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STUDIES ON THE LIZARD
HOLBROOKIA TEXANA (TROSCHEL)
WITH DESCRIPTIONS OF TWO NEW
SUBSPECIES

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THE rapid growth in collections of herpetological material in the United States which has taken place in the past 50 years has made possible the reinspection and detailed study of many species long considered monotypic, with subsequent definition of well-marked geographic or ecologic forms. Many of these studies have entailed the application of statistical methods toward their completion (producing, on occasion, subspecies recognizable only to statisticians), in contrast with the time-honored method of recognizing only clearly marked and simply described variations. The present study of the iguanid lizard, *Holbrookia texana* (Troschel), has lent itself admirably to a combination of both methods of approach, because the statistics served principally as a tool to substantiate subspecies which are definable, and usually recognizable, down to the level of the individual specimen, on the basis of nonstatistical differences.

METHODS, MATERIALS, AND ACKNOWLEDGMENTS

In making the counts and measurements on these lizards I have attempted to standardize my procedure as much as possible, and the methods used were as follows: The ventrals are counted in a straight line from the posterior edge of the last gular fold to the anal fold along the mid-ventral line. The head length, measured with dividers, is taken as the distance from the anterior edge of the rostral to the posterior edge of the interparietal. The number of dorsal scales in the head length are counted from the mid-point between the shoulders posteriorly on the vertebral line. Only labials which are actually in the lip line are included in labial count; this was done to eliminate bias

concerning the scales in the labial line which lie beneath the eye in such a position that they are crowded off the lip by granules from the angle of the jaw.

In accordance with the practice which is being broadly adopted by workers in systematic zoology, the holotypes are not emphasized as individuals in the descriptions of the subspecies. This procedure is based upon the concept that a subspecies is composed of populations whose range of variation is confined to a limited part of the range of variation for the species. This range cannot be demonstrated by any individual specimen. However, since the status of a name must be determined by the status of the holotype of that name, sufficient data are included concerning the holotype to make future identification of the individual possible.

In all, 1254 specimens from the various collections in the United States were examined, and I extend my sincere thanks to the persons who made it possible for me to see the material in their care. Specimens have been loaned by the following institutions and individuals (with the abbreviations used in reference to their specimens in this paper): American Museum of Natural History (AMNH); Baylor University Museum (BUM); Bryce C. Brown (BCB); Carnegie Museum (CM); Chicago Academy of Sciences (CAS); Chicago Natural History Museum (CNHM); Edward H. Taylor (EHT); Frederick A. Shannon (FAS), Museum of Comparative Zoology, Harvard College (MCZ); Stanford University Natural History Museum (SU); Sherman A. Minton (SAM); Texas Agricultural and Mechanical College (TAM); Thomas H. Lewis (THL), United States National Museum (USNM), University of Illinois Museum of Natural History (UIMNH), University of Michigan Museum of Zoology (UMMZ), and University of Texas (UT).

I am also indebted to Mr. John Werler, who expended much personal time and effort in order to obtain topotypes of Troschel's species for me. Dr. Norman Hartweg has, as always, been extremely liberal with time, advice, comments, and criticisms, and his efforts to inject intelligibility have not, I hope, gone unrewarded.

HISTORY OF THE SPECIES

The first known description of *Holbrookia texana* was published in 1852 by Troschel, who described it as a new genus and species, which he called *Cophosaurus texanus*. In the original description, Troschel stated that he had 2 specimens available, one of which was deposited in the museum at Bonn and the other in the museum at Hildesheim.

Dr. A. Reichensperger, director of the Zoological Institute of the University of Bonn, which operates the museum, wrote me that the museum was completely destroyed during the war and that the type of *Cophosaurus texanus* is not to be found. The city of Hildesheim was almost totally leveled during the war, and requests for information concerning the collections have gone unanswered. It seemed advisable, therefore, to designate a neotype to replace Troschel's original cotypes, and this has been done under the discussion of the typical subspecies.

Baird and Girard (1852: 125) placed the species in the genus *Holbrookia*, where it has since remained undisturbed.

Strecker (1909: 12) was the first to comment upon the differences in coloration between specimens from 2 areas, stating that "the examples collected [in Brewster County] were so brilliantly colored that I could hardly realize that they were of the same species that occurs in Central Texas." Schmidt (1922: 713) suggested that 2 fairly distinct subspecies would probably be recognizable upon examination of larger series. Baird and Girard (1852: 125) described *Holbrookia affinis* from a single specimen from within the range of what is here considered to be the typical subspecies, and later Baird (1859: 8) recorded another specimen of *H. affinis* from Sonora, Mexico. I have seen the 3 cotypes of this species,¹ and they fall within the limits of the typical subspecies, although they are somewhat intermediate between *texana* and *scitula*. The type locality is on the eastern edge of the zone of intergradation. Cope (1900: 286) thoroughly discussed the synonymy of *affinis* with *texana*, first pointed out by Boulenger (1885: 208).

In addition to the sources mentioned, there has been little published concerning the species, and, with the exception of very recent works by Ramsey and by Cagle, that which has been published is merely recapitulation. Reference to the species in recent literature has been practically confined to local and faunal listings.

LIFE HISTORY

By far the most widely recorded habitat for the species is that composed of open rocky desert flats with scattered bushes, such as creosote bush and greasewood. It is also common on sandstone and limestone or on shale cliffs and bluffs along streambeds. Of 36 specimens in Bryce C. Brown's collection for which habitat data are available, 29

¹ Although Baird and Girard mentioned only a single specimen in their description, the United States National Museum has 3 specimens with identical data which apparently were available to the authors if not used. There are 2 females in this series, neither of which can be definitely shown to be the type.

were taken on or under rocks, 6 on open ground, and 1 in weeds. Most of the specimens came from sandstone hills or dry creek beds. Jameson and Flury (1949) found specimens in 5 different ecological associations, but in all of them they were practically restricted to the rocky areas, their preference obviously being for the rocks and not for the floral association.

