American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 1813

DECEMBER 23, 1956

A Survey of the Frogs of the augusti Group, Genus Eleutherodactylus

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As presently understood, the augusti group of the genus Eleuthero-dactylus is comprised of five species with an aggregate range including part of the Central Plateau region of Mexico and adjacent mountain ranges, from the Isthmus of Tehuantepec on the south to southern Arizona, southeastern New Mexico, and the edge of the Edwards Plateau of Texas. Species currently recognized in the group are Eleuthero-dactylus augusti Dugès, E. bolivari Taylor, E. cactorum Taylor, E. latrans Cope, and E. tarahumaraensis Taylor. Formerly, E. laticeps Duméril was placed together with these species, but Firschein (1951) has shown that it is better placed with E. stantoni Schmidt in a separate group.

Two of the species in the augusti group, bolivari and tarahumaraensis, have been known only from the type specimens. In 1953, William J. Riemer and I collected several individuals of tarahumaraensis in Chihuahua and Durango. This new material provided the impetus for a review of the group, as the specific status of tarahumaraensis has been questioned (Bogert and Oliver, 1945, pp. 405–406), and these authors considered that full specific status of latrans and augusti was doubtful. Also, Mocquard (1899) considered latrans and augusti to be conspecific, and Kellogg (1932, pp. 101–102) discussed the close relationship of the two, noting, however, that they were not identical.

In the most recent key to the members of this group (Smith and Taylor, 1948, p. 50), the principal characters used to separate the species involve body proportions. *Eleutherodactylus tarahumaraensis* is differentiated in addition by the absence of an intertympanic fold present in all

others, and color and pattern characters are mentioned in some instances. *Eleutherodactylus tarahumaraensis* appears to be distinct from the other species with which it is associated in the group, and deserves to be ranked as a full species. It is treated in a subsequent section of this paper. There exists, however, some doubt as to the specific distinctness of the other forms. An analysis of variation in size, proportions, and color pattern has been made for populations of the other forms, with a view towards finding similarities and differences that might serve as a basis for inference as to relationships of the several populations.

Material available for this analysis has included specimens from the following states: Texas, 38 males, 14 females, one juvenile; New Mexico, one juvenile; Arizona, one female; Sonora, two males; Sinaloa, two females; Navarit, one female; Jalisco, one female, one juvenile; Guerrero, seven males, 11 females, one juvenile; Oaxaca, two males, three juveniles; Puebla, two males (one a topotype of cactorum); Morelos, one female; México, one male (type of bolivari), one female; Guanajuato, one female; Ouerétaro, one male; San Luis Potosí, one male, one female; Tamaulipas, eight males, three females, two juveniles; Nuevo León, one female; Hidalgo, one male; Coahuila, two males, five females; a total of 117 specimens. All measurements were taken with a vernier caliper and were recorded to the nearest tenth of a millimeter. Head width was measured behind the angle of the jaws at the level of the tympanic membranes. Body length was taken as the distance from the tip of the snout to the tip of the urostyle, with the body forcibly straightened if necessary. Tibia length was measured as the distance from the fold of skin at the knee to the heel. Foot length was from the tip of the longest toe (the fourth) to the proximal side of the inner metatarsal tubercle. The length of the tympanum was measured horizontally and included the tympanic ring.

The relatively few specimens of frogs of the *augusti* group are scattered throughout many collections. Hence I am indebted to many persons for the loan of specimens or for information: Dr. W. Frank Blair, University of Texas; Dr. Doris M. Cochran, United States National Museum; Dr. William B. Davis, Agricultural and Mechanical College of Texas; Miss Alice G. C. Grandison, British Museum (Natural History); Dr. Robert F. Inger, Chicago Natural History Museum; Dr. William J. Koster, University of New Mexico; Mr. John M. Legler, University of Kansas; Dr. Paul S. Martin, Osborn Zoological Laboratory, Yale University; Dr. Loye H. Miller, Museum of Vertebrate Zoology, University of California; Dr. William J. Riemer, Florida State Museum; Dr. Frederick A. Shannon, Wickenburg, Arizona; Mr. Joseph

Slevin, California Academy of Sciences; Dr. Hobart M. Smith, University of Illinois; Dr. Robert C. Stebbins, Museum of Vertebrate Zoology, University of California; Dr. Charles F. Walker, University of Michigan. I am grateful to all these persons, and to Mr. Charles M. Bogert, who read and helpfully criticized the manuscript.

