l'activité thryoidienne et des phénomènes cycliques de la mue. Bull. Soc. Zool. France 86: 59–67.

———, AND R. DUGUY. 1963. Notes de cytologie sanguine comparée sur les reptiles de France. Bull. Soc. Zool. France 88: 613–624.

SAINT GIRONS, M., AND H. SAINT GIRONS. 1969. Contribution à la morphologie comparée des érythrocytes chez les reptiles. Br. J. Herpetol. 4:67–82.

SLONIMSKI, P. 1934. Sur les elements du sang chez *Vipera russelli* et *Python regius*. C. R. Assoc. Anat. 1:25–28.

VLĂDESCU, C. 1965. Glycaemia in the *Vipera berus*. Rev. Roumaine Biol. Ser. Zool. 10:43–46.

WIRTH, T. 1972. Hématologie comparée—contribution à l'étude des lignées médullaires chez les reptiles: les lignées granulocytaires, lymphocytaires et monocytaires. C. R. Acad. Sci. Paris 274:1871–1873.

ZAIN-UL-ABEDIN, M., AND M. QAZI. 1965. Blood sugar levels of some reptiles found in Pakistan. Can. J. Biochem. Physiol. 23:173–177.

Received: 14 June 1972
Accepted: 7 August 1972

Department of Animal Health, New York Zoological Society, Bronx Park, Bronx, New York 10460

VARIATION IN THE CANYON LIZARD, *SCELOPORUS MERRIAMI* STEJNEGER

R. EARL OLSON

ABSTRACT: Habitat and range of *Sceloporus merriami* are briefly discussed. Geographic and nongeographic variation are given detailed treatment involving analyses of several characters of scutellation and pattern. A new race is described from Presidio County, Texas.

SINCE Stejneger described *Sceloporus merriami* in 1904, the species has received little attention. Smith (1937) described the subspecies *S. m. annulatus* from the Chisos Mountains, Brewster County, Texas. Williams et al. (1960) named *S. m. australis* from central and southwestern Coahuila, Mexico; populations of uncertain taxonomic relationship were reported from La Mota Mountain, Presidio County, Texas (Milstead, 1953) and from north-central Chihuahua, Mexico (Smith et al., 1963). Subsequently, specimens have been taken from several localities along the Rio Grande in southern Presidio County. The present study was undertaken in order to gain a better understanding of variation within the species.

MATERIALS AND METHODS

During this study, about 1600 specimens were examined, including numerous living animals. The dorsal scales were counted from the occiput to a point above the posterior edge of the insertion of the hind limbs. Ventral scales were counted from a point opposite the anterior edge of the insertion of the forelimbs to a point between the femoral pores. Counts were also made of femoral pores, scales between the pore series, and subdigital lamellae of the fourth hind toe. Other scutellation characters noted were the degree of rugosity of the head plates, number of frontoparietals, condition of the anterior section of the frontal, number of prefrontals, and anterior position of the labiomentals. Snout-vent measurements (SVL) were made routinely, but total length was not, because the tail of most specimens was missing.

Pattern features of taxonomic significance are the throat markings, degree of proximity of the belly patches in males, and subcaudal banding. Paravertebral spots designated as small are generally rounded and involve one or two scales, whereas large spots are usually more nearly square and occupy four or more scales.

Distribution

Sceloporus merriami occurs in southwestern Texas and central Coahuila, Mexico (Fig. 1). In Texas, the known range extends from extreme western Edwards and Crockett counties westward along the Rio Grande as far as Shafter, Presidio County. The species is found somewhat farther to the west in Mexico along the Río Conchos. Another series of populations is known from central Coahuila.

The range of the species is almost entirely within the Chihuahuan Biotic Province (Dice, 1943), but peripherally enters the Balconian Biotic Province (as delimited by Blair, 1950). A range involving these two provinces in Texas is not a unique distribution pattern; many forms range throughout much or all of the Chihuahuan Province and portions of or the entire Balconian Province (*sensu* Blair) but do not occur elsewhere in Texas adjacent to either the Chihuahuan Province or the Edwards Plateau (Balconian Biotic Province). Amphibians and reptiles known to range throughout both provinces include *Syrrhophus marnocki*, *Hylactophryne augusti latrans*, *Sceloporus poinsetti poinsetti*, *Gerrhonotus leiocephalus infernalis*, *Thamnophis cyrtopsis*, *Ficimia cana*, *Crotalus lepidus*, and *Crotalus molossus*. Chihuahuan Province forms ranging eastward onto the western periphery of the Edwards Plateau are *Sceloporus merriami*, *Lampropeltis mexicana*, and *Elaphe subocularis*.

Sceloporus merriami inhabits rocky areas where the soils are well drained. The eastern populations inhabit gently-rolling regions of light-colored Cretaceous limestone and live among low-lying rocky hills, low breaks or outcrops, and canyons. Elsewhere steep-walled gorges and ruggedly-broken country, especially large boulders and cliff faces near the upper regions of talus slopes, are preferred; most of these areas are composed of dark rock, generally of igneous origin. Hot dry situations seem to be the most favored by this species. In Texas, the outlines of the known range encompass areas with very high summer temperatures and marked moisture deficiency.

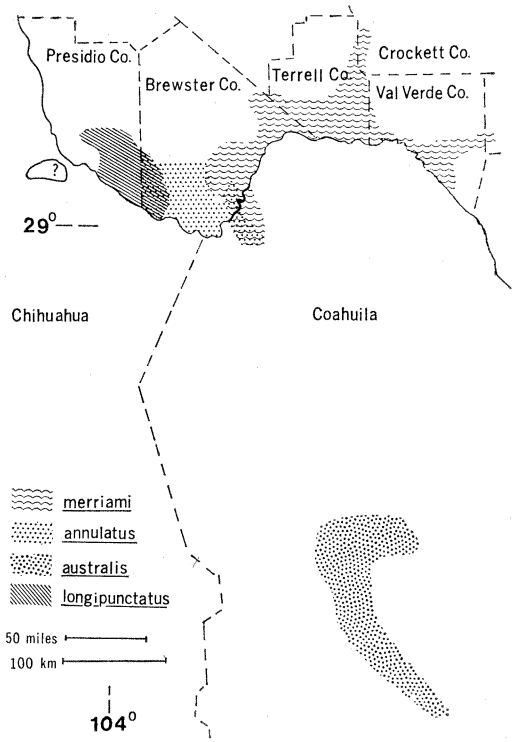

Fig. 1.—Distribution of the subspecies of *Sceloporus merriami*.

Sceloporus merriami occurs where vegetation is sparse or absent. Nowhere have I known this lizard to utilize vegetation except for occasional concealment behind grass at the bases of some cliffs and rocks. Several locations almost devoid of vegetation support dense populations of these lizards.