The species is well known to collectors for its rapidity of movement and the effectiveness of its protective coloration. An individual often seeks no cover when trying to escape, but merely runs a few yards and settles to the sand, practically disappearing (Bailey, 1905: 41). It frequently curls its tail over its back while running, displaying the black bars. Mertens (1946: 12) suggested that this is a fear or warning reaction. Possibly the tail is vital as a balance in those species which curve it over the back, and loss of the tail may be a serious handicap to locomotion. Strecker easily caught a lizard that lacked a tail, and he (1928: 4) remarked upon its seeming incapacitation.

Members of the species are known to "bob" in the manner of most iguanids, pumping up and down on the forelegs (Murray, 1939: 6). Strecker (1909a: 4) chased them into water and watched them swimming. He also (1928: 4) reported a young *H. texana* in the stomach of a *Cnemidophorus gularis*.

Cagle, whose recent study (1950) is the most detailed yet made (his work is based upon specimens of the subspecies *t. texana* as here considered), found that the species inhabits a home range to which it eventually returns after being disturbed. He observed courtship behavior during June and July, but not the time of egg deposition, although eggs he dissected from a female on June 26 hatched 50 days later. He stated that females lay several broods a season, a conclusion based upon the discovery of oviducal eggs in the females throughout the summer, but with a consistent reduction in number of eggs in the later months.

Smith (1946: 136) reported the clutch size as 8 to 12. The eggs are deposited to a depth of 5 to 6 inches. Ramsey (1949: 125) noted newly hatched young as numerous by August 1. Cagle found that the young attained sexual maturity during the first year of life. It appears from his data that the species not only reaches maturity but also near-maximum size within the first year.

During the winter of 1947 Ramsey (1948:223) took 5 females (belonging to the typical subspecies) which he thought were hibernating. The lizards, inert when found, were under 3 inches of loose shale on a river bluff, about 9 feet above water level. The population which these

individuals represented was apparently almost completely destroyed by spring floods in 1949. He (1949) had found as many as 30 dormant individuals of this species at one time at the locality, but obtained only 2 widely separated individuals in the entire area after floods on the river had inundated the shale under which the lizards were buried. I suspect this type of dormancy results from occasional chilling and probably does not continue unbroken throughout the winter period. My suspicion is partly verified by Ramsey (1949), for he mentioned that February 17, 1949, was a warm day and that "some of the lizards were fairly active." Ramsey's reports, as far as I know, are the only published records of instances of winter inactivation for the species.

DISCUSSION OF THE SPECIES

Holbrookia texana (Troschel)

DIAGNOSIS.—Tail flattened, longer than head and body, barred beneath with 5 to 9 (usually 7) black bands; paired lateroventral black stripes placed far posteriorly, enclosed in a broad blue patch; size large (maximum for males, snout to vent, 81.5 mm.; for females, 73 mm.); hind legs long.

Within the species I have been able to define 3 subspecies.

Holbrookia texana texana (Troschel)

Cophosaurus texanus Troschel, *Arch. f. Naturg.*, I, 1850 (1852): 389, Pl. VI.

Holbrookia texana, Baird and Girard, *Proc. Acad. Nat. Sci. Phila.*, VI (1852): 125.

Holbrookia affinis Baird and Girard, *Proc. Acad. Nat. Sci. Phila.*, VI (1852): 125.

TYPE LOCALITY.—New Braunfels, on the Guadalupe River, Texas (types, formerly in Bonn and Hildesheim, now destroyed.)

NEOTYPE.—UMMZ 100811, Northeastern edge of city of New Braunfels, Comal County, Texas, collected by John Werler, October 11, 1949.

DIAGNOSIS.—Ventrals from collar to anus 79 or less (80 per cent); number of scales in head length 40 or more (86 per cent); sum of femoral pores 27 or less (83 per cent); color as described below.

DESCRIPTION OF SUBSPECIES.—Ventrals 67–87, usually less than 80; scales in head length 36–54, usually more than 39; sum of femoral pores 20–32, usually less than 28; upper labials 6–8, usually 7 or less; small scales of back extend up to and come in contact with the interparietal.

Dorsal color, slate gray to dark brown; vertebral spots, when present, not prominent; usually no orange or yellow stippling dorsally, little laterally, where it is confined to the axillary region. Ventral color, cream to dark cream; paired ventrolateral black stripes lighter on sides, but extending almost to vertebral line; chin occasionally with black lines converging toward mid-line posteriorly.

NEOTYPE.—74 ventrals; 44 scales in head length; femoral pores 12–12 (10th and 11th pore on a single scale on right side); upper labials 6–7.

Ground color, dark gray; some black vertebral spots present, not paired but alternating; small white spots scattered dorsolaterally, more abundant between the axillary region and the ventrolateral stripes than between the stripes and the groin. Chin and throat dark gray with yellowish spots. Body cream ventrally; arms, legs, and tail white below. Tail with 7 bars below, the first of which is incomplete.

