129 (in *M. f. fuliginosus*).

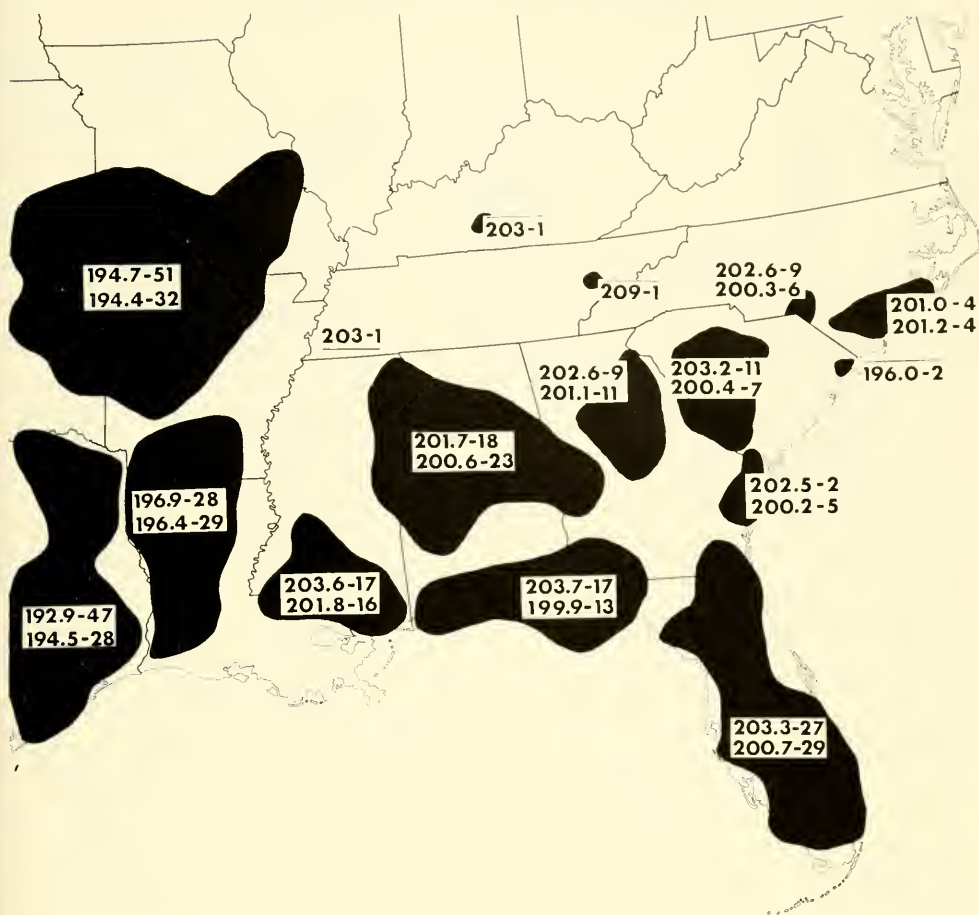


Figure 26. Geographic variation of ventral number in *Masticophis flagellum* in the eastern United States. Black blotches represent the areas from which samples were taken. The upper numbers associated with each blotch are the sample mean and sample size (separated by a dash) for males; the lower numbers present the same data for females. When a line appears in place of either the upper or lower figures, it signifies that no specimens of that sex were present in the sample.

Variational trends are similar to those observed for ventrals but are not identical. The mean number of subcaudals east of the Mississippi River is relatively high, but means for various populations are not so constant as are those of the ventrals in this area (Fig. 29). West of the Mississippi River the mean number of subcaudals decreases rather sharply and continues to decrease through western Oklahoma and eastern and central Texas (Fig. 30). Except for an increase in the male mean in eastern New Mexico, the decrease continues in western New Mexico and Arizona. The mean in-

creases again in southern California, except for populations from the central valley and adjacent areas where there are fewer subcaudals. The mean continues to increase, with some variation, southward through the peninsula of Baja California; means for the southern portion of the peninsula are the highest anywhere within the range (Fig. 31). In Sonora the mean tends to decrease from north to south, rather than increase as does the mean for the ventrals. This trend continues into northern Sinaloa where the mean is the lowest anywhere within the range, with the exception of Chihuahua



Figure 27. Geographic variation of ventral number in *Masticophis flagellum* in the western United States. Explanation as for Figure 26.

where the female mean is lower than that for females from northern Sinaloa. Although based on relatively few counts, the mean number of subcaudals for central and eastern Mexico is similar to that for central and southern Texas.

Sexual dimorphism in subcaudals is evident, with males having, usually, a higher mean number. The amount of difference between the sexes varies from population to population and ranges from about 2 to 8 scales in the majority of populations.

Apical Pits.—The number of apical pits in *Masticophis flagellum* is 2 over most of the body. I examined the shed skin of a *M. f. piceus* and found that not all dorsal body scales have 2 apical pits nor do all all have apical pits. In the neck region

scale pits are present on all rows except the first two lateral rows. On most scales the number of pits is 2, but on some scales there is only 1. On the other scales the two apical pits show varying degrees of divergence. On a few scales scattered along the dorsum there are no pits. On the anterior portion of the body there are no pits on the first two lateral rows and on the third they appear but faintly. The pits are more prominent dorsad. At midbody there are no pits on rows 1 through 4 and they appear but faintly on row 5. In the anal region few scales have apical pits. No pits are present on the scales of the tail.