Description of Species

Adult canyon lizards average about 49 mm SVL (maximum 59 mm) and 150 mm total length. Postfemoral dermal pockets are lacking and the lateral body scales are granular. Dorsal body scales are small, averaging 52.8 (40–70, $N = 940$). Ventral scales average 67.9 (55–79, $N = 751$). There are typically two postrostrals, four internasals, three frontonasals, and two prefrontals. The frontal is divided transversely into

anterior and posterior sections; the anterior section is entire or longitudinally divided. Frontoparietals number one or two on either side with a large interparietal. A rudimentary gular fold is present. Postanal scales are enlarged in males. The femoral pores average 25.2 (19–32, $N = 803$) per side. The series is usually narrowly interrupted at the midline; it is rarely continuous (<1%).

Dark blue belly patches are well developed in males. Barring on the throat and subcaudal regions is variable. Dorsal coloration varies from sandy tan to dark brown. The head pattern, when visible, consists of dark bars on most of the plates. The pattern of the dorsum is comprised of 7–10 pairs of dark paravertebral spots alternating with 2 series of smaller dark lateral spots. Spots in the outermost row are sometimes fused to form a longitudinal dark stripe. The tail is banded dorsally by dark bands three or four scales long and light bands one to three scales long. Limbs and toes are also banded. An extensive dark bar is always present on each shoulder; these bars are rarely in contact ventrally, but by joining the paravertebral spots above them, they occasionally appear to be continuous dorsally. There is light dorsal spotting generally, which is most noticeable on the sides of the body. Spots are occasionally large, imparting a reticulated appearance among ground color.

Nongeographic Variation

Ontogenetic Variation.—Little or no ontogenetic change occurs in dorsal pattern and color in the few juveniles examined. A general darkening of ground color with age may be exhibited in those localities where the dorsum is usually dark in adults.

The most noticeable ontogenetic differences are seen in ventral pattern. Juveniles are either unmarked or inconspicuously marked beneath. The smallest specimen (20 mm SVL; KU 118321) is unmarked below; slightly larger examples (21 mm SVL) are either unmarked (KU 118530) or have faint throat bars evident (UMMZ 114219). Two lizards (22 and 23 mm SVL) bear markings similar to the 21 mm SVL specimens, but a specimen 25 mm SVL (USNM 159551) has light-shaded subcaudal bands. No belly patches are present in males as large as 30 (UMMZ 66174), 32 (UMMZ 114215), or 34 mm SVL (UMMZ 66195), but they are indistinctly evident in several specimens 37 mm SVL.

The umbilical scar remains evident at a snout-vent length of 27 mm (FMNH 75888). The skull in the region of the interparietal remains distinctly bulbous until the lizard reaches a length of 30 mm SVL.

Sexual Variation.—The dorsal pattern is similar in both sexes. The ventral pattern of males is generally darker than in females, and males have well-defined belly patches. The throat pattern is usually similar in both sexes, however females may not be as darkly barred as males. In some northeastern populations (16–24 km NW Del Rio, 21 km SE Sheffield, 10.5 km SE Sanderson, and 1.6 km E Langtry), throat markings are faint or absent in females but present in males. Subcaudal banding, when present, also may be less pronounced in females than in males from the same populations, a situation which is most evident in southern Brewster County populations.

Geographic Variation

Dorsal Scales.—The smallest number of dorsal scales occurs in southern populations, around Cuatro Ciénegas [45.9 (42–53), $N = 85$]. The counts are higher in the Chisos Mountains area [50.4 (42–59), $N = 137$] and increase slightly to the northwest of the Chisos Mountains [52.1 (44–60), $N = 107$], except at La Mota Mountain [49.5 (40–56), $N = 47$]. There is a greater increase northeast of the Chisos Mountains from the lowlands of the Big Bend National Park to Del Rio [59.5 (51–70), $N = 166$].

Although the mean number of dorsal scales in most eastern populations exceeds 60, the mean for a series of 25 animals taken 42 km E Marathon, Brewster County is 56.0, which approaches those of western populations. Consequently I suspect that there are populations occurring west-southwest of Marathon, perhaps at Santiago Peak, Nine-Point Mesa, and Bandera Mesa.

TABLE 1.—Population variation in certain meristic and pattern features of *Sceloporus merriami*. Data presented as means.

Locality	Ventral scales	4th toe lamellae	Interfemoral pore scales	Frontoparietals	% separations by labiomentals	% population with extended paravertebral spots
Sheffield area	69.0(63–75) 25	29.5(27–34) 44	2.3(1–4) 41	1.9(1–5) 44	97.4 (38)	2.9 (35)
Del Rio	71.6(67–75) 7	27.2(24–30) 12	2.0(1–3) 9	1.2(1–2) 12	100 (11)	0 (11)
Devils-Pecos Rivers	69.3(62–76) 32	26.5(23–31) 50	1.7(0–2) 41	1.3(0–2) 47	94.8 (96)	0 (3)
SE Sanderson	70.0(68–72) 3	26.8(25–30) 6	2.0(1–3) 6	1.3(1–2) 6	83.3 (6)	0 (3)
42 km E Marathon	71.7(63–76) 16	25.8(23–30) 23	2.5(1–4) 24	1.1(1–2) 25	80.0 (25)	0 (23)
Black Gap area	71.6(64–79) 19	25.8(23–29) 32	1.4(0–2) 29	1.2(1–2) 28	67.9 (26)	0 (9)
Boquillas Rgr. St.	67.8(62–71) 7	27.0(22–31) 23	2.0(1–2) 25	1.0(all) 20	87.5 (32)	9.1 (22)
Grapevine Hills	69.1(61–78) 39	25.3(22–29) 81		1.2(1–2)100	68.1(116)	13.8(101)
Persimmon Gap	71.4(62–76) 9	26.7(23–30) 9	1.5(0–3) 9	1.4(1–2) 8	88.9 (9)	0 (9)
Hot Springs	64.3(60–68) 3	26.7(24–29) 6	1.8(1–3) 6	1.1(1–2) 6	71.4 (7)	0 (6)
Chilocotal Mt.	72.4(70–76) 51	23.2(20–26) 11	2.6(2–4) 9	1.8(1–2) 11	0 (11)	18.1 (11)
Glenn Draw	72.7(69–75) 3	23.6(22–25) 5	2.0(1–3) 6	1.8(1–2) 6	0 (7)	15.0 (19)
E. Slope Chisos Mts.	69.0(60–78) 40	23.5(20–27) 64	2.6(1–4) 67	1.8(1–3)100	3.6(112)	8.3(133)
Chisos Basin	68.0(58–75) 14	24.3(21–29) 14	2.3(1–3) 14	1.6(1–2) 14	7.7 (13)	12.5 (8)
22.5 km N Terlingua	65.4(65–67) 5	24.0(22–27) 9	2.2(2–3) 4	1.9(1–3) 10	0 (11)	0 (2)
Santa Elena Canyon	68.5(64–73) 6	25.5(23–28) 8	2.0(1–3) 8	1.4(1–2) 8	0 (9)	0 (3)
Terlingua to Lajitas	67.6(58–79)100	24.3(20–29)150	2.4(1–4)175	1.9(1–3)180	2.7(187)	23.1(108)
4.8–9.7 km NW Lajitas	66.6(59–75) 50	24.8(21–29) 60	2.4(0–4) 60	1.8(1–4) 46	1.6 (61)	75.1 (46)
Closed Canyon	67.9(60–75) 26	24.5(22–28) 77	2.9(1–6) 82	1.9(1–3) 75	7.0 (86)	84.6 (91)
12.1–19.3 km SE Redford	68.3(63–70) 35	24.7(22–27) 43	3.0(2–4) 40	1.9(1–2) 55	7.0 (43)	86.5 (52)
San Jacinto Mt.	67.5(64–70) 6	25.6(22–28) 5	3.5(2–5) 6	1.9(1–2) 4	0 (6)	100 (6)
La Mota Mt.	66.5(62–73) 34	25.0(23–29) 53	2.8(1–4) 50	1.7(1–3) 90	31.0 (92)	40.3 (67)
Rio Conchos	66.7(62–67) 7	25.7(24–29) 7	3.0(all) 7	1.5(1–2) 7	52.7 (7)	16.7 (6)
Central Coahuila	64.3(55–71) 62	24.3(20–29) 76	1.9(0–4) 78	1.7(1–3) 84	1.1 (87)	16.9 (71)