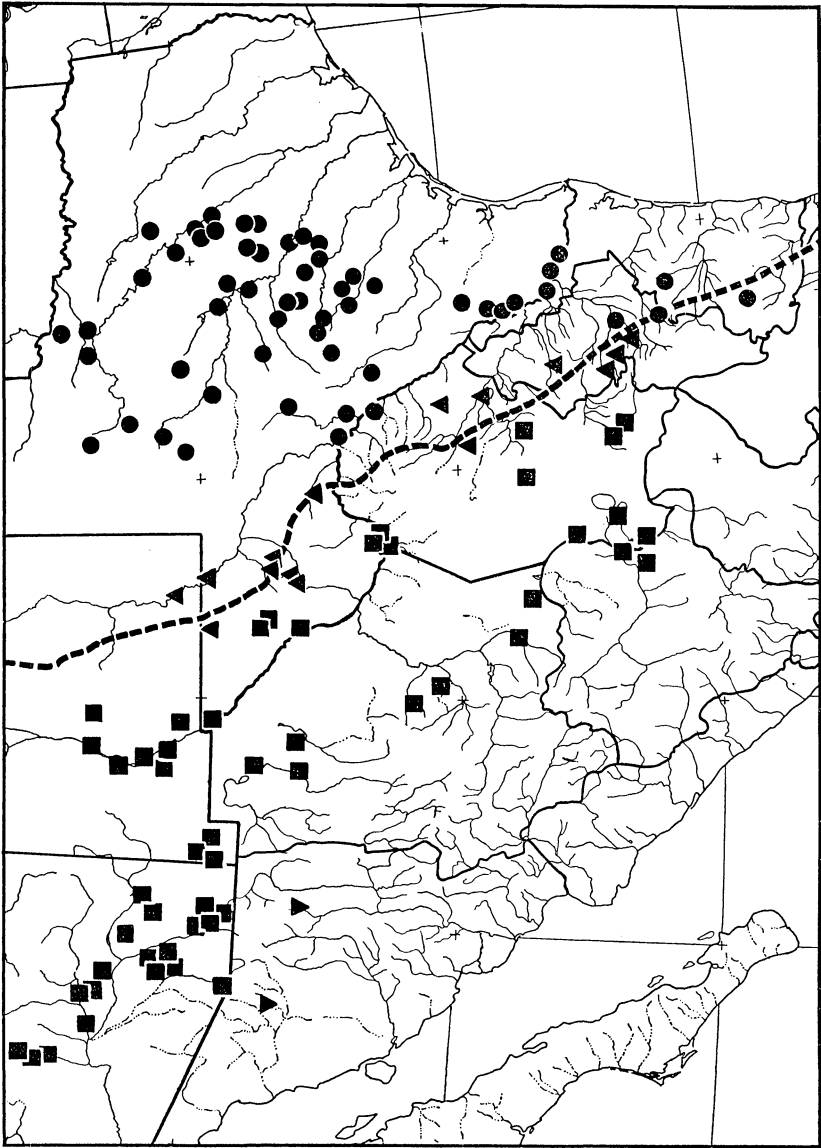
Body length 66 mm., tail length 76 mm., total length 142 mm., hind-leg length 58 mm., hind foot 26.5 mm., longest toe 18 mm., head length 15.5 mm., head width 12.5 mm.

RANGE.—Texas west of the Balcones escarpment to Reeves and Terrell counties, south to southern Tamaulipas, eastern Nuevo León, and eastern Coahuila (Map 1).

REMARKS.—The following notes were made by John Werler concerning the neotype and several topotypes: "Collected October 11, 1949, at the northeastern edge of the city of New Braunfels, Comal County, Texas. All were taken in the vicinity of an old rock quarry where they were found under small rocks. The locality supported only sparse vegetation and few trees. Collecting in other parts of New Braunfels for *texana* was futile."

The following specimens of this subspecies have been examined:

TEXAS: *Atascosa Co.*, (CM 8479). *Baylor Co.*, Lake Kemp (BUM 4096–99). *Bell Co.*, Cedar Creek, 7 miles from Belton (BUM 5280); Copperas Cave (TAM 1045), 3 miles west of Holland (TAM 1908). *Bexar Co.*, Helotes (BCB 14, BUM 4817–19, CM 8480, 21124–26), 8 miles northwest of Helotes (BCB 2237–39), 5½ miles north of Helotes (TAM 1902), 8 miles north of Helotes (TAM 1909), San Antonio (AMNH 43222, 44371, 44401–3, 46086–87, 59669). *Blanco Co.*, (CNHM 18352). *Borden Co.*, 7 miles north of Vincent (BCB 4047–53). *Bosque Co.*, Clifton (BUM 3813), Childress Creek, D. B. Hill Farm (BUM 5284), 10 miles north of China Spring (CNHM 46715–21). *Brown Co.*, mouth of Brady Creek, 60 miles southeast of Brownwood (CNHM 15953), *Burnet Co.*, (CM 1001–2, 1004–7), Honey Creek Road (CNHM 1823), Burnet (UMMZ 42333). *Coke Co.*, 17 miles north of San Angelo (SU 9940). *Comal Co.*, near Guadalupe River (AMNH 62306–8), 6 miles southeast of Fischer's Store (BCB 1871). *Crosby Co.*, 5 miles east of Crosbyton (CNHM 46008). *Gillespie Co.*, 3 miles north of Fredericksburg (BCB 13). *Hays Co.*, San Marcos (AMNH 32435–36, 32448–53, 32455, 32467, 32473–78), Nance Ranch (TAM 1903–6); 2 miles west of Wimberley (BCB 459–60), 5 miles east of Wimberley (BCB 2100), 3 miles south of Wimberley (BCB 3807). *Hidalgo Co.*, 10 miles west of Mission (BCB 684–85). *Howard Co.*, 1 mile south of Big Spring (SU 9941). *Kent Co.*, 20 miles north of Snyder (UMMZ 69055, 70810–15). *Kerr Co.*, Raven Ranch, 19 miles south of Kerrville (CAS 7173–74, 7177), Turtle Creek, 8 miles southwest of Kerrville (CNHM 30595–96), 8 miles southwest of Ingram (TAM 113), 20 miles west of Hunt (TAM 114), 11 miles west of Kerrville (TAM 115), Hunt (TAM 1102–3). *Kinney Co.*, 5 miles east of Brackettville (TAM 641). *Knox*



MAP 1. Locality records for the subspecies of *Holbrookia texana* in southwestern United States and northern Mexico. The circles represent localities for *H. t. texana*; squares, *H. t. scitula*; triangles, *texana-scitula* intergrades; and inverted triangles, *H. t. reticulata*. The heavy dashed line is the approximate boundary between the Basin and Range physiographic province, in the United States, and the piedmont and low plateau, in Mexico.