Dorsal Scale Rows.—The dorsal scale rows in *Masticophis flagellum* are normally 19-17-15-14-13. This pattern includes two lat-

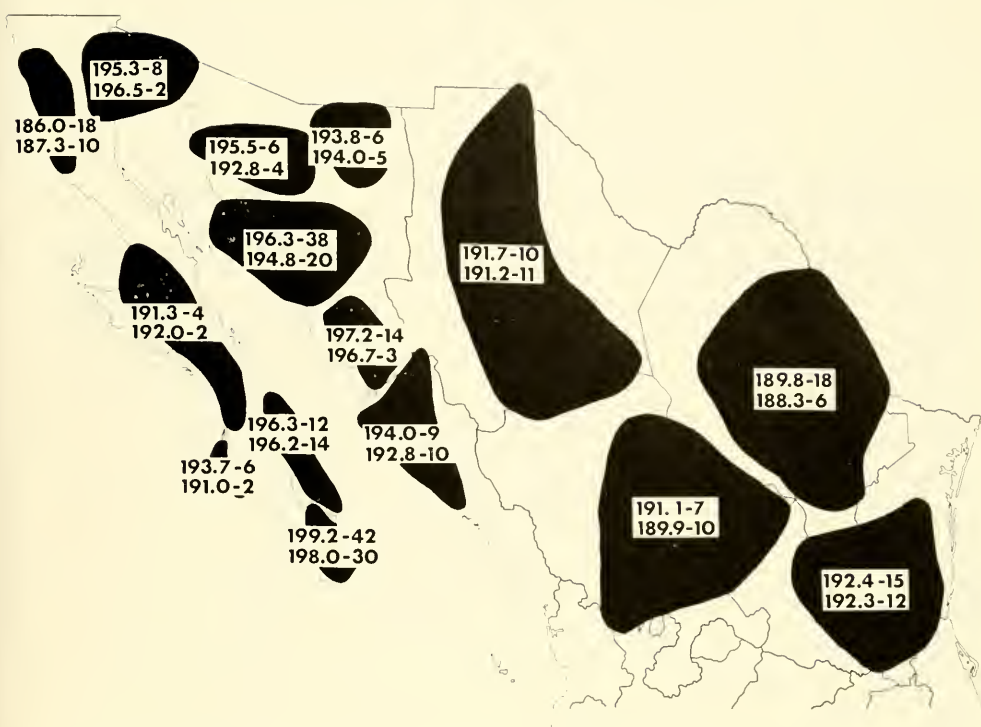


Figure 28. Geographic variation of ventral number in Mexico. Explanation as for Figure 26

eral reductions and two middorsal reductions. Scale reduction patterns were determined for 461 specimens from all portions of the range, including 339 from the United States and 122 from Mexico. Approximately 20% of the patterns may be summarized as follows:

$$19 \frac{3+4 (6-35)}{3+4 (6-33)} \quad 17 \frac{3+4 (85-139)}{3+4 (86-142)}$$

$$15 \frac{7+8 (91-159)}{7+8 (98-174)} \quad 14 \frac{7+8 (98-174)}{7+8 (98-174)} \quad 13$$

Several distinctive types of deviations from the standard pattern given above were noted. These deviations may be grouped as follows:

1. Lateral Reduction Substitution. In this pattern fusion of rows 2 and 3 or 4 and 5 replaces that normally occurring between rows 3 and 4. This substitution may occur in either the first or second lateral reduction as shown in the following examples:

AU 409 (Alabama)

$$19 \frac{4+5 (14)}{4+5 (16)} \quad 17 \frac{3+4 (138)}{3+4 (138)}$$

$$15 \frac{7+8 (168)}{7+8 (156)} \quad 14 \frac{7+8 (168)}{7+8 (156)} \quad 13$$

UAZ 9336 (Sonora)

$$19 \frac{3+4 (13)}{3+4 (13)} \quad 17 \frac{4+5 (113)}{4+5 (112)}$$

$$15 \frac{8+9 (116)}{8+9 (116)} \quad 14 \frac{7+8 (122)}{7+8 (122)} \quad 13$$

Fifty specimens (10.9%) show this deviation in the first lateral reduction and 51 (11.1%) show it in the second lateral reduction.

2. Occurrence of First and/or Second Middorsal Reductions Anterior to Second Lateral Reduction. This type of pattern is relatively common (41.2%), although it is more common for the first middorsal reduction to appear anterior to the second lateral reduction (34.2%). The two types of patterns are illustrated by the following examples:

MCZ 12779 (Alabama)

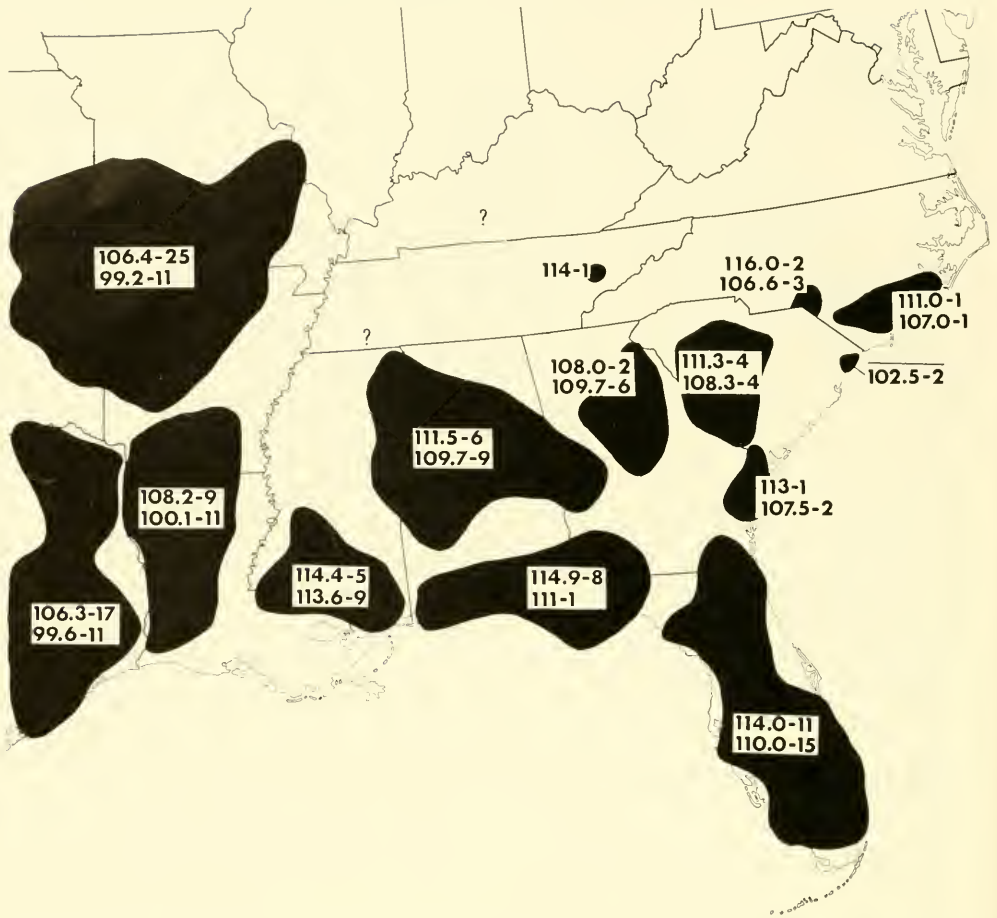


Figure 29. Geographic variation of subcaudal number in the eastern United States. Explanation as for Figure 26.