Throughout most of the range, changes in number of dorsal scales from population to population occur rather gradually. However, in areas north and east of the Chisos Mountains, Brewster County, marked changes occur over a short distance. Thus, counts for Chilocotal Mountain and Glenn Draw average 50.7 and 50.2, respectively, whereas 16 km eastward at Hot Springs, counts average 55.1. In the Rosillos Mountains, dorsal counts average 52.4, while 16 km northeastward near Persimmon Gap the mean is 59.1; 4.8 km E Park Headquarters the mean count is 48.7, while 9.6 km N Headquarters it is 61.2.

Ventral Scales.—The number of ventral scales varies but little throughout the range of the species and is taxonomically useful only in conjunction with other features. There is a slight increase from 64.3 (55–71, $N = 62$) in the south to 67.7 (58–79, $N = 255$) in the northwest, 69.1 (58–78, $N = 129$) in the Chisos Mountains area, and 70.0 (60–76, $N = 157$) in the northeast.

Subdigital Lamellae of Fourth Hind Toe.—From southern to northwestern populations, almost no change in number is noted [24.6 (20–30), $N = 1025$], but in Terrell County, near Sheffield, this count is higher [29.5 (27–34), $N = 44$].

Femoral Pores.—Little difference in mean femoral pore counts was noted. The lowest counts occur in central Coahuila [25.0 (20–31), $N = 77$] and in the northwestern portion of the range [24.5 (20–29), $N = 235$]; they are highest in the northeast [26.1 (19–32), $N = 206$].

The number of scales between the femoral pore series in the Cuatro Ciénegas area averages 2.5, as it does in the Chisos Mountains area. The mean is 2.9 (0–7, $N = 448$) in southern Presidio County populations. In northeastern populations, the mean number is 2.1 (0–4, $N = 207$).

Frontoparietals.—In northeastern populations, frontoparietals generally number one per side, elsewhere there are usually two (Table 1).

Frontal.—The anterior section of the frontal shield may or may not be divided longitudinally by a median suture. This plate is usually divided in the Chisos Mountains (81%, $N = 49$), in southern Presidio County (61.1%, $N = 345$), and the Río Conchos populations (57.2%, $N = 7$) but only rarely in Terrell and Val Verde counties to the northeast (8.1%, $N = 307$) or in central Coahuila (24.1%, $N = 87$).

Divergence from the condition seen in surrounding populations is noted at La Mota Mountain (46.6%, $N = 73$) and in the Lajitas-Terlingua area in extreme southwestern Brewster County (41.2%, $N = 160$); nearby populations have higher incidences. In the Grapevine Hills in southern Brewster County the incidence is high (30.2%, $N = 116$) compared with that of populations just to the north (0–3.0%) but low compared with that of populations to the south and west in the Chisos Mountains area. In the Sheffield area the frequency of occurrence is surprisingly high (26.3%, $N = 38$) compared with that of nearby populations.

First Labiomental.—The frequency with which the first labiomental is wedged between the first infralabial and the first postmental shows some interesting geographic trends. The frequency is high in Terrell County, near Sheffield (97.4%, $N = 38$), in the Pecos-Devils Rivers region (94.8%, $N = 96$), the Boquillas area (87.5%, $N = 32$), and in the Sanderson-Marathon area (81.5%, $N = 31$). The frequency is somewhat lower in the Grapevine Hills and Black Gap Wildlife Management Area (68.0%, $N = 154$) and is very low in western populations (0–7.7%, $N = 395$), the La Mota Mountain population (31.0%, $N = 92$), and the Río Conchos, Chihuahua sample (54.6%, $N = 7$).

Paravertebral Spots.—The size and shape of the paravertebral spots vary geographically (Fig. 2). They are small or medium size, rounded, without sharply defined borders, and only occasionally modified with lateral extensions (16.9%, $N = 71$) in central Coahuila specimens. In northeastern populations paravertebral spotting resembles that of the Coahuila specimens, but only very rarely are there lateral extensions (2.6% of 38 specimens from southeast of Sheffield, absent elsewhere), except at Grapevine Hills (13.8%, $N = 101$) and at the Boquillas Ranger Station (9.1%, $N = 22$).

Specimens from southern Brewster County have large, square, sharply defined spots. In these populations lateral extension of the spots occurs infrequently, 6.7% ($N = 31$) at Glenn Spring, 5.0% ($N = 20$) at Juniper Canyon, 0% ($N = 16$) at Oak Creek, 15.0% ($N = 19$) at Glenn Draw, 0% ($N = 2$) at Corazones Peak, and 12.5% ($N = 8$) in the Rosillos Mountains. Paravertebral spots on individuals from southern Presidio County usually bear dark lateral extensions so that each mark somewhat resembles a comma (75.1%, $N = 46$, 5–10 km NW Lajitas; 84.6%, $N = 91$, Closed Canyon; 86.5%, $N = 52$, 12–19 km SE Redford; and 100%, $N = 6$, San Jacinto Mountain). The frequency is markedly lower at La Mota Mountain (40.3%, $N = 67$).