Co., 8 miles north of Vera (CNHM 48674-82). *Llano Co.*, (CNHM 27179, SAM R-162), 18 miles north of Fredericksburg (BCB 673, 683). *McLennan Co.*, Waco (BUM 3134-38, 3710-37, 3783, 3794, 5680), 6 miles northeast of Waco (BCB 2489, 2956), Lake Waco (BUM 4025-28), China Springs (BUM 3041, 5678-79), 5 miles north of China Springs (BCB 2776), White Rock Creek (BUM 3875), Rock Creek (BUM 5244), Childress Creek (BUM 5535), Eagle Branch (BUM 4993-94), Crawford (BUM 2926-28). *Mason Co.*, 4 miles south of Mason (TAM 1098). *Medina Co.*, Diversion Lake (CM 8478, 8481). *Menard Co.*, Menard (BCB 2044). *Mills Co.*, near Goldthwaite (UMMZ 70146). *Palo Pinto Co.*, Palo Pinto (CAS 13097-99, 13149-52), 8 to 10 miles south of Mineral Wells (BCB 3999-4000, 4128, 4163, CNHM 48683). *Real Co.* (BUM 5178, 5182). *San Saba Co.* 2 miles east of San Saba (BCB 1654-55), 6 miles west of Bend (BCB 3397-3407). *Scurry Co.*, 2 to 3 miles south of Knapp (BCB 3974-77, 4062, 4150). *Somervell Co.*, Paluxy River (BUM 5403-4, 5406-7), Glenrose (UMMZ 42337). *Starr Co.*, 5 miles east of Rio Grande City (CAS 6454-56), Rio Grande City (EHT A935), 2 miles northwest of Roma (UMMZ 74759). *Sutton Co.*, vicinity of Sonora (SU 9882-83). *Tarrant Co.*, 5 miles southwest of Tarrant (UIMNH 4485-86). *Taylor Co.*, 25 miles southwest of Abilene (CNHM 41858-59, 41876), near Lake Abilene (TAM 1907). *Terrell Co.*, near Sanderson (UMMZ 69788). *Travis Co.*, Onion Creek (BCB 266), 2 miles northwest of Oak Hill (BCB 771-72), Marshall Ranch (BUM 3991), 14 miles northwest of Austin (CM 25832-33), 10 miles south of Austin (CAS 6457), Marshall Ford Reservoir (UIMNH 2638-40). *Val Verde Co.*, mouth of Pecos River (TAM 642), 5 miles east of mouth of Pecos River (EHT A932), Devils River (CAS 11411). *Webb Co.*, near Laredo (EHT A922), 30 miles southeast of Laredo (CAS 5335-36), 54 miles northeast of Laredo (UMMZ 69803). *Wilbarger Co.*, Hilltop Oil Field (BUM 4048-49). *Zapata Co.*, 20 miles north of Zapata (CAS 11410), 4 miles west of San Ignacio (UMMZ 74761-62), Arroyo Villeno (UMMZ 74760).

MEXICO: *Nuevo León*, 14 miles north of Villagran (UIMNH 3985-97), 14 miles east of Cadereyta (UIMNH 3998). *Tamaulipas*, Jaumave (USNM 46725-26), Marmalejo (UMMZ 69216-17).

Holbrookia texana scitula, new subspecies

HOLOTYPE.—UMMZ 100818, male.

TYPE LOCALITY.—On rocks at mouth of small arroyo entering Cañada del Oro, 16 miles north of Tucson, Pima Co., Arizona; collected by Dr. Howard K. Gloyd, August 12, 1930.

DIAGNOSIS.—Ventrals from collar to anus 80 or more (84 per cent); number of scales in head length 39 or less (80 per cent); sum of femoral pores 28 or more (82 per cent); color as described below.

DESCRIPTION OF SUBSPECIES.—Ventrals 74-97, usually more than 79; scales in head length 29-45, usually less than 40; sum of femoral pores 24-40, usually more than 27; upper labials 6-9, usually 7 or more; granular scales of the back separated from the interparietal by at least 1 row of larger scales.

Dorsal color, light gray, with prominent paired black vertebral spots; sides reticulated from axilla to groin, with a black ground color and

numerous orange, red, or yellow spots throughout, except in the region about the ventrolateral black bars, which extend far up the sides above the lateral fold. The colored spots often form regular series which parallel the ventrolateral bars. Ventral color, light cream to white, with a pinkish cast on the chests of males. Chin and sides of neck often reticulated, with throat blackish, or with irregular black bars directed back and in toward center.

HOLOTYPE.—83 ventrals; 36 scales in head length; femoral pores 15–15; upper labials 8–7.

Black vertebral spots present, not prominent. The paired black stripes are bordered both anteriorly and posteriorly by a zone of light yellow as wide as the stripes themselves. Tail with 8 bands below, the first only a spot in the mid-line, the remaining 7 extending the width of the tail; a half spot near the tail tip, on the right side only.

Body length 64.5 mm., tail length 80.5 mm., hind leg length 59 mm., hind foot length 28 mm., longest toe length 18 mm., head length 15 mm., head width, 12.5 mm.

RANGE.—Central and southeastern Arizona east to New Mexico and western Texas, south through Chihuahua and Coahuila to the eastern edge of Durango and western Nuevo León (Map 1).

REMARKS.—Lewis (1950: 7) had this subspecies in hand when he discussed the variance in color pattern from that of published descriptions. His remarks are of particular value as they are concerned with the living coloration of the subspecies. To quote them in part: “. . . the lateral black bars are bordered by brilliant green . . . and [there is an] absence of blue on the belly. Large males . . . show a faint flush of pink on the throat, yellow chest, abdomen, and ventral surfaces of anterior limbs, metallic blue-gray on head and nape, changing over the shoulder to alternating bars of gray and orange, which curve laterally and caudally from the midline. In the field the males appear metallic-iridescent dorsally.”