$$19 \frac{3+4 (12)}{3+4 (14)} \quad 17 \frac{8+9 (128)}{8+9 (128)}$$

$$16 \frac{3+4 (128)}{3+4 (130)} \quad 14 \frac{7+8 (156)}{7+8 (156)} \quad 13$$

NCSM 5872 (Mississippi)

$$19 \frac{3+4 (14)}{3+4 (15)} \quad 17 \frac{8+9 (132)}{8+9 (132)}$$

$$16 \frac{8+9 (139)}{8+9 (139)} \quad 15 \frac{3+4 (140)}{3+4 (145)} \quad 13$$

An example of this type of pattern is presented below:

NCSM 5170 (North Carolina)

$$19 \frac{3+4 (8)}{3+4 (9)} \quad 17 \frac{3+4 (127)}{3+4 (125)}$$

$$15 \frac{6+7 (142)}{6+7 (142)} \quad 14 \frac{6+7 (145)}{6+7 (145)}$$

$$13 \frac{6+7 (175)}{6+7 (175)} \quad 12$$

3. Lateral Displacement of the First and/or Second Middorsal Reductions. This pattern is characterized by the substitution of the fusion of scale rows 6 and 7 on either side of the body for the usual 7 + 8 fusion. This substitution is relatively common, occurring in 34.1% of the patterns determined.

4. Preanal Decrease. In this pattern there is a further decrease from the usual number of thirteen scale rows at the anus to twelve. This occurs in 38.9% of the patterns determined and involves usually a middorsal fusion of rows 6 and 7. An example is shown below:

UCM 19721 (Colorado)



Figure 30. Geographic variation of subcaudal number in the western United States. Explanation as for Figure 26.

$$\begin{array}{l} 19 \frac{3+4(12)}{3+4(17)} \quad 17 \frac{3+4(114)}{3+4(115)} \\ 15 \frac{7+8(116)}{7+8(124)} \quad 14 \frac{7+8(124)}{7+8(124)} \\ 13 \frac{6+7(148)}{6+7(148)} \quad 12 \end{array}$$

5. Preanal Increase. This type of pattern is characterized by an increase from thirteen rows to fourteen or fifteen rows or from fourteen rows to fifteen or sixteen rows. This increase may take place either by a lateral or middorsal division of one scale row into two. This deviation occurs in 4.6% of the patterns. An example is shown below:
UNM 8329 (Texas)

$$19 \frac{3+4(17)}{3+4(14)} \quad 17 \frac{3+4(118)}{3+4(118)}$$

$$\begin{array}{l} 15 \frac{7+8(129)}{7+8(129)} \quad 14 \\ 7+8(132) \quad 13 \frac{3=3+4(188)}{2=2+3(187)} \quad 15 \end{array}$$

6. Sporadic Increase and Decrease. In this pattern there is an irregular increase and decrease of dorsal scale row number at various points along the body. This deviation occurs in 2.0% of the patterns. An example is shown below:
CM 9533 (South Carolina)

$$\begin{array}{l} 19 \frac{3+4(9)}{?} \quad 17 \frac{3+4(127)}{3+4(128)} \quad 15 \frac{7+8(135)}{7+8(135)} \\ 14 \frac{7+8(145)}{7+8(145)} \quad 13 \frac{6+7(169)}{6+7(169)} \\ 12 \frac{2+3(177)}{2+3(177)} \quad 11 \frac{2=2+3(178)}{2=2+3(178)} \\ 12 \frac{2+3(181)}{2+3(181)} \quad 11 \frac{2+3(186)}{2+3(186)} \end{array}$$



Figure 31. Geographic variation of subcaudal number in Mexico. Explanation as for Figure 26.

$$10 \frac{2 = 2 + 3 (191)}{2 = 2 + 3 (199)} \quad 11 \frac{2 + 3 (192)}{2 = 2 + 3 (201)}$$

7. Simultaneous Paravertebral Fusion. Fusion of rows 6 and 7 on both sides of the body at the same place replaces the first two middorsal reductions. This deviation occurs in 3.7% of the patterns. An example of this type of pattern is shown below:

UMMZ 79621 (Arkansas)

$$19 \frac{?}{3 + 4 (13)} \quad 17 \frac{3 + 4 (119)}{3 + 4 (117)}$$

$$15 \frac{6 + 7 (130)}{6 + 7 (131)} \quad 13$$

8. Fusion of Middorsal with Two Paravertebral Scales. Fusion of rows 6, 7, and 8 at one spot replaces the normal first two middorsal reductions in 0.9% of the patterns as shown below:

MCZ 12778 (Alabama)

$$19 \frac{3 + 4 (9)}{3 + 4 (9)} \quad 17 \frac{3 + 4 (116)}{3 + 4 (116)}$$

$$15 \frac{6 + 7 + 8 (128)}{6 + 7 + 8 (128)} \quad 13$$

The variation exhibited by the individual

components of the scale reduction pattern will be considered next.

First Lateral Reduction. The reduction from 19 to 17 rows most commonly involves the fusion of the third and fourth scale rows (93.1% of the patterns determined exhibit this condition), but may also involve the fourth and fifth rows (4.8%) or the second and third rows (2.1%). The range in point of reduction is from the 4th to the 35th ventral (mean 11.6).

Second Lateral Reduction. The reduction from 17 to 15 rows most commonly involves the fusion of the third and fourth scale rows (92.9%), but may also involve the fusion of the fourth and fifth (6.3%) or the second and third rows (0.8%). The range in point of reduction is from the 85th to the 173rd ventral (mean 118.5).