An occasional male is reticulated laterally. This phenomenon is seen in examples from Devils River (3 of 14), Persimmon Gap (3 of 6), Boquillas (1 of 4), Grapevine Hills (10 of 75), Black Gap (7 of 25), eastern Chisos Mountains (6 of 50), 21 km SE Sheffield (2 of 14), Chilocotal Mountain (1 of 8), Carmen Mountains (1 of 1), 9.7 km N Park Headquarters (2 of 3), 4.8–6.4 km E Park Headquarters (1 of 3), and near Boquillas Ranger Station (3 of 15).

Throat Bars.—The throat bears dark, moderately broad to broad, diagonally confluent bars (Fig. 2) in specimens from the Chisos Mountains, 16 km E Terlingua, 23 km N Terlingua, and Chilocotal Mountain. Northeastern lizards usually have the throat unbarred or with only faint bars and a free-form dark patch posteriorly. The latter condition has been noted from southwestern Crockett County, Carta Valley, the mouth of Devils River, Shumla, 1.6 km E Langtry, the mouth of Pecos River, Dog Canyon (Santiago Mountains), 48 km SE Sheffield, 21 km SE Sheffield, Black Gap Wildlife Refuge, and 42 km E Marathon. Occasionally throat markings are faint or absent in some northeastern populations so that certain females are immaculate ventrally

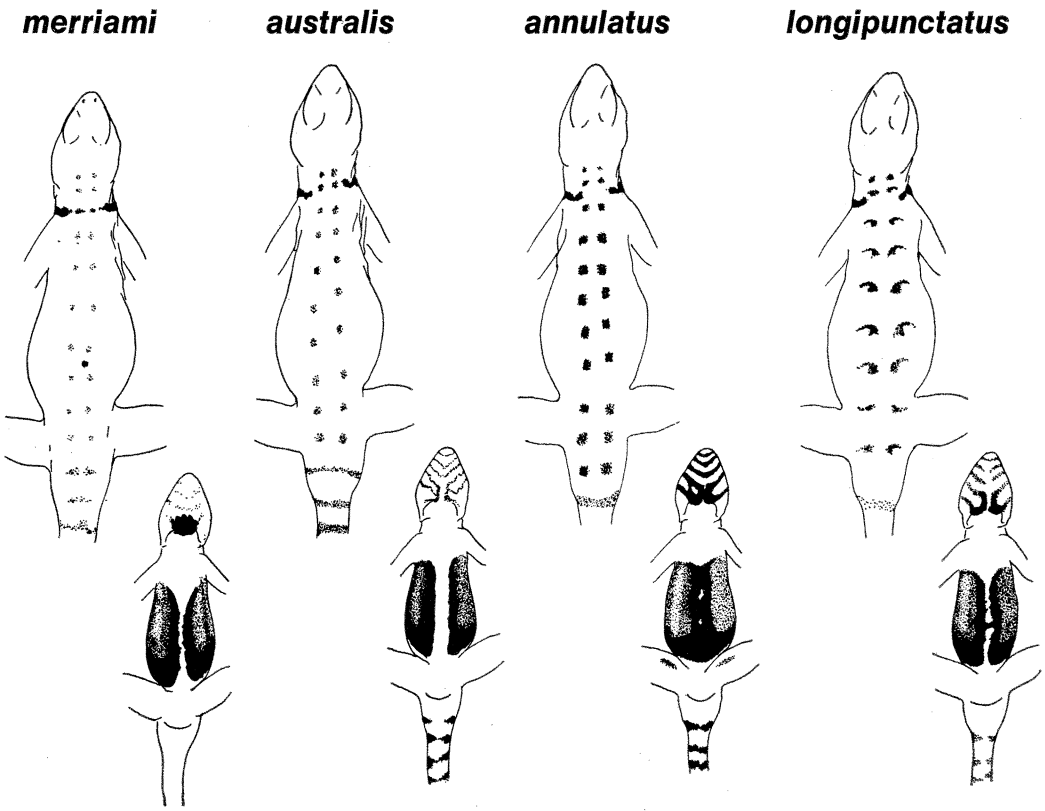

FIG. 2.—Diagrammatic representation of the predominating types of paravertebral spots (upper) and ventral patterns (lower) seen in populations of *Sceloporus merriami.*

(16–24 km NW Del Rio, 21 km SE Sheffield, 10.5 km SE Sanderson, and 1.6 km E Langtry).

Specimens from central Coahuila very often (62.2%, $N = 90$) have narrow, uneven dark blue lines on the throat, but broader, light blue, continuous (23.3%) or discontinuous (14.5%) barring is also seen. The presence of narrow throat lines is seen in Santa Elena Canyon specimens (45.0%, $N = 14$) and occasionally in examples from northwest of that locality.

Belly Patches.—Belly patches in males are usually (78.2%, $N = 101$) confluent in populations from the Chisos Mountains area but are separated (or barely in contact) elsewhere. In specimens from central Coahuila the belly patches are separated medially by a light area four or more scales wide. In northeastern examples the belly patches are usually separated medially by two light scales. In northwestern parts of the range, the belly patches are generally separated by a median light area averaging two scales in width but with occasional contact along the midline. The latter situation also occurs at Black Gap Wildlife Management Area (15%, $N = 40$) and Grapevine Hills (27.3%, $N = 66$), localities which lie between populations characterized by nonconfluent belly patches and those in which the marks are confluent.

Subcaudal Banding.—Presence or absence of dark subcaudal bands is of geographic importance in *Sceloporus merriami.* The bands are broad in specimens from the Chisos Mountains (79.8%, $N = 59$), at Chilocotal Mountain (90.9%, $N = 11$), the Rosillos Mountains (67.0%, $N = 9$) and localities lying between the Chisos Mountains and Corazones Peak (65.7%, $N = 35$). In central Coahuila, banding is generally

present (72.7%, $N = 55$), but the bands are often narrow and of a lighter shade.

Northwestern populations generally have incomplete bands or none at all; complete bands are present in only 15.5% ($N = 212$) of the specimens. Northeastern animals do not possess subcaudal bands.

Discussion

The number of dorsal scales, ventrals, and subdigital lamellae on the fourth hind toe increase from south to north. The lowest counts for all of these characters occur in central Coahuila. The numbers are higher in the Big Bend area of Texas, increasing slightly to the northwest in Presidia County and markedly to the northeast (Table 1). The frequency with which the anteriormost of the outer row of labiomentals is wedged between the first infralabial and the first postmental increases from south to north. The series from the Río Conchos in Chihuahua, the westernmost population, show development of meristic features similar to those of the northeastern populations, but there are few specimens and critical material from nearby areas is lacking.