PARATYPES.—ARIZONA: Pima Co.; UMMZ 69801 (topotype); SU 10061–62, Sabina Canyon; UMMZ 69792–93, 69799–800 (6) Catalina Mountains; UMMZ 64071 (5), 65087 (3), Tucson; AMNH 62697–98, 3½ miles west of Tanque Verde; AMNH 2465–68, Tucson; AMNH 64287–90, base of Agua Caliente Mountains.

The following additional specimens of this subspecies have been examined:

ARIZONA: *Cochise Co.*, 10 miles east of Benson (AMNH 67570), Tombstone (CNHM 908), Charleston (UMMZ 69791), between Hereford and Mule Mountains (UMMZ 69798), 30 miles southwest of Wilcox (UMMZ 71048), 9 miles west of Tombstone

(UMMZ 85625), Fort Lowell (SU 2454). *Gila Co.*, Roosevelt Lake (UMMZ 64911). *Graham Co.*, Solomonville (AMNH 62914), Jacobson Creek, southeast slope of Mount Graham (CAS 10005), 1 to 3 miles northeast of Klondyke (FAS 220, 273, 290, 296-97, 805-7, 819-48). *Maricopa Co.*, Mormon Flat (CAS 9829), 2 miles southwest of Wickenburg (FAS 619-26, 678, 709), Phoenix (UIMNH 2013-14), Wickenburg (UMMZ 90698). *Pima Co.* (AMNH 26202-19, 26198); 9 miles north of Rillitos (UMMZ 68684), Sabina Creek (UMMZ 84971); Sabina Canyon (AMNH 340, SU 10063-64). *Pinal Co.*, Boyce Thompson Southwestern Arboretum, 4 miles west of Superior (AMNH 66307-11, CAS 9530, 9733, 9888, 10213-15, 13527-33), 6 to 8 miles southeast of Superior (CAS 9583-84), Oak Flat, 5 miles northeast of Superior (CAS 9610-14, 9624-30), base of Picket Post Mountain (CAS 9686, 9730, 9745, 9775-79, 9819-20, 9826), base of Superstition Mountain (CAS 9702-3, 9711-15), 2 to 3 miles north of Superior (CAS 9804-16); 5 miles west of Superior (CAS 9906), 1 mile west of Superior (FAS 161, 201, 853), 5 miles southwest of Superior (FAS 214, 229, 849-52), near Oracle (UMMZ 69802), 3 miles southeast of Oracle (UMMZ 72618-19), 5 miles north of Oracle (UMMZ 72620). *Santa Cruz Co.*, Ruby (UMMZ 91588). *Yavapai Co.*, near Kirkland (AMNH 20363-70), Weaver Mountains, near Congress (AMNH 67573-74), 5 miles north of Wickenburg (CAS 2864, 2894, 2898, 2933, 2940, 2956-58, 2977-89, 3071, 3088-89, 3144, 3431), Yarnell (CAS 3155, 3247-48, 3262-67, 3301-2, 3358-60, 3419, 3662), Martinez Creek, 7 miles southwest of Yarnell (CAS 3674, 3695-96), Peeples Valley, 6 miles north of Yarnell (CAS 3711).

NEW MEXICO: *Dona Ana Co.*, 17 miles northwest of Las Cruces (CM 18261), 10 miles north of Radium Springs (CM 18330), Sierra de Cristo Rey (CNHM 47481), eastern slopes of Organ Mountains (THL 287-301), 14 miles east of Las Cruces (UMMZ 60067). *Eddy Co.*, Carlsbad (UIMNH 2015). *Hidalgo Co.*, 28.4 miles southwest of Lordsburg (UIMNH 5894), near Rodeo (UMMZ 69797), west side of Playas Lake (UMMZ 90769). *Luna Co.*, 8.6 miles southwest of Hatch (UIMNH 5895). *Sierra Co.*, Rio Grande River, 8 miles above Garfield (UMMZ 60061-62), 15 miles east of Hermosa (UMMZ 60063), Elephant Butte Dam, near Cuchillo (UMMZ 60064-66, 60068). *Socorro Co.*, San Marcial (CNHM 15956), 4 miles south of Oscura (EHT 925, 928).

TEXAS: *Brewster Co.*, "Big Bend Region" (AMNH 62968-73), Iron Mountain (BUM 5494), Boquillas (CAS 4895, UMMZ 66343), foothills of Chisos Mountains (CAS 4893-94, UMMZ 66331-32), Chisos Mountains (CAS 4891-92, 11412-14, UMMZ 66341, 69789-90), Glenn Spring (UMMZ 66311-27, 66330, 66334-36, 66345, 69796, 72078), 5 miles north of Glenn Spring (UMMZ 66337-40), 4 miles south of Glenn Spring (UMMZ 72079), 3 miles southeast of Glenn Spring (UMMZ 72080), Rice Draw (UMMZ 66328-29), Chilocal Mountains (UMMZ 66333, 66342, 66344, 69795), Hot Springs (UMMZ 69794, TAM 1110), Pinnacle Spring (UMMZ 81991), McKinney Spring (TAM 1114-18), Tornillo Creek (TAM 1119-23), mouth of Santa Elena Canyon (TAM 1124), 1 mile east of Burro Spring (TAM 1125). *Culberson Co.*, 16 miles southeast of Van Horn (TAM 402), 1 mile northwest of Van Horn (UMMZ 91494). *El Paso Co.*, El Paso (CNHM 1680, 2810, UMMZ 71046), Fort Bliss (CNHM 4369, 4782-84). *Presidio Co.*, San Carlos (CNHM 46023), 3 miles northeast of Porvenir (CNHM 46009-21), 8 miles north-northeast of Porvenir (CNHM 46022), 5 miles north of Porvenir (UT T4209, T4229); San Esteban Dam (SU 7389) C. E. Miller Ranch, 11 miles west of Valentine (UT 2780, 2853, 2856-57, 2880, 3064-65, 3069, 3075, 3112-13, 3120-21, 3127, 3338, 3341-43, 3356, 3389, 3463-68, 3530-34, 3641, 3860-61, 3882, 3893, 3898, 3937, 4010-13, 4088, 4090-91, 4114, 4163-64, 4229, 4260-61, 4268, 4279).