First Middorsal Reduction. The reduction from 15 to 14 rows most commonly involves the fusion of the seventh and eighth rows (50.0%), but may also involve the fusion of the eighth and ninth rows (when the first middorsal reduction occurs anterior to the second lateral reduction) (27.1%),

the seventh and eighth rows counting from the right side (7.7%), the sixth and seventh rows (4.2%), or a miscellaneous number of rows (11.0%). Occurrence of the first middorsal reduction anterior to the second lateral reduction takes place in 34.2% of the patterns determined. In 7.0% of the patterns the second middorsal reduction also occurs anterior to the second lateral reduction.

Second Middorsal Reduction. The reduction from 14 to 13 scale rows most frequently involves the fusion of the seventh and eighth rows (67.8%), but may also involve the eighth and ninth rows (when the second middorsal reduction occurs anterior to the second lateral reduction) (5.1%), the sixth and seventh rows on the right (2.9%) or the left (16.9%), or a miscellaneous number of rows (7.3%). The range in point of reduction is from the 98th to the 191st ventral (mean 129.5).

Third Middorsal Reduction. The reduction from 13 to 12 rows most commonly involves the fusion of the sixth and seventh rows (98.2%), but may also involve the sixth and seventh rows on the right side (1.8%). The range in point of reduction is from the 130th to the 194th ventral (mean 160.7).

Geographical Aspects of the Dorsal Scale Reduction Formula

Most of the types of deviation from the standard pattern have no geographic significance or have a very low frequency of occurrence within the species. These deviations include the lateral reduction substitution, occurrence of the second middorsal reduction anterior to the second lateral reduction, lateral displacement of the first and second middorsal reduction, preanal increase, sporadic increase and decrease, simultaneous paravertebral fusion, and fusion of the middorsal with two paravertebral scales. The geographic variation exhibited by the percentage of occurrence of the first middorsal reduction anterior to the second lateral reduction is highly erratic (Table 11). Adjacent states often have very different percentage values. For example, Mississippi has a value of 66.7%, but Louisiana has a value of only 10.0%. Likewise, Arkansas has a value of 16.7%, but Missouri has a value of 52.6%. Although this character is geo-

graphically variable there apparently is no consistent pattern.

Another geographically variable aspect of the scale reduction pattern is the frequency of reduction to twelve scales anterior to the vent (Table 11). Much of this variation is also erratic, except that the subspecies *lineatulus* characteristically has a high frequency of preanal decrease to 12 rows. Of the patterns determined for this subspecies, 90.6% had this deviation. In contrast, the values for Texas and Tamaulipas are 22.7% and 20.0%, respectively. Interestingly enough, those areas immediately adjacent to the range of *M. f. lineatulus* also have high values. The value for Coahuila is 68.4%, from which state I determined patterns of 17 *testaceus* and two *lineatulus*. In New Mexico, where *lineatulus* and *testaceus* intergrade over a large area, 11 out of the 12 *lineatulus* × *testaceus* intergrades examined have 12 rows at the vent, while only two out of eight *testaceus* have this condition.

Proportions

Relative Tail Length.—The relative tail length changes little during ontogeny and there is likewise little difference between the sexes. The mean for the tail length/total length ratios for snakes under 900 mm in total length is 0.249, for those over 900 mm it is 0.248. The means for this ratio for males and females of the seven subspecies are as follows (males listed first, females second; the number in parentheses following the mean value for the tail length/total length ratios is the number of observations): *flagellum*—0.248 (65), 0.247 (82); *testaceus*—0.246 (36), 0.244 (45); *lineatulus*—0.241 (29), 0.243 (17); *piceus*—0.252 (83), 0.258 (77); *cingulum*—0.247 (33), 0.253 (20); *ruddocki*—0.253 (3), 0.257 (1); *fuliginosus*—0.256 (37), 0.261 (27). A slight amount of geographic variation is indicated in the above data. Snakes from the western portion of the range of the species have longer tails than those snakes from the eastern portions of the range.

Hemipenis

The following description was taken from the two organs of UG 431. Each hemipenis is bilobed with a single, oblique sulcus sper-

TABLE 11
Percent frequency of deviations observed in the scale reduction pattern of *Masticophis flagellum*.