Pattern and coloration features exhibit different geographic trends than that of the scutellation. Dorsal spots are small and not sharply outlined in southern populations; they increase in size and boldness of outline to the northwest but become smaller and less sharply defined to the northeast. On the other hand, the throat bars, narrow and complete in southern examples, are darker and broader in the Chisos Mountains area; they tend to be incomplete to the northwest and are reduced to a blotch to the northeast. The same geographic trend is true of subcaudal banding. The belly patches are broadly separated ($\geqslant 4$ scales) in the south, but the dark borders are expanded and contact in the Chisos Mountains area; incidence of complete contact decreases somewhat to the northwest, more so to the northeast.

The populations of *Sceloporus merriami* appear to be divisible into four major assemblages. The population clusters occur in central Coahuila, southern Presidio County, Texas, southern Brewster County, Texas, and the region from the lowlands northeast of the Chisos Mountains to Crockett County, Texas.

Northeastern populations exhibit a considerable amount of uniformity in the characters considered. The only notable exception within the geographic area occurs 42 km E Marathon, where the mean dorsal scale count drops to 56.0 (means of 59.1–64.2 in other populations), the number of interfemoral pore scales becomes 2.5 (compared to 2.0), and the fourth toe lamellae decreases to 25.8 (compared to 28.5). The other characteristics of this population agree with those of the other northeastern populations.

In almost every character considered, northwestern populations differ from those to the northeast of the Chisos Mountains. However, there is much variability among the western populations.

Specimens from southern Brewster County and southern Presidio County show little difference in scutellation: dorsals 50.4 ($N = 136$) and 52.1 ($N = 107$) respectively; ventrals 68.3 ($N = 105$), 67.5 ($N = 245$); fourth toe lamellae 23.6 ($N = 130$), 24.7 ($N = 410$); femoral pores 23.4 ($N = 81$), 24.1 ($N = 433$); interfemoral pore scales 2.6 ($N = 76$), 2.9 ($N = 415$); frontoparietals 1.8 ($N = 82$), 1.9 ($N = 243$); and frontal divided anteriorly 80.2% ($N = 113$), 58.0% ($N = 445$). In pattern features, considerable variation is seen. Comma-shaped paravertebral spots are rarely seen in specimens from southern Brewster County (<15%) but are more common between Terlingua and Lajitas (23.1%, $N = 108$); they are of general occurrence in southern Presidio County (>80%), except at La Mota Mountain. Broad, confluent throat bars, confluent belly patches, and complete subcaudal bands are seen in southern Brewster County examples but infrequently in Presidio County specimens.

Specimens from central Coahuila show considerable uniformity of characters: dorsal scales 45.9 (42–53, $N = 85$); ventrals 64.3 (55–71, $N = 62$); subdigital lamellae

of fourth toe 24.3 (20–29, $N = 76$); femoral pores 25.0 (20–31, $N = 77$); interfemoral pore scales 1.9 (0–4, $N = 78$); frontoparietals 1.7 (1–3, $N = 84$); anterior portion of frontal divided 22.4% ($N = 107$); anterior extension of labiomentals 1.1% ($N = 87$); lateral extension of dorsal spots 16.9% ($N = 71$); complete subcaudal bands 72.7% ($N = 55$); no medial confluence of belly patches in males ($N = 53$).

One of the most striking problems concerns the Río Conchos population; it inhabits the western extremity of the known range but resembles eastern examples in several characters. Smith, Williams, and Moll (1963) suggested that the two groups represent the same race and that they might be joined by intermediate populations via the Sierra del Carmen. I doubt this hypothesis in view of the fact that intermediate populations at Sierra del Carmen are unlike northeastern examples in several respects so that they do not seem to form such a link. I believe that the Río Conchos population is not closely allied with the northeastern populations. I also suspect that the Río Conchos and Redford area (Presidio County) populations, being physically separated by only about 64 air km, are isolated from one another by habitat barriers; the intervening area is low-lying and alluvial. Pending the acquisition of material from critical areas, I feel that it is best not to speculate as to the relationships of the Río Conchos population. Specimens are needed from northern Coahuila, between Cuatro Ciénegas and the Rio Grande.

The La Mota Mountain series indicates divergence from trends seen elsewhere in southern Presidio County. Dorsal scale counts are slightly lower [49.1 (40–56), $N = 47$, opposed to 52.1], separation of the first postmental and first infralabial by the anterior labiomental is more frequent (31.0%, $N = 71$, opposed to 6.2%), and presence of comma-shaped paravertebral spots is of moderate frequency (40.3%, $N = 67$, contrasted with 81.4%). I suspect that the population at La Mota Mountain is separated from other Presidio County populations by filter barriers. It is interesting that similar trends are not apparent in the small series from nearby, somewhat isolated San Jacinto Mountain.

Subspecies Accounts

Sceloporus merriami merriami Stejneger

Sceloporus merriami Stejneger, 1904:17–20.
Sceloporus merriami merriami Smith, 1937: 83–86.

Holotype.—USNM 33039, adult male from "East Painted Cave, near mouth of Pecos River," Val Verde County, Texas, collected 2 September 1890 by W. Lloyd.

Comparisons.—*S. m. merriami* can be distinguished from all other races by the high number of dorsal scales (56 or more in 97.8% of *merriami*, but 55 or less in more than 94% of members of the other races), incidence of separation of the first infralabial from the first postmental by the labiomental (92.7% for *merriami*, but less than 5% for other races), and absence of subcaudal bands and throat bars.

Sceloporus merriami annulatus Smith

Sceloporus merriami annulatus Smith, 1937: 83–86.

Holotype.—UIMNH 25058, adult male from east slope of the Chisos Mountains, Brewster County, Texas, collected August 1931 by E. H. Taylor and J. Wright.

Comparisons.—*S. m. annulatus* is separable from the other races by combination of broad, dark, and complete subcaudal bands (81.7% of *annulatus*, less than 15% elsewhere, except in central Coahuila populations where the bands are narrow and hourglass-shaped), confluent belly patches in males (78.2% of *annulatus*, but less than 12% in other races), and large, bold, squared paravertebral spots.

Sceloporus merriami australis Williams, Smith and Chrapliwy

Sceloporus merriami australis Williams, Smith, and Chrapliwy, 1960:38–39.

Holotype.—UIMNH 43319, adult male from 15.6 miles (25.1 km) E Cuatro Ciene-

gas, Coahuila, collected 9 July 1958 by P. S. Chrapliwy and K. S. Williams.