MEXICO: *Chihuahua* (USNM 8310, 14238), Chihuahua City (CNHM 992, SU 1971, USNM 46652), Jiménez (CNHM 992a), 18 miles north of Escalon (EHT 15418-19), between Chihuahua and Naica (EHT 15420-22), Lago Santa María (USNM 47415), 6 miles southwest of Rancho Nuevo (USNM 104755-60), Río Santa María near Progreso (USNM 104761), between El Paso and Janos (USNM 4118). *Coahuila*, Las Delicias (AMNH 67397-401, CNHM 46111-12), 20 miles west of Saltillo (AMNH 67366-67), Jaral (CNHM 1550), Hermanas (CNHM 47302-15), between Hermanas and Monclova (CNHM 47316-20) Monclova (CNHM 47326, USNM 46703-4, MCZ 4558, 4562), Cuatro Ciénegas (CNHM 47327-34), Castanuelas (USNM 2663), Alamo des Parnas (USNM 2677), Jimulco (USNM 46646), Saltillo (USNM 46696, 46705-6, 47487-88), 21 miles north of Saltillo (USNM 105991-93), 4 miles north of Saltillo (EHT A1342, A1345, A1348), 1.5 miles west of Saltillo (EHT A1360, A1363, A1366, A1369), San Pedro (EHT A1351, A1354), 23 miles southeast of San Pedro (USNM 105984-85), Hipolito (USNM 105989-90), 30 miles west of La Rosa (EHT A1372). *Durango*, Lerdo (CNHM 1295), 3 to 3½ miles southwest of Lerdo (AMNH 67477-87), 7 kilometers west of Torreón (CNHM 17106-9), between Lerdo and La Goma (USNM 105955-61), Pedricana (USNM 105971-83), 14 miles north of Pedricana (USNM 105962-70).

The following intergrades between *scitula* and *texana* have been examined:

TEXAS: *Culberson Co.*, Guadalupe Canyon, Frijole (UMMZ 70079). *Jeff Davis Co.*, Cherry Canyon (UMMZ 51438-45), Fort Davis, Davis Mountains (UMMZ 52723, 52869-82), 5 miles southeast of Fort Davis (UMMZ 93091), Limpia Canyon, Davis Mountains (UMMZ 69804, 71047). *Loving Co.*, 40 miles south of Carlsbad, New Mexico (UMMZ 86092). *Reeves Co.*, Toyahvale (SU 7390), Weinacht's Draw (UMMZ 51446-92), 15 miles east of Balmorhea (UMMZ 67368).

MEXICO: *Coahuila*, Muquiz (CNHM 28658-62, 47292-93), Juarez (CNHM 47294-301), 4 miles south of Allende (CNHM 47321-25). *Nuevo León*, Sabinas Hidalgo (CM 9786, EHT A1336), Montemorelos (CNHM 1307), Río Pesquería (MCZ 46376-79), Cadereyta (UMMZ 90615, USNM 2861), Monterey (UMMZ 69410, EHT 27056, USNM 2669, 2822), 20 kilometers northwest of Montemorelos (TAM 899, 948), 13 miles southwest of Sabinas Hidalgo (TAM 783-85), 45.2 miles north of Sabinas Hidalgo (UIMNH 6707-20), 13 kilometers south of Sabinas Hidalgo (USNM 113221), Pesquería Grande (USNM 2665), Santa Caterina (USNM 2791, 46695, 105994).

Holbrookia texana reticulata, new subspecies

HOLOTYPE.—UMMZ 100817, male, collected by Berry Campbell, July 14, 1935.

TYPE LOCALITY.—Pilares, Sonora.

DIAGNOSIS.—Ventrals more than 82 (94 per cent); sum of femoral pores less than 31 (100 per cent); scales in head length less than 36 (85 per cent); black lateroventral bars do not extend above the lateral fold; color as below.

DESCRIPTION OF SUBSPECIES.—Ventrals 80-96; scales in head length 30-39; sum of femoral pores 19-30; upper labials 6-9, usually 7.

The ventrolateral black bars are exceedingly faint and do not extend over the lateral fold in males. The head is light brown, distinctly lighter than the back; two pale cream stripes from eye to lip. Chin and throat heavily suffused with dark brown; indistinct light striping directed posteriorly and toward the center. Ventral surfaces cream, somewhat suffused with light brown; the ventral blue patch is very bright, occasionally extending into groin and onto the ventral surface of the femur, and blending with the black bars. The black bars are replaced above the lateral fold by dark brown stripes which are mottled and spotted with orange. The males are heavily spotted dorsally, the females stippled with orange or yellow from cheek to base of tail and from lateral fold to level of vertebral spots. Black vertebral spots present, but often indistinct.

DESCRIPTION OF HOLOTYPE.—96 ventrals; 32 scales in head length; femoral pores 12–13; upper labials 7–7.

Ventral surfaces cream, somewhat suffused with light brown. Tail with 7 black bands, the first beginning only 2 scales behind the post-anal pocket, confined to the mid-line and joining the second band, which is broader than long but does not extend to full width of the tail, the remaining 5 bands entire.

Body length 62 mm.; tail length 72 mm.; hind-leg length 61.5 mm.; hind-foot length 27 mm.; longest hind-toe length 17.5 mm.; head length 14.5 mm.; head width 12 mm.