Following is a list of abbreviations used in this paper:

A.M.N.H., the American Museum of Natural History

C.A.S., California Academy of Sciences

C.N.H.M., Chicago Natural History Museum

E.H.T.-H.M.S., Edward H. Taylor, H. M. Smith collection

F.A.S., Frederick A. Shannon collection

M.V.Z., Museum of Vertebrate Zoology, University of California

T.C.W.M., Texas Cooperative Wildlife Museum, Agricultural and Mechanical College of Texas

T.N.H.C., Texas Natural History Collection, University of Texas

U.I.M.N.H., University of Illinois Museum of Natural History

U.K.M.N.H., University of Kansas Museum of Natural History

U.M.M.Z., University of Michigan Museum of Zoology

U.N.M., University of New Mexico

U.S.N.M., United States National Museum

The trip on which Riemer and I collected *Eleutherodactylus tarahu-maraensis* was made possible through funds furnished by the Annie M. Alexander Memorial Fund, kindness of Mrs. Martha Alexander Gerbode, and through the Revolving Research Fund of the American Society of Ichthyologists and Herpetologists.

ANALYSIS OF VARIATION

VARIATION IN MAXIMUM SIZE

The greatest size is attained by frogs of the Texas population. One of 13 females measures 94.0 mm. snout to vent, and six others in the sample are greater than 70 mm. long. The largest of 35 males from Texas measures 77.2 mm.; 16 of these specimens are 70 mm. or more in length. Apparently females attain a greater size than the males.

The largest of 10 adult males from Tamaulipas, San Luis Potosí, and Querétaro measures 67.3 mm.; the largest of three females, 72.5 mm. The Guerrero sample of 11 males and seven females contains as its largest individuals a male 68.4 mm. and a female 62.5 mm.

None of the other scattered Mexican specimens exceeds in size those already mentioned. The single female from Arizona measures 77 mm. The difference seen between frogs from Texas and those of Mexico probably reflects a real difference in maximum size attained by individu-

als of the respective populations inasmuch as the samples consist largely of adult individuals.

VARIATION IN HEAD WIDTH

To judge from the Texas sample, there seems to be little or no sexual dimorphism. The regression of head width on body length has been calculated separately for male (n=35+1) juvenile) and female (n=13+1) juvenile) samples, the formulas being Y = 0.440X + 0.6 and Y = 0.424X + 1.4. When plotted, the lines fall very nearly atop each other. The correlation coefficients are high (r = 0.978, r = 0.996). The samples include very few immature individuals, so that the calculations may be unduly influenced by a preponderance of adults. However, it is probably safe to conclude that head width increases in a rectilinear fashion with respect to body length, at least in adults, and that males and females do not differ in relative head width.

The regression equation for 15 males and females from Tamaulipas, Nuevo León, San Luis Potosí, and Querétaro is Y=0.418X+2.0. The coefficient of correlation is similarly high, r=+0.997. The plotted line nearly coincides with those lines calculated for Texas specimens. Individual specimens from other regions fall sufficiently close to the Texas regression lines that it is assumed that intra-population variation in relative head width is of no significance.

The rectilinear nature of head width increase, at least among adult individuals, allows head width to be used as a base for computing proportions of other body parts. This is desirable where it is convenient to use a smaller base than body length, or where it is felt that the body length measurement is not sufficiently precise.

VARIATION IN TIBIA LENGTH

The length of the tibia (and the length of the foot, to be discussed subsequently) may be used to compare relative leg lengths among several samples, on the assumption that differences in total leg length are reflected in all segments of the limb. As the tibia length and the body size as a whole do not seem to increase at the same relative rate, it has not been practical to compare the various populations by means of ratios. Scatter diagrams serve to illustrate differences and similarities of the populations (figs. 1, 2). The greater absolute size of the specimens from Texas is at once evident (fig. 2). The growth curve of the Guerrero-Puebla males (fig. 1) is similar to the comparable segment of the Texas sample (fig. 2), but the smaller individuals from Tamaulipas and adjoining states are noticeably longer-legged; the curve for this group has

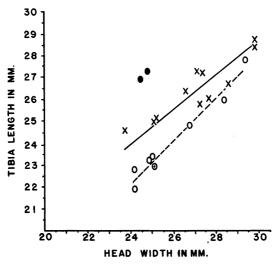


Fig. 1. Regression of tibia length on head width, adult male specimens of *Eleutherodactylus augusti*. \times , *E. a. augusti*, specimens from Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo; O, *E. a. cactorum*, specimens from Guerrero and (\odot) Puebla; \bullet , *E. a. cactorum*, specimens from Oaxaca. Regression lines fitted by least squares method. Regression formulas are: *augusti*, Y = 0.816X + 4.4; *cactorum*, Y = 1.01X - 2.1.

a rather different slope. Specimens from other regions are too few to be more than suggestive. The two males from Oaxaca are much longer-legged than any others of comparable size, while two from Coahuila (not plotted on the diagram) fall with the short-legged Texas and Guerrero specimens. The only Sonoran specimen in the size group studied has rather long legs.