Comparisons.—*S. m. australis* is distinguishable from *merriami* by a lower number of dorsal scales (48 or less in 84.8% of *australis*, 56 or more in 97.8% of *merriami*), and presence of subcaudal bands and throat bars (absent in *merriami*); from *annulatus*, *australis* is distinguished by possessing narrow rather than broad throat bars, hourglass-shaped as opposed to broad subcaudal bands, markedly less medial confluence of belly patches in males (0% for *australis*, 78.2% of *annulatus*), and medium-sized, rounded paravertebral spots rather than large, squared spots.

Sceloporus merriami longipunctatus subsp. nov.

Holotype.—USNM 192744 (formerly REO 3286), an adult male from Closed Canyon, 14.3 road miles (23.0 km) SE Redford, Presidio County, Texas, collected 31 May 1971 by R. Earl Olson.

Paratopotypes.—REO 877, 894, 939, 2223–2226, 2233–2235, LSUMZ 23001–19, CNM 13242–43, 13267, SRSU 188–198, 210, 216, 232–233, 235–236, 254–255, 261, 264, 268, 287–292, 299, 508, 598–599, 628–635, 653–656, 658–659, 668–670, 679, 681–683, 721, 723, 772–776, 790, 792–793, 811–825, 828, 847, 863–864, 868–869, 873, 1211–12.

Definition.—Adults average about 50 mm SVL; anterior section of frontal entire as often as divided; frontoparietals generally two per side; anterior scale of outer row of labiomentals not wedged between first infralabial and first postmental; dorsal scales average 52.1; throat with broad bars, more often incomplete than continuous medially; subcaudal region with bluish wash, usually with incomplete bands; paravertebral spots usually bearing lateral extensions, resembling a comma.

Comparisons.—The race *longipunctatus* can be separated from all other races by the presence of laterally elongate paravertebral spots (83.5% in *longipunctatus*, but 16.9% in *australis*, 5.2% in *annulatus*, and 1% in *merriami*).

Description of Holotype.—Snout-vent length 49.0 mm, head length 10.8 mm (to posterior edge of interparietal), head width 10.0 mm, left femur length 11.5 mm, longest hind toe length 9.0 mm (measurements of preserved specimen).

Dorsal scales 54, ventrals 69, fourth toe lamellae 25–26, femoral pores 26–?, interfemoral pore scales 3, lamellae of longest front toe 20–21, frontoparietals 2–2; frontal transversely divided, anterior section entire; one prefrontal on each side separated medially by one azygous scale about one-fourth the size of prefrontals; frontonasals 3; internasals 4; postrostrals 2; supraorbitals 5–5; canthals 2–2; supraciliaries 5–5; supralabials 5–5; infralabials 8–6; postmentals 6–8; labiomentals 9–8; auricular lobules 4–5.

Dorsal head plates moderately rugose and extensively pitted; several dorsolateral head scales, numerous enlarged scales among the granular lateral nuchals, and many granular lateral body scales pitted; rostral three times as long as high, with median dorsal region convex; anteriormost point of labiomentals on both sides reaching along one-fourth the length of the first infralabial; auricular lobules along upper half of the anterior edge of ear opening covering little of the ear opening, third is longest on both sides.

Dorsal color medium brown, head plates with suffusion of black in some areas; black spots on posterior sides of interparietal and parietals; a semicircle of black spots from each supratemporal region posteriorly, semijoining along the midline on the sixth scale posterior to the interparietal; a dark bar on each side of the head beneath the eye from the center of the suborbital across the posteriormost lorilabials and the fourth supralabials; a dark spot above and below the angle of the mouth; a temporal spot on each side; a circumauricular series of six spots, the anterior three dark, posterior three faint; a series of nine pairs of paravertebral spots, the first pair unelaborated, but the others bearing lateral dark extensions, the second pair separated along the midline by one scale, but joining the dark shoulder bars laterally; the shoulder bars black, becoming fainter on the ventral side with eight light intermediate ventral scales; a series of bold dark spots lateral to each paravertebral pair along the juncture of the enlarged dorsal scales and the granular lateral body scales; dorsum of tail with black band (tail incomplete); the body laterally with large light spots among unclear suffusion of gray; forelimbs with two dark bars proximally, two dark bars distally, and lighter bands on the foot and digits; posterior limbs with three dark bands proximally, three dark bands distally, two dark bands on the foot, and lighter bands on the digits.

Ventrally, ground color white; three series of anterior throat bars gray, broad (one and one-half to three scales wide), continuous medially, extending across the infralabials on both sides; posterior throat bars dark blue, faint laterally, the anterior pair arising laterally near an imaginary line joining

the angles of the mouth, curving caudad to join the posterior pair at a point two scales anterior to and midway between the ends of the incomplete gular folds, the fourth pairs arising in a position anteroventral to the ear openings, curving sharply posteriorly, then extending straight across the gular region; belly patches extending from 18 scales posterior to the gular bar to within 3 scales of the groin, the patches in contact medially for 15 scales; tail incomplete at tip, with faint, narrow, incomplete bands.

KEY TO SUBSPECIES OF *SCELOPORUS MERRIAMI*

1. Anterior labiomental usually wedged between first postmental and infralabial scales; dorsal scales more than 55; frontoparietals usually 1 per side; throat unbarred or faintly barred with dark, irregular posterior patch; no subcaudal bands; extreme west-central Crockett and southwestern Edwards counties, Texas westward to eastern Brewster County, thence southwestward to an imaginary line joining Boquillas, the Grapevine Hills, and Persimmon Gap (Fig. 1) ..... *merriami*

   Anterior labiomental usually not wedged between first labiomental and infralabial scales; dorsal scales less than 55; frontoparietals often 2 per side; throat with distinct bars or lines; subcaudal bands usually present but may be incomplete 2

2. Paravertebral spots usually comma-shaped, extending laterally; southern Presidio County, Texas from the Brewster County line westward to near Redford, thence northwestward through the La Mota and San Jacinto Mountains to Shafter ..... *longipunctatus*

   Paravertebral spots usually without lateral extensions 3

3. Subcaudal bands broad and dark; throat with broad, dark bars; belly patches in males completely in contact or closely approaching each other medially; southern Brewster County, Texas, from Chilocotal Mountain and Glenn Draw westward to Study Butte thence northward to Corazones Peak ..... *annulatus*

   Subcaudal bands narrow and light blue, often complete; throat with narrow blue bars; belly patches in males separated medially by four light scales; central Coahuila ..... *australis*

Intergradation of *S. m. merriami* with *S. m. annulatus* occurs to the north and east of the Chisos Mountains, Brewster County. Specimens from 3–5 km W Boquillas Ranger Station are mostly similar to northeastern populations in coloration, ventral pattern, dorsal scale number (60.0), number of subdigital lamellae of fourth toe (27.0), number of femoral pores (25.7), number of interfemoral pore scales (2.0), frontoparietal number (1.0), and the frequency of anterior frontal shield division (3.2%). Boquillas lizards reflect influence of *annulatus* in the reduced values of ventral scale averages (67.8 instead of 70 or more in *merriami*) and anterior extension of labiomentals (87.5% opposed to 92% or more in *merriami*).