REMARKS.—The Stanford University specimens collected on the Cerro Santa Teresa were taken by Mr. Jay M. Savage, in 1950, and he has furnished additional information concerning the subspecies in life. He stated: "The *Holbrookia* were found on small rocks along the base of the Cerro. The rock and ground had a definite reddish tinge which was characteristic of the dorsal color of the lizards . . . The gular color is reddish-orange in life." This series, due to differences between it and the topotypical population, is not included among the paratypical specimens listed below. The only specimens included in this subspecies which have less than 83 ventrals or more than 35 scales in head length are those found among the Cerro Santa Teresa specimens, and they are, therefore, considered somewhat atypical. Among other species taken at the same time and place were *Holbrookia maculata approximans* and *Callisaurus draconoides ventralis*.

RANGE.—Northern Sonora (known from 2 localities, Map 1).

PARATOPOTYPES.—MEXICO: Sonora, Pilares (UMMZ 78366–72).

Additional specimens examined:

MEXICO: *Sonora*, north slope of Cerro Santa Teresa, 4.5 to 5 miles south of Tubutama (SU 12758–67).

VARIATION WITHIN THE SPECIES

Variation within the species has been investigated in 3 directions: racial, sexual, and populational. Only the characters which have shown significant variations are discussed here. These are primarily the ventrals, femoral pores, scales in head length, and color. Other characters, such as the postanal pocket, are mentioned when significant.

RACIAL.—A detailed account of the variations expressed by the subspecies of *Holbrookia texana* is given below (Table I). Although as shown later, there are no significant differences between the sexes in the characters listed, the data are itemized by sex to facilitate the work of future investigators. *Holbrookia texana texana* is quite distinct from both *reticulata* and *scitula* in all 3 of the characters used (Table I), whereas the close relationship of the latter 2 subspecies can be easily seen.

Comparison of the subspecies on the basis of ventral count shows that 80 per cent of the individuals of *texana* have 79 or less; 84 per cent of the *scitula* have 80 or more; and 100 per cent of the *reticulata* have 80 or more. Only 2 of the *reticulata* have less than 83 ventral scales. Eighty-three per cent of the individuals of *texana* have 27 or less femoral pores, while 82 per cent of the *scitula* have 28 or more. The subspecies *reticulata* differs from *scitula* in this character, in that 76 per cent have 27 or less, none having more than 30, while *scitula* has approximately 56 per cent of its individuals above that figure. Both *scitula* and *reticulata* have a low number of dorsal scales contained in the head length, with 97 per cent in *reticulata* and 80 per cent in *scitula* having 38 or less, while in *texana* 86 per cent have 39 or more.

The zone of intergradation between the subspecies *texana* and *scitula* parallels the line of demarcation between the Great Plains province² (*texana*) and the Basin and Range province (*scitula*), and continues into Mexico along the eastern escarpment of the plateau, with *texana* occupying the lowlands or piedmont area, and *scitula* the low plateau. Intergrades between the 2 subspecies are known from Jeff Davis, Reeves, and Loving counties in Texas, and from Coahuila and Nuevo León in Mexico.

No intergrades between *reticulata* and *scitula* are known at present, but they may be anticipated in the Arizona-Sonora border region. I have considered *reticulata* a subspecies regardless of the absence of intergrades, because of the close similarity between it and *scitula* and the geographic relationships that exist.

² As shown on the United States Geological Survey map of the physical divisions of the United States, by N. M. Fenneman and D. W. Johnson.

TABLE I
 RACIAL VARIATION IN SUBSPECIES OF *Holbrookia texana*

Character	<i>H. t. texana</i>		<i>H. t. scitula</i>		<i>H. t. reticulata</i>	
	Males	Females	Males	Females	Males	Females
Ventrals						
Mean	76.68 ± .36	75.30 ± .36	84.40 ± .40	82.80 ± .37	90.64 ± .69	85.94 ± .89
Range	67-87	65-86	74-97	71-95	85-96	80-94
Number of specimens	174	123	154	147	20	16
Femoral pores						
Mean	25.70 ± .17	25.37 ± .20	30.97 ± .26	29.52 ± .30	26.65 ± .40	25.43 ± .67
Range	20-32	20-32	25-40	21-40	24-30	19-28
Number of specimens	175	120	146	131	20	14
Scales in head length						
Mean	42.47 ± .29	42.68 ± .36	35.90 ± .25	36.55 ± .28	33.67 ± .44	34.73 ± .76
Range	33-54	36-53	29-45	30-49	30-38	32-39
Number of specimens	170	119	146	134	18	15

SEXUAL.—For comparison of the sexes, populations from restricted areas were chosen in order to exclude differences due to the influence of geographic variation. The areas selected are from those parts of the range of the species from which statistically suitable samples are available. Although they are listed by county, most of the samples come from even more restricted localities. For example, the Pinal County, Arizona, series is almost entirely from an area within 8 miles of Superior, and the Brewster County, Texas, series is practically confined to the Chisos Mountains region. Direct comparison of the figures for each sex in a single population shows that in only 4 times out of 18 (ventrals, Presidio Co.; femoral pores, Brewster and Presidio counties; scales in head length, Brewster Co.) is the difference between the means greater than twice the sum of their standard errors (Table II). The variations between the sexes in ventrals, femoral pores, and scales in head length are negligible, and in no instance are the differences that exist statistically significant.

The sexes are easily recognized throughout this species, however, because the coloration is strongly dimorphic, and the scutellation of the postanal pockets is an infallible guide. The males are much more brightly colored, with the prominent paired black bars on the sides just anterior to the insertion of the hind legs. These bars extend onto the ventral surface, and are surrounded by a blue or green area. These brightly colored areas often come within 5 or 6 scale rows of each other at the mid-ventral line. In females the black bars are quite often reduced to paired spots or slight bars, which seldom extend far onto the ventral surface, and the areas of dark or blue ventral color surrounding them are small or absent. The postanal pockets in the males are large, and each has a very large scale on its posterior wall, against which, apparently, the base of the hemipenis rests during copulation. The females also possess the postanal pockets, but they are lined with small scales no larger than those of the tail proper.