Geographic differences of the sort apparent in the male frogs are not seen in the females or, if truly present, are of too small magnitude to be evident in the face of individual variation. The only individual that falls much out of the general trend is a conspicuously long-legged frog from Nayarit, unfortunately the only specimen from that region available to me.

Females from Texas are relatively longer-legged, on the average, than males, at least among the larger individuals (fig. 2). Such a difference is not apparent in the Guerrero-Puebla sample, and there are too few female specimens from other regions to indicate trends.

VARIATION IN FOOT LENGTH

As seen on a scatter diagram (not reproduced here), the foot lengths of male frogs from Tamaulipas, San Luis Potosí, Hidalgo, and Queré-

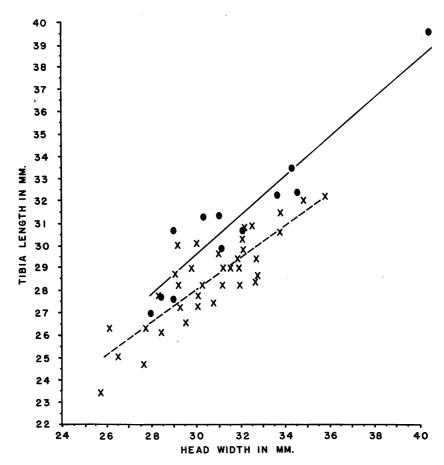


FIG. 2. Regression of tibia length on head width, adult males (\times) and females (\bullet) of *Eleutherodactylus augusti latrans* from Texas. Regression lines fitted by least squares method. Formulas are: males, Y = 0.904X + 2.5; females, Y = 0.740X + 5.9.

taro average greater than those of Texas males. Nine of 10 specimens fall above a regression line calculated for males from Texas. Two males from Oaxaca are well up in the range of the sample from Tamaulipas and adjoining states, and two from Coahuila are below the Texas regression line. The sample of seven males from Guerrero and one from Puebla fits neatly about the Texas regression line. Thus it is seen that variation in foot length among the male specimens parallels that seen in tibia length in the several populations.

Females from the several localities appear to fall within the same range

of variation on a scatter diagram, except those from Coahuila, which consistently have shorter feet.

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Sexual dimorphism in foot length, while not marked, appears to be present. This may be shown by means of a comparison of foot length/body length ratios. Some effect of ontogenetic change may be present, however. For 11 females from Texas, the mean foot length/body length ratio is 0.457 ± 0.008 , range 0.41-0.49. For 32 males the mean is 0.432 ± 0.003 , with a range of 0.39-0.48. All frogs are from 60 to 78 mm. in snout to vent length, except one 94-mm. female. The difference between the means is statistically significant, $d/d\sigma = 3.6$, P = <0.001. Average differences between males and females are slight, but in the same direction as seen in tibia length, namely, relatively longer limb segments in females.

VARIATION IN TYMPANUM SIZE

The relative size of the tympanum has been used as a character differentiating northern (*latrans*) and southern (*augusti*) forms, hence is of some taxonomic importance.

The differences between the populations and between sexes are shown

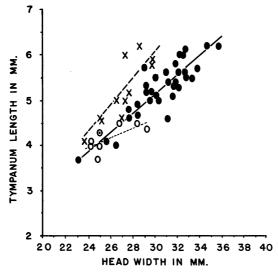


FIG. 3. Regression of tympanum length on head width, adult males of *Eleutherodactylus augusti*. \times , *E. a. augusti*, specimens from Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo; \odot , *E. a. latrans*, specimens from Texas; O, *E. a. cactorum*, specimens from Guerrero and (\odot) Puebla. Regression lines fitted by least squares method. Formulas are: *augusti*, Y = 0.295X - 2.80; *latrans*, Y = 0.214X - 1.29; *cactorum*, Y = 0.105X + 1.45.

TABLE 1

RELATIVE SIZE OF TYMPANUM, EXPRESSED AS RATIO OF TYMPANUM LENGTH TO HEAD WIDTH, IN ADULT SPECIMENS OF THE SUBSPECIES OF Eleutherodactylus augusti

Subspecies		Tympanum Length/Head Width		
	N	$\bar{X} \pm \sigma_{\bar{x}}$	Range	
latrans ^a				
Males	35	0.172 ± 0.001	(0.15-0.20)	
Females	11	0.184 ± 0.006	(0.16-0.21)	
$fuscofemora^b$,	
Males	1	0.19 —		
Females	5	0.174 —	(0.17-0.18)	
$augusti^c$,	
$\overline{\mathrm{Males}}$	10	0.192 ± 0.005	(0.17-0.22)	
Females	4	0.180 —	(0.17-0.19)	
$cactorum^d$,	
Males	8	0.161 ± 0.003	(0.15-0.17)	
Females	15	0.149 ± 0.002	(0.13-0.17)	