At Black Gap Wildlife Management area, intergradation is evident in dorsal scale count (57.5 compared to 59.1 or more in *merriami*), number of lamellae on the fourth hind toe (25.8 opposed to 28.5 in *merriami*), separation of first infralabial and postmental scales by the anterior labiomental (67.9% compared to 80% + in *merriami*), irregular variation of throat markings, and frequent contact of belly patches (15.0%, but <5% in *merriami*). Specimens from Hot Springs show intergradation in the frequency of division of the anterior section of the frontal (22.2%, usually <10% elsewhere in *merriami*), number of dorsals (55.7 opposed to 59 or more in *merriami*) and ventrals (64.3 rather than 69+ for *merriami*), separation of the first infralabial and first postmental by the labiomentals (71.4%, but usually more than 85% in *merriami*), and irregular variation in throat bars.

Although there is not enough material available at present, I suspect that the Sierra del Carmen, Coahuila sample represents intergrades of *S. m. merriami* × *S. m. annulatus*. They resemble *S. m. merriami* in most respects, but there are relatively few dorsal scales (54.0 rather than 59.1 or more) and femoral pores (24.0 opposed to 26.1), the anterior section of the frontal is divided in one specimen and the throat bars are variable.

It is interesting that in certain areas there is no apparent intergradation although the populations approach each other closely, whereas nearby populations show intergradation. *Sceloporus m. merriami* occurs 10 km N Big Bend National Park Headquarters, but *S. m. annulatus* occurs 5 km

E the headquarters. Intergrade populations exist both to the east and northeast (Dog Canyon, 10 km SE Persimmon Gap, Boquillas) and to the west (Grapevine Hills) of the locality.

Intergradation between *Sceloporus merriami annulatus* and *S. m. longipunctatus* occurs in a narrow zone on the extreme southwestern edge of Brewster County. There is an increase in dorsal scales from the average of 50.4 for *annulatus* (52.7 at Terlingua, 53.5 from 5.1 km W Terlingua), increase in presence of elongated paravertebral spots (2 of 3 at Terlingua, 1 of 4, 5.1 km W Terlingua, and 2 of 3 from 14.3 km E Lajitas), and reduction in the incidence of complete subcaudal bands (2 of 3 at Terlingua, 0 of 4 from 5.1 road km W Terlingua, and 1 of 3 from 14.3 km E Lajitas). Animals from Terlingua and 5.1 km W Terlingua are light-colored dorsally, but there they inhabit areas with a light-colored substrate.

The narrow and occasionally interrupted zone of intergradation between *Sceloporus merriami merriami* and *S. m. annulatus* to the northeast of the Chisos Mountains indicates secondary intergradation in that region. By contrast, the gradual transition between the rather similar races *annulatus* and *longipunctatus* indicates the probability of primary intergradation following a relatively brief period of differentiation. I suspect that the species has invaded (or reinvaded) northern areas postglacially. It may be that the eastern and central populations came to occupy the northern part of the range by separate routes. Perhaps the central group invaded the Chisos Mountains area, while the eastern group crossed the Rio Grande and expanded its range east and west, contacting the more westerly populations in Brewster County.

The hypothesis of the northward dispersal by two (or three) routes would be enhanced by finding primary intergradation between races in northern Coahuila and Chihuahua. It might also be that what appears to be intergradation among the geographic races north of the Rio Grande is simply the result of recontact of the ends of clines. However, the presence of apparent *merriami* populations at La Linda, Coahuila, and *merriami* × *annulatus* in the Sierra del Carmen seems to negate such a possibility. *Sceloporus merriami* is a highly variable species. This lizard inhabits rather specialized sites, resulting in a fair degree of isolation. Isolated populations tend to exhibit divergence.

The series from La Mota Mountain indicates that isolation or semi-isolation allows a population to diverge considerably from others nearby. More intensive investigation of this area (and San Jacinto Mountain) might serve to reveal something of the way in which isolation factors function in this species.

Material Examined

Sceloporus merriami merriami.—Texas: *Brewster Co.* Black Gap Wildlife Management Area (SRSU 598–9; KU 118165–268); 42 km E Marathon (KU 118955–72); 74 km S Marathon [UMMZ 102677 (6)]; 9.6 km N Park Headquarters (UCM 14568–69; REO 900, 3309–10); 4.8 km SE Persimmon Gap (INHS 7988–92); Santiago Mountains near Persimmon Gap (FMNH 75891–93). *Crockett Co.* Lancaster Hill, 48 km W Ozona (KU 118801–02); 9.6 km E Sheffield (TNHC 7352–54). *Edwards Co.* 0.8 km W Carta Valley (KU 88166). *Terrell Co.* 10.0–10.7 km SE Sanderson (REO 919–24); 48 km SE Sheffield (SRSU 723; KU 118614–26); 21 km SE Sheffield (KU 118632–51). *Val Verde Co.* 5.8 km SE Comstock (TNHC 32418); 29 km NE Comstock (TNHC 32425); Del Rio, T. Rose Ranch (TNHC 21619–22); 19 km NW Del Rio (TNHC 32420, 32426); 20 km NW Del Rio (TNHC 32415–17); 21 km NW Del Rio (TNHC 32413a); 22 km NW Del Rio [TNHC 32412, 32413 (2)]; near mouth of Devils River (KU 10840, 10843–44, 10846, 10850, 10853, 14962); 1.6 km E Langtry (TNHC 32419, 32421–24); 8 km E mouth of Pecos River (KU 14957–92); mouth of Pecos River (USNM 33039–40; UIMNH 21395–96; KU 10854–56); 3.2 km SW Shumla (TNHC 11688). Mexico: *Coahuila.* 6.4 km S La Linda (AMNH 106341–43).

Sceloporus merriami annulatus.—Texas: *Brewster Co.* Cattail Falls (SRSU 721); Chilocotal Mountains [UMMZ 69856 (9)]; east slope of Chisos Mountains (KU 15059–61, 16063–67); Chisos Mountains Basin [USNM 103633; UMMZ 114217 (2)]; 13 km S Chisos Mountains (KU 15068); Corazones Peak (FMNH 75889–90); Glenn Draw (UMMZ 66215–24); Glenn Spring (UMMZ 72077; USNM 120770); Oak Creek, Chisos Mountains (USNM 103647; FMNH 27406–

22); 4.8 km E Panther Junction (AMNH 106331–38); Rosillos Mountains [UMMZ 114216, 114219, 114220 (3)]; 16 km E Terlingua (KU 15162–64); 23 km N Terlingua (KU 15988–98).