State	1°		2		3		4		5		6		7		8	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Florida	14.3	9.5	33.3	—	—	—	4.8	—	19.0	—	—	—	—	—	—	—
Georgia	5.0	10.0	25.0	10.0	—	—	15.0	25.0	42.9	19.0	—	—	—	—	—	—
Alabama	38.5	23.1	23.1	—	—	—	30.8	23.1	45.0	15.0	—	—	—	—	—	—
Mississippi	16.7	16.7	66.7	16.7	—	—	25.0	16.7	38.5	7.7	—	—	—	—	—	7.7
South Carolina	28.6	14.3	—	—	—	—	28.6	28.6	33.3	8.3	—	—	—	—	—	—
North Carolina	6.3	6.3	18.8	—	—	—	18.8	25.0	71.4	14.3	14.3	—	14.3	—	—	—
Kentucky	100.0	—	—	—	—	—	100.0	—	37.5	—	—	—	6.3	—	—	—
Tennessee	100.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Louisiana	5.0	15.8	10.0	—	—	—	20.0	35.0	20.0	—	—	—	10.0	—	—	—
Missouri	—	—	52.6	15.8	—	—	10.5	21.1	42.1	5.3	—	—	—	—	—	—
Illinois	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Arkansas	—	5.6	16.7	5.6	—	—	—	22.2	27.8	11.1	—	—	11.1	—	—	—
Kansas	13.3	20.0	13.3	—	13.3	—	13.3	13.3	13.3	—	—	—	—	—	—	—
Nebraska	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oklahoma	10.0	25.0	30.0	—	—	—	5.0	35.0	35.0	5.0	5.0	—	10.0	—	—	—
Texas	4.5	—	22.7	4.5	9.1	—	20.0	13.6	22.7	18.2	—	—	—	—	—	—
Colorado	—	20.0	30.0	5.0	20.0	—	—	15.0	40.0	5.0	—	—	10.0	—	—	—
Tamaulipas	20.0	10.0	—	—	—	—	—	30.0	20.0	—	—	—	—	—	—	—
Veracruz	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nuevo Leon	—	25.0	—	—	—	—	—	—	50.0	25.0	—	—	—	—	—	—
San Luis Potosí	11.1	—	22.2	11.1	33.3	—	—	11.1	55.5	—	44.4	—	11.1	—	—	—
Coahuila	15.8	21.1	42.1	—	5.3	—	—	15.8	68.4	—	5.3	—	—	—	—	—
Chihuahua	7.1	—	50.0	—	—	—	—	21.4	92.9	—	—	—	—	—	—	14.3
Durango	10.0	20.0	60.0	20.0	10.0	—	10.0	10.0	90.0	—	—	—	—	—	—	—
Zacatecas	50.0	—	50.0	—	—	—	—	—	50.0	—	—	—	—	—	—	—
New Mexico	20.0	10.0	40.0	5.0	10.0	—	—	15.0	65.0	—	—	—	20.0	—	—	—
Utah	—	7.7	46.2	7.7	7.7	—	—	15.4	7.7	—	—	—	—	—	—	—
Nevada	9.1	13.6	36.4	13.6	9.1	—	—	18.2	36.4	—	—	—	4.5	—	—	4.5
California	14.8	7.4	59.3	18.5	14.8	—	—	11.1	11.1	3.7	—	—	—	—	—	—
Arizona	10.3	13.8	44.8	10.3	37.9	—	—	20.7	24.1	—	—	—	—	—	—	—
Sonora	9.1	9.1	54.5	13.6	9.1	—	—	18.2	36.4	—	4.5	—	—	—	—	—
Sinaloa	15.4	7.7	23.1	—	—	—	—	7.7	7.7	—	—	—	—	—	—	—
Baja California	11.1	5.6	33.3	5.6	22.2	—	—	27.8	33.3	—	—	—	11.1	—	—	—

* The numbers 1 through 8 refer to types of deviations seen in the scale reduction formula. The letters refer to subdivisions within the major types of deviations. 1—Lateral reduction substitution; A—substitution appears in first lateral reduction, B—substitution appears in second lateral reduction. 2—Occurrence of first and/or second middorsal reductions anterior to second lateral reduction; A—first middorsal reduction, B—second middorsal reduction. 3—Lateral displacement of first and/or second middorsal reductions; A—first middorsal reduction, B—second middorsal reduction. 4—Preanal decrease. 5—Preanal increase. 6—Sporadic increase and decrease. 7—Simultaneous paravertebral fusion. 8—Fusion of middorsal with two paravertebral scales. The numbers in the body of the table are percentages.

maticus extending onto the left lobe of the organ. Distally each organ is covered with calyces in about 13 rows on the sulcate side and about 9 rows on the absulcate side. The micro-ornamentation of the calyces is spinulate. The apex of the organ is smooth. The proximal area is spinose, the spines increasing in size proximally. There are about 6 rows on the absulcate side, 4 on the sulcate side. Two enlarged basal spines are present, one on either side of the sulcus spermaticus. The lateral spine is the larger. The basal area is naked save for some very small, scattered spinules.

The *in situ* hemipenis extends about to the level of subcaudal 11 (range 6-13).

Anal Sacs

The anal sacs extend about to the level of subcaudal 5 (range 4-6). The length of anal sacs was determined for only 21 specimens and the degree of sexual dimorphism, if any, is slight (average of 5.17 for males, 5.36 for females).

Dentition

Very few tooth counts were made and the majority of those were made on the maxilla. The number of teeth on the maxilla ranges from 16 to 21 (mean 18.6). Observed ranges and means for the number of teeth on the other dentigerous bones are as follows: palatine—12 to 15 (13.3); pterygoid—17 to 25 (21.0); dentary—19 to 24 (21.7).

Umbilicus

The number of scales involved in the umbilical scar ranges from 2 to 7 (mean 3.7). The beginning point of the umbilical scar ranges from the 146th to the 185th ventral (mean 164.4). The position of the umbilical scar is not sexually dimorphic as suggested by Edgren (1951) for *Heterodon platyrhinos*, but rather is related to the total number of ventrals. Thus, if there was much sexual dimorphism in the number of ventrals in *Masticophis flagellum*, which there is not, the position of the umbilical scar would reflect that dimorphism if considered alone and without relation to the total number of ventrals (see Martof, 1954, for a discussion of the position of the umbilical scar in *Thamnophis s. sirtalis*).

DISTRIBUTION AND HABITAT

Masticophis flagellum inhabits relatively dry, warm situations ranging from the deserts of the southwestern United States to the pine forest of the southeastern United States. This snake occurs in the southern half of the United States from coast to coast, thence south into Mexico the length of the peninsula of Baja California and as far south as Sinaloa on the west coast, Zacatecas on the central plateau, and extreme northern Veracruz on the east coast (Figs. 2 and 3).

In Florida *M. f. flagellum* is distributed throughout the state. Carr (1940) reported the coachwhip as an occasional inhabitant of wire-grass flatwoods, palmetto flatwoods, upland hammock, and a frequent inhabitant of limestone flatwoods, rosemary scrub, and highpine. Carr also noted that "although alert and very active creatures, coach-whips are frequently killed by groundfires in the flatwoods, more often apparently than any other snake; I once found seven dead after a fire which burned ten or twelve acres of flatwoods in Collier County." Charles W. Myers (*in litt.*) gave the following information regarding habitat distribution in Florida: "It was my impression that they are most common in Coastal Scrub vegetation . . . , but they also occur in Pine Flatwoods, Mixed Pine-hardwood Forest, and Mesophytic Hammock. One of the scrub specimens was almost in the Grassy Beach Front and I have no doubt that they also prowl that environment." In southern Florida, Duellman and Schwartz (1958) found that "most of the specimens of *Masticophis* come from the eastern rim [as opposed to the interior lowlands] where they are found in the pine woods. One has been found on a sandy island off the Gulf coast and another at Pinecrest, an isolated pine 'island' in the Everglades. These snakes have never been observed in the Everglades."