[&]quot; Specimens from Texas.

in table 1 and figures 3 and 4. If the frogs are compared on the basis of tympanum length/head width ratios, females from Texas appear to have, on the average, slightly larger ears than males. The difference between the means is statistically significant at the 1 per cent level, $d/d\sigma = 2.79$, P = <0.01. However, there is much overlap in the ratios, and a larger sample of females might invalidate the assumption that females truly have larger ears, on the average. Where sexual dimorphism is present in ear size among anurans, it is usual that the male has larger ears. This appears to be the case among the frogs of the southern part of the range—Guerrero, Morelos, Nayarit, Jalisco, Puebla, and México. In the relatively small sample of 15 females and eight males, the males have larger ears. The difference between the mean tympanum length/head width ratios is statistically significant at the 1 per cent level, t = 2.9, P = 0.01.

While there is some question as to the validity of apparent differences between the sexes, it is quite evident that some populations differ from others in ear size. Thus males from Tamaulipas and adjoining states have

^b Specimens from Coahuila.

^e Specimens from Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo.

^d Specimens from Guerrero, Puebla, Morelos, México, Jalisco, and Nayarit.

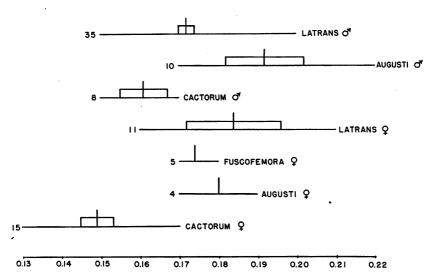


FIG. 4. Ratio of tympanum length to head width in adult individuals of subspecies of *Eleutherodactylus augusti*. Horizontal line indicates range of variation in sample; vertical line, the mean; rectangles indicate two standard errors on either side of the mean. If rectangles of two sets of data do not overlap, a statistically significant difference between the means is suggested. Sizes of individual samples are given to the left of each figure.

relatively large ears, and those from the southern Mexican states have small ears. The tympanum length/head width ratios for the two groups barely overlap (fig. 4). Males from Texas tend to be intermediate but are still significantly different from each of the other two groups. As the sample of frogs from Texas includes individuals of greater size than do the other samples, it might be thought that this difference in size contributes, by way of ontogenetic variation, to the differences seen. However, the 11 Texas specimens in the same size range as the Tamaulipas series (25–30 mm. in head width) have the same range and almost the same mean (0.171) as the entire Texas sample. A single small adult male from Coahuila has large ears, the ratio being 0.19.

The few female specimens from Texas, Coahuila, and Tamaulipas have ears of similar sizes, relatively large. Those from the southern states have much smaller ears. A single large female from Arizona also has relatively small ears; tympanum length/head width ratio is 0.16.

All variation considered in the previous paragraphs has to do with adult frogs. Juveniles probably have relatively smaller ears than adults. For example, two females from Texas with head widths of 21.6 and 17.2 mm. each have tympanum length/head width ratios of 0.15. This is well

below the average figure of 0.184 ± 0.006 seen for adult females from Texas, and below the minimum of 0.16 found among those adults.

VARIATION IN COLOR PATTERN

Adults and young differ widely in pattern. The juvenile pattern, as seen in small individuals from Oaxaca, Guerrero, Jalisco, Tamaulipas, New Mexico, and Texas, consists of dark head and shoulder region, a light band across the middle of the back, and dark posterior third of the body. Darker spots are discernible through the dark anterior and posterior regions and also invade the light area but do not conceal the very evident banded effect. Photographs of such juveniles are presented by Wright and Wright (1949, pl. 80, figs. 2–3, p. 375).

In adults, the banded effect usually disappears, though it is faintly seen in many individuals and is quite distinct in some. The neotype of *Eleutherodactylus augusti* belongs in the latter category (Smith and Necker, 1943, pl. 1, fig. 1). A description of adult color patterns of various populations follows:

Specimens from Texas: The dorsal ground color in preservative is usually light brown. On the back and head there are numerous darker brown, irregular blotches that measure from 3 or 4 mm. to 10 mm. in greatest diameter. In many specimens the blotches are outlined in a lighter shade than the ground color. The hind limbs are barred. Usually there are three primary dark bars on the tibia and two or three on the femur. These bars are, as are the dorsal spots, often outlined with a lighter shade, so that with the ground color, the pattern of the dorsal surfaces of the hind limbs gives the impression of alternating dark and light bars separated by narrow, irregular, lighter lines. The bars on the femur are almost always fainter and less well defined than those on the tibia (fig. 5A).

Color in Life: Stebbins (