POPULATIONAL.—Since subspecies are usually defined on the basis of lack of homogeneity between populations, it seems advisable to look at comparisons of populations as well as of races and sexes. (Table II can be used to illustrate this comparison, if the figures are read horizontally rather than vertically.) These populations, which can be assumed to represent the closest approach possible to closely knit, completely interbreeding groups of individuals, with unrestricted gene flow throughout, must be the units upon which a subspecific classification is based.

In the 6 populations listed, the first 4 are in the subspecies *scitula*

TABLE II
SEXUAL AND POPULATIONAL VARIATION IN SUBSPECIES OF *Holbrookia texana*

Character	Yavapai Co.	Pinal Co.	Presidio Co.	Brewster Co.	Llano Co.	McLennan Co.
Ventrals						
Males	83.62 ± 1.12	84.74 ± 1.72	86.10 ± 2.18	87.22 ± 1.85	76.51 ± 1.23	77.19 ± 1.04
Females	81.76 ± 1.49	81.87 ± 1.68	82.18 ± 1.44	84.90 ± 2.06	77.17 ± 1.61	76.42 ± 1.22
Femoral pores						
Males	30.96 ± .81	30.37 ± .93	29.72 ± .77	31.15 ± 1.45	25.92 ± .55	24.17 ± .49
Females	29.62 ± 1.12	30.66 ± 1.18	27.83 ± 1.03	28.59 ± .92	26.38 ± .85	25.00 ± 1.05
Scales in head length						
Males	35.23 ± .77	36.53 ± 1.10	35.92 ± .97	36.22 ± 1.01	43.95 ± 1.31	43.06 ± 1.06
Females	36.88 ± 1.02	36.75 ± 1.08	35.51 ± .85	38.43 ± 1.14	43.50 ± 1.64	43.05 ± 1.25

Figures represent the mean ± twice the standard error of the mean.

and the last 2 are included in *texana*. The third subspecies, *reticulata*, has not been included because of the lack of a sufficiently large sample. The Brewster County, Texas, population is geographically near the area of intergradation, and it shows the influence of both subspecies in its characters, although it has been included as a member of the subspecies *scitula*. For example, although the ventral count in the males is the highest of all those in the table, the femoral pore count in the females shows the closest approach of any *scitula* population to those of *texana*, and this is also true in the count of scales in head length for the females. This intermediacy is emphasized more strongly in all intergrading populations, such as those from Reeves County, Texas, and from several localities in Coahuila and Nuevo León, Mexico. On the other hand, in Presidio County, Texas, which is just west of Brewster County, the population is typically *scitula* in all respects except that the femoral pore count in females is rather low.

If the data for 1 population from each subspecies are used, the difference between any 2 of the populations is below the level of statistical significance only once. If data from 2 populations of a single subspecies are used, only 4 times out of 42 does the difference reach the level of significance.

Yavapai County, Arizona, and McLennan County, Texas, are the westernmost and easternmost counties, respectively, in which the species is found. The differences between the populations of the 2 counties are statistically significant on every count shown, but they do not always represent the extremes. Although occupying peripheral positions geographically, these 2 counties do not show any abnormal deviations from the other populations of their respective subspecies, nor from the norm of the subspecies taken as a whole.

A small sample of the population (44 individuals) from Durango, Mexico, is available, and presents several interesting deviations. Although more than 90 per cent of the specimens have more than 27 femoral pores and 75 per cent have more than 80 ventrals, only 66 per cent have less than 40 scales in the head length, which is a much lower percentage than is expected in a population of *scitula*. This tendency toward *texana* in the Durangan population is also seen in the color, in that 16 per cent have the typical dorsal color of *texana*, and lack vertebral spots and yellow dorsolateral reticulations; 52 per cent have more or less distinct paired vertebral spots; 45 per cent have the yellow reticulation; and 27 per cent have both vertebral spots and yellow reticulation. This change of character is probably due to the peripheral nature of the population, and perhaps to the distance geographically

from the center of the distribution of the species. This population is considered part of the subspecies *scitula*, since the majority of the characters considered indicate such an affinity.

EVOLUTION OF SPECIES

The close resemblance of the subspecies of *Holbrookia texana* and those of *Callisaurus draconoides* is well known. They occupy mutually exclusive ranges, with some overlap in Arizona and Sonora. The subspecies *H. t. scitula* resembles *C. d. ventralis* very closely and, through the loss of the ear opening, is possibly derived from it directly. These two forms occupy the area of overlap between the 2 genera in Arizona.

It thus appears that the species has found its origin in Arizona, somewhere within the range of the subspecies *scitula*. This subspecies has given rise directly to the Sonoran subspecies *reticulata*, the Texan subspecies *texana*, and the variant populations contained within its limits in Durango and Coahuila. Each of these has been derived independently, although *texana* and the Mexican populations are the results of the same trend in differentiation. This hypothesis of the origin and center of distribution for the species is in contradistinction to the postulation of Jameson and Flury (1949: 74), who suggested a Mexican center for the species. They do not amplify this statement or give reasons for the assumption.

The formation of the subspecies *reticulata* involved a loss of the black bands above the lateral fold, a reduction of the number of femoral pores, and further emphasis of the reticulate pattern of *scitula*, although the vertebral spots are reduced. The subspecies *texana* resulted from a reduction in number of femoral pores, a decrease in the number of ventrals, an increase in the granulation of the dorsal scales, and a general darkening in color with loss of reticulation. It seems probable that *scitula* spread throughout most of its present range in the Basin and Range area of the United States and Mexico before its invasion of Texas and Tamaulipas. This is indicated by the variable populations of *texana* in southern Texas and Tamaulipas, which seem to be the result of successful invasions by *scitula* on several fronts. The general trend is a reduction in number of femoral pores and a general darkening in coloration toward the east and south, culminating in the very dark individuals from Tamaulipas, which have the lowest femoral pore count known, 9-9, in a specimen (USNM 46726) from Jaumave.

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