There is only scanty information available on the habitat distribution of *M. f. flagellum* in the states of Georgia, North and South Carolina, and Alabama. Martof (1956) reported the distribution in Georgia as statewide and the habitat as "rock piles in fields, open woods." Charles W. Myers (*in litt.*) stated that he has collected specimens in "rolling farm and pasture land" and an "overgrown field on river floodplain" in

Georgia. Löding (1922) remarked that in Alabama the eastern coachwhip is "not uncommon in dry fields and cut-over pine lands in Mobile County" and that he has seen "this snake in pine forest on and near the mountains in Cleburne and Clay counties." Myers (*in litt.*) reported that he collected an Alabama specimen that was "... dug from a small mammal burrow in grassy pinewoods." Collector's field notes accompanying specimens in the North Carolina State Museum from North Carolina indicate the following habitat designations: "sandy, open field" and "plum thicket." DePoe, Funderburg, and Quay (1961) gave the distribution of the eastern coachwhip in North Carolina as the southern half of the Coastal Plain. This information is borne out by the specimens I have examined.

The single specimen available from Kentucky was collected in a "broomsage field" (Chenoweth, 1949).

I have seen only two specimens from Tennessee, one from Knoxville, Knox County (the locality data may be in error as the area is relatively mountainous), and one from 3 miles E Hornsby, Hardeman County. In reference to the distribution of the coachwhip within the state, Glenn Gentry (*in litt.*) wrote that "in my 30 years of miscellaneous collecting I have talked with many natives throughout the state and most of them (especially the older people) has heard the 'folk tales' about the coachwhip snake and/or had seen them. The same was true of the ground rattler and the bull (pine) snake. The distribution of the last two in particular is very spotty. Evidently the destruction of timber and cultivation have severely reduced the suitable habitat for these and no doubt to some extent for the coachwhip."

Cook (1954) stated that the distribution in Mississippi is state wide, "including all faunal regions."

Fitch (1949) noted that in western Louisiana *M. flagellum* occurs "in all habitats, especially dry uplands, often near cultivated areas." Strecker and Frierson (1926) dug one out of a hole in the bank of Wallace Bayou, a bayou separating a portion of DeSoto and Caddo parishes. My own experience with the coach whip in Louisiana is rather limited, primarily because the species is relatively uncommon in the state. I have

found the species in the longleaf pine hills of central and west-central Louisiana. Locality data for specimens I have examined from the state indicate that it is found, in addition to the habitat mentioned above, in the longleaf pine hills of the upper tier of Florida parishes, the shortleaf pine-oak-hickory hills of northwestern and north-central Louisiana, and a few have been collected in the prairie region in southwestern Louisiana. The species is missing from the marshland of southern Louisiana.

Very little information is available on the habitat distribution of *M. f. flagellum* in Arkansas. Dowling (1956) stated that the coachwhip snake is found in the Ozark Plateau, Arkansas River valley, and Ouachita Mountain region, and later (1957) expanded the range to include the entire state. Available locality records suggest that this snake is found everywhere in Arkansas except for the Mississippi alluvial plain of eastern Arkansas. A specimen (LSUMZ 14145) collected 2 miles SE Gamaliel, Baxter County, was noted by the collector to have come from "hardwood forest in mountains."

Anderson (1965) stated that "coachwhips occur in Missouri in rough, rocky terrain in rather exposed situations. They have also been observed in open grassy areas on timbered hillsides and in low bushes." Locality records indicate that *flagellum* occurs in the southwestern Missouri prairie and the Ozark region (Anderson, 1965, p. xiv).

The few specimens collected in Illinois have come from the lower Mississippi border counties in the Mississippi River bluff and dissected upland (Smith, 1961).

Smith (1950) stated that "this terrestrial species is usually found in grassy areas more or less devoid of trees..." in Kansas. Taylor (1929) and Brennan (1934) noted that the western coachwhip is usually found in open prairie country in Kansas.

Force (1930) reported that in the region of Tulsa County, Oklahoma, the eastern coachwhip is "common on sunny slopes, under rocks and in brush piles." The eastern coachwhip is found mainly in the oak-hickory hardwood forest of eastern Oklahoma and the western coachwhip in the tall-grass and short-grass areas of western Colorado.

The coachwhip occupies all types of habitat in Texas. I have already mentioned the vegetation types which *M. f. flagellum* inhabits in eastern Texas. Brown (1950) indicated that the western coachwhip is found in the following "natural regions": Trans-Pecos—a high plateau, the vegetation of which is typically Chihuahuan Desert in type, *i.e.*, desert scrub with creosote bush, yucca, lechuguilla, sotol, and several species of cacti. High Plains—a level to slightly rolling plain in the Panhandle, the primary vegetation of which is short and bunch grasses with scattered shrubs and mesquite in some areas. North Central Plains Region—a rolling plain in the north central portion of the state, the predominant vegetation of which is bunch and short grasses with scattered timber, mostly post oak, blackjack oak, and mesquite. Edwards Plateau—a limestone plateau with a rolling topography and a vegetation cover composed primarily of short grasses with scattered live oaks, shin oak, and cedar. Rio Grande Embayment—a rolling plain with some open prairie with a chaparral type of vegetation, with the exception of the grassy prairies, composed of mesquite, acacia, mimosa, prickly pear, and other cacti. *M. f. testaceus* also occurs marginally in the Coastal Prairie, a grass-covered plain with coarse grasses predominating, the Post Oak Belt, a region of rolling hills and a few prairies with post oak and other hardwoods dominant on the uplands and bunch and short grasses in the prairies. It is this latter area where *M. f. flagellum* and *M. f. testaceus* intergrade (information on Texas vegetation compiled from Brown, 1950; McDougall and Sperry, 1951; and Raun, 1965).