Sceloporus merriami australis.—MEXICO: *Coahuila.* 5.3 km NNW Cuatro Ciénegas (KU 80296–300); 4.8 km NW Cuatro Ciénegas (KU 39947); 16 km S Cuatro Ciénegas (KU 47041–44; KU 47056–70); 25 km E Cuatro Ciénegas (UIMNH 43321); 24 km E Cuatro Ciénegas (TNHC 32898–900); 9.2 km W Cuatro Ciénegas (UIMNH 46945–51); 9.7 km W Cuatro Ciénegas (KU 47045–55); 10.0 km W Cuatro Ciénegas (UIMNH 43321–24); 11.3 km SW Cuatro Ciénegas (USNM 159545–54); 47 km W Cuatro Ciénegas (UIMNH 46956–57); 24 km SSW Cuatro Ciénegas (TNHC 32870–73); 4.5 km Hac. Guadalupe (UIMNH 43307–17); Jaral (FMNH 1544); Las Delicias (FMNH 46113); 3.2 km S, 4.8 km E Muralla (KU 39945–46); 10.5 km W Nadadores (TNHC 33479–84); 12.9 km W Nadadores (KU 53738); 48 km NW San Pedro (FMNH 44318).

Sceloporus merriami longipunctatus.—TEXAS: *Presidio Co.* Closed Canyon (REO 868–73, 875–78, 939, 2223–25, 2233–36, 3282–89, 3334; LSUMZ 23001–19; SRSU 188–98, 210, 216, 232–3, 235–6, 254–5, 261, 264, 268, 287–92, 299, 508, 598–9, 628–35, 653–6, 658–9, 668–70, 679, 681–3, 721, 723, 772–6, 790, 792–3, 811–25, 828, 847, 863–4, 868–9, 873, 1211–12); 9.7 km NW Lajitas (KU 118847–57); 4.8 km NW Lajitas (KU 118887–918); 4.8 km W Lajitas (SRSU L870–71, four unnumbered specimens); 8.0 km W Lajitas (SRSU L255, L635, L882–3); La Mota Mountain (KU 118652–749); 50.0 road km SE Redford (REO 2307–8, 2317); 35.7 road km SE Redford (REO 2244); 34.3 road km SE Redford (REO 2245–6); 18.8 road km SE Redford (LSUMZ 23146–47); 16.9 road km SE Redford (REO 1568–73, 2695, 3292–94); 15.1 road km SE Redford (LSUMZ 23032–34); 13.7 road km SE Redford (REO 2217–19); San Jacinto Mountain (REO 3254, 3269–73); 3.5 road km SW Shafter (LSUMZ 23145); Tapado Canyon, 12.1 road km SE Redford (LSUMZ 23031, 23035–53; REO 888–94, 904–05, 2214–16, 2309–10, 3295–98).

Sceloporus merriami merriami × *S. m. annulatus.*—TEXAS: *Brewster Co.* Boquillas (KU 118580); 3.2 km WNW Boquillas Ranger Station (KU 118600–13); 4.8 km WNW Boquillas Ranger Station (KU 118581–99); Dog Canyon, Santiago Mountains (UMMZ 114215, 3 specimens); Grapevine Hills (SRSU L847; KU 118466–579); Hot Springs [UMMZ 66163–67 (8), 69855 (2)]; 9.6 km SE Persimmon Gap (INHS 7828). MEXICO: *Coahuila.* Carmen Mountains (FMNH 42383–85).

Sceloporus merriami annulatus × *S. m. longipunctatus.*—14.3 road km E Lajitas (LSUMZ 23020–22); 9.6 km N Lajitas (KU 118302–60); 16 km ENE Lajitas, near Mariposa Mine (KU 118372–449); Terlingua (KU 15063); 3.2 km W Terlingua (KU 118768–800); 5.1 road km W Terlingua (LSUMZ 23023–24; REO 2228–29).

Acknowledgments.—For the loan of specimens I wish to thank Mr. Roger Conant and Drs. Charles A. Douglas, William E. Duellman, Donald F. Hoffmeister, Robert F. Inger, T. Paul Maslin, James A. Peters, Douglas A. Rossman, James C. Scudday, Philip W. Smith, and Donald W. Tinkle. I am grateful to Dr. James Scudday for his helpfulness, and to Dr. Robert H. Carcasson, with whom stimulating discussions have been highly rewarding.

I owe a special word of thanks for critical reading of the manuscript and for suggestions to Drs. Kenneth C. Corkum, Blanche Jackson, George H. Lowery, Jr., Douglas A. Rossman, and Hobart M. Smith.

Initials used in the text represent specimens seen from the following institutions: AMNH, American Museum of Natural History, New York; CNM, Canadian National Museum, Ottawa; FMNH, Field Museum of Natural History, Chicago, Illinois; INHS, Illinois Natural History Survey, Urbana; KU, University of Kansas Museum of Natural History, Lawrence; LSUMZ, Louisiana State University Museum of Zoology, Baton Rouge; REO, R. E. Olson; SRSU, Sul Ross State University, Alpine, Texas; TNHC, Texas Natural History Collection, Texas Memorial Museum, Austin; UCM, University of Colorado Museum of Natural History, Boulder; UIMNH, University of Illinois Museum of Natural History, Urbana; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, United States National Museum, Washington, D. C.

LITERATURE CITED

BLAIR, W. F. 1950. The biotic provinces of Texas. Texas J. Sci. 2:117–143.

DICE, L. R. 1943. The biotic provinces of North America. Univ. Michigan Press, Ann Arbor.

MILSTEAD, W. W. 1953. Ecological distribution of the lizards of the La Mota Mountain region of Trans-Pecos, Texas. Texas J. Sci. 5:403–415.

SMITH, H. M. 1937. A new subspecies of the lizard genus *Sceloporus* from Texas. Proc. Biol. Soc. Washington 50:83–86.

———, K. WILLIAMS, AND E. O. MOLL. 1963. Herpetological explorations on the Río Conchos, Chihuahua, Mexico. Herpetologica 19:205–225.

STEJNEGER, L. 1904. A new lizard from the Rio Grande Valley, Texas. Proc. Biol. Soc. Washington 17:17–20.

WILLIAMS, K. L., H. M. SMITH, AND P. S. CHRAPLIWY. 1960. Turtles and lizards from northern Mexico. Trans. Illinois Acad. Sci. 53:38–39.

Received: 4 February 1972
Accepted: 1 May 1972

Department of Biology, University of Colorado, Boulder, Colorado 80302