In addition, Fouquette and Lindsay (1955) noted that *M. f. testaceus* occurred in Dawson and Hutchinson counties in the Panhandle most commonly in the flood plain association, and that it also was found in deep sand and on rocky slopes. In Terrell County, Milstead, Mecham, and McClintock (1950) reported that "three specimens were collected in the cedar savannah, 15 in the mesquite-creosote, three in the mesquite-sumac-condalia, and two in the live-oak association." Jameson and Flury (1949) stated that in the Sierra Vieja Range of Presidio County the western coachwhip is more common "in the Plains belt than in the Roughland belt. Of 10 specimens collected, only

two were from the Roughland belt. One of these was in the stream bed association, and the other was in the lechuguilla-beargrass association on top of the mesa. Specimens from the Plains belt were from the following associations: catclaw-tobosa, four; creosote-bush-catclaw-blackbush, one; mesquite-huisache-blackbush, one; and yucca-tobosa, one." In the Black Gap Wildlife Management Area in eastern Brewster County, Axtehl (1959) found seven specimens, five of which came from the floodplain, one from the stream bed, and one from the low, limestone gravel hills.

In Colorado the distribution of *M. f. testaceus* is limited to the short-grass areas east of the Rocky Mountains.

In New Mexico *M. f. testaceus* is found mainly in the short-grass areas of eastern New Mexico. This subspecies intergrades with *lineatulus* over the broad expanse of mesquite grassland and Chihuahuan Desert in central and southwestern New Mexico. Gehlbach (1965) mentioned a *M. f. lineatulus* $\times$ *testaceus* intergrade which came "from the Plains Life Belt at 6300 feet, where narrow-leaved yucca and one-seed junipers are prevalent." In the Tularosa Basin of western Otero and eastern Dona Ana counties, Lewis (1950) found *M. f. testaceus* (most likely *lineatulus* $\times$ *testaceus* intergrades) in the yucca grassland zone and the *Atriplex* (saltbush)-*Allenrolfea occidentalis* (iodine bush) association.

The habitat distribution of *Masticophis flagellum* in Mexico has been little studied. With respect to *M. f. testaceus*, Martin (1958) stated that in southern Tamaulipas this snake is found in the thorn forest, and areas "characterized by low trees and shrubs, usually thorny and deciduous, and either microphyllous or compound-leaved," and the low tropical deciduous forest "formed of trees of medium height (12-15 m.) which are rather widely spaced and rise out of a dense, almost impenetrable, understory of lower trees, about 5 m. in height."

A large portion of the range of *M. f. lineatulus* lies within the boundaries of the Chihuahuan Desert in the Mesa del Norte section of the Central Mexican Plateau. This desert is characterized by the presence of low shrubs and lies mostly above 3500 ft in elevation (Lowe, 1964). The main shrubs are *Larrea tridentata* (creosotebush), *Acacia*

cymbispina, *Flourensia cernua* (tarbush), and *Prosopis juliflora* (mesquite in shrub form). Low leaf succulents such as *Agave lechuguilla* (lechuguilla), *Agave falcata*, and *Hechtia* sp. (a member of the family Bromeliaceae) are also present. Several species of *Yucca* are also represented (Shreve and Wiggins, 1964).

Some information on habitat distribution of the subspecies of *Masticophis flagellum* in Arizona has already been discussed in the section on *M. f. lineatulus*. The main portion of the range of *M. f. piceus* lies within the Sonoran Desert, but it also extends into the Mohave Desert in Mohave County. The Sonoran Desert is a complex grouping of several, more or less distinct, biotic communities. These include the paloverde-sahuaro (*Cercidium-Cereus*) community, the creosote-bur sage (*Larrea-Franseria*) community, and the saltbush (*Atriplex*) community (Lowe, 1964). The Sonoran Desert is the hottest and the lowest in elevation of the four North American deserts. The Mohave Desert includes creosotebush, Joshua-tree, blackbush, and saltbush as principal association-types. There is a striking paucity of desert trees and the Mohave Desert is essentially transitional between the warmer, lower Sonoran Desert to the south and the cooler, higher Great Basin Desert to the north (Lowe, 1964). Lowe (1964) noted that it ranges to approximately 4,500 ft in elevation.

In California *M. f. piceus* occurs in the Lower Colorado Valley section of the Sonoran Desert (Shreve and Wiggins, 1964), east of the Peninsular Ranges and the Mohave Desert in San Bernardino and Inyo counties. In addition, the range of *piceus* extends into the Chaparral and Coastal Sagebrush vegetation of the Peninsular and Transverse Mountain ranges. In the Death Valley of Inyo County, Turner and Wauer (1963) found *piceus* to be "the most common snake of the Valley oases . . . It occurs about the mesquite and tamarisk groves . . . and frequents the washes and canyons and the open sage flats below the pinyon-juniper association." In the area around Indian Wells, Riverside County, Mosauer (1935) found *piceus* "in the dune region" and "in the sand hills."

The red racer also extends into the Great

Basin Desert in southern and western Nevada and in extreme southwestern Utah.

The subspecies *M. f. ruddocki* is confined to the Central Valley of California, occurring in both the San Joaquin and Sacramento portions. Brattstrom and Warren (1953) stated that "the dominant vegetation is grassland or Oak-Savannah," and Shelford (1963) reported that the primary original vegetation was composed of various species of grasses in bunch form (bunch-grass grassland). Much of the Central Valley is now under cultivation, which may account for the apparent scarcity of *ruddocki*; this seems also to be the case with *Crotaphytus wislizenii silus*, another valley endemic (Montanucci, 1965).

In Baja California *Masticophis flagellum* is found in all the major phytogeographic areas of the peninsula. *M. f. piceus* is found in that section of the Lower Colorado Valley desert that extends into Baja California, east of the San Pedro Mártir Mountains, about as far south as Bahía de Los Angeles. This area is characterized by a simplicity of floral elements. *Larrea tridentata* and *Franseria dumosa* (burweed) are dominant shrubs (Shreve and Wiggins, 1964).

The major portion of the range of *M. f. fuliginosus* lies within the boundaries of the Sonoran Desert in Baja California, but it also extends into the California phytogeographic area (chaparral and sclerophyll woodland) and the Cape Region phytogeographic area (Wiggins, 1960; Shelford, 1963). The latter area is one in which the vegetation is similar to that of the tropical scrub lowlands of Sinaloa (West, 1964). A number of tropical deciduous plants of mainland affinity occur in this region. The other Baja California subdivisions of the Sonoran Desert in which *M. f. fuliginosus* occurs include the Vizcaino Region, the Central Gulf Coast, and the Magdalena Region. The Vizcaino Region is distinctive because of the presence of several leaf-succulent plants. The Central Gulf Coast flora is dominated by sarcocaulous trees of the genera *Bursera* and *Jatropha*, which have trunks of an exaggerated diameter. The Magdalena Region is characterized by a shared dominance of trees and large succulents (cacti) (Shreve and Wiggins, 1964). Linsdale (1932) mentioned that a speci-

men of the black phase of *fuliginosus* was "shot while lying in the sun at the edge of brush on a sandy bank near a marsh" and a specimen of the light phase was "found among rocks" at Comandú and another was "found under a low bush on the desert" on Isla Santa Magdalena. Leviton and Banta (1964) saw two specimens that were "very active on the leeward side of sand dunes" at Bahía de Los Muertos and 4.9 miles SE Pescadero. Another was found coiled up inside a cardón log.

Etheridge (1961) reported collecting one specimen on Isla Cerralvo and seeing others in the high, rolling sand dunes at the southern end of the island.

In Sonora, *M. f. piceus* is found in the Gran Desierto and is apparently restricted to it, although there are no records between the road from Sonoita and Punta Peñansco, and from along the road from Desemboque to Nogales. The distribution of *M. f. cingulum* in Sonora is mainly within the limits of the Sonoran Desert (Shreve and Wiggins, 1964). The range also extends somewhat farther north and east into the area around Cananea, and farther south into the thorn forest of southern Sonora. The distribution of *M. f. cingulum* to the east is effectively limited by the pine-oak woodland and, at higher elevations, the coniferous forests of the Sierra Madre Occidental. *M. f. cingulum* is completely isolated along the greater part of its eastern range limits from *M. f. lineatus* to the east (there is almost certainly some contact between *cingulum* and *lineatus* in the area to the north of the main ranges of the Sierra Madre Occidental, e.g., in the low areas between the Sierra Pulpito and Sierra de San Luis; however, no specimens are available from this area).

Within the Sonoran Desert, *M. f. cingulum* is found in all subdivisions. It occurs in the Lower Colorado Valley, the Arizona Upland, the Plains of Sonora, an area of transition between the very arid type of desert vegetation to the north and the more humid subtropical thorn forest vegetation typical of west coast Mexico, the Central Gulf Coast, an area very similar in vegetational characteristics to that of the eastern coast of Baja California below Bahía de Los Angeles, and the Foothills of Sonora, a fairly rugged area with elements of both the des-

ert vegetation and the thorn forest vegetation (Shreve and Wiggins, 1964).

The distribution of *Masticophis flagellum* in Sinaloa is apparently limited to the thorn forest of the northern portion of the state; the vegetation of the area around El Dorado, the southernmost locality for *Masticophis flagellum* in the Pacific coastal lowlands of Mexico, is described by Fugler and Dixon (1961) as being originally composed of "a heavy forest of mixed native hard- and softwoods." They further stated that "the heavy clayish soils, not utilized for agriculture, bear typical desert vegetation, such as saguaro, yucca, sparse brush of various types, and desert softwoods." The southward dispersal of *Masticophis flagellum* in this region would seem to be limited by the appearance of elements of the tropical lowland vegetation in central Sinaloa.

SUMMARY AND CONCLUSIONS

The generic name *Masticophis* is used for the whipsnakes instead of the taxonomically unstable name *Coluber*. *Masticophis mentovarius* is not considered to be close to the basic stock from which the *flagellum* group arose, but rather to be an advanced form that has the fourth and fifth supralabials fused into a single scale.

Color pattern proved to be the most taxonomically useful character complex; the most important aspects are summarized below. *Masticophis flagellum flagellum* has two adult pattern types, a pale tan pattern resembling that of the juvenile of that subspecies, and a more typical pattern that is dark brown anteriorly and tan posteriorly. The extent of dark brown pigment on the anterior portion of the body and the coloration of the posterior portion of the body are geographically variable, specimens from the southeastern portions of the range being paler than specimens from the northwestern portions of the range.

Masticophis flagellum testaceus has two types of ground color and three types of color pattern. One ground color is pink or red, this phase characterizing three disjunct populations in Trans-Pecos Texas, eastern New Mexico, and eastern Colorado. A tan ground color is found throughout the remainder of the range of the subspecies. The three types of color pattern (a unicolor dor-

sum, a narrow-banded dorsum, and a wide-banded dorsum) occur throughout the range of *M. f. testaceus*.

Masticophis flagellum lineatus is one of two subspecies that shows little pattern variability. Intergradation between *M. f. lineatus* and *M. f. testaceus*, and between *M. f. lineatus*, *M. f. piceus*, and *M. f. cingulum* takes place over a large area in western New Mexico and southeastern Arizona, respectively.

Masticophis flagellum piceus has two phases, one black, the other red. The black phase occurs in south-central Arizona and is most common within a 20-mile radius of Tucson, Pima County.

Masticophis flagellum ruddocki is the other subspecies that shows little pattern variability. Intergradation between *M. f. ruddocki* and *M. f. piceus* occurs in low montane passes at the southern end of the San Joaquin Valley.

Masticophis flagellum cingulum, as envisioned in this study, has a range that encompasses all of Sonora, with the exception of the Gran Desierto of the northwestern portion of the state, and extreme south-central Arizona. This subspecies exhibits considerable variation in color pattern, ranging from a banded phase to one in which the dorsum is uniformly black or red. These pattern changes are clinal in nature.

The subspecies name *Masticophis flagellum fuliginosus*, a new combination, is applied to the form inhabiting the peninsula of Baja California. This subspecies has a pale and a dark phase, each of which exhibits variability in both color and pattern. The two phases occur on the islands on both sides of the peninsula.

A distinctive, but poorly known, pattern variant occurs in northern Sinaloa.

Ventrals and subcaudals exhibit both geographic and individual variation. The subcaudals also are subject to sexual dimorphism to a slight degree. The scale reduction pattern exhibits considerable individual variation, but certain aspects appear to have geographic significance. Only individual variation is exhibited by the head scutellation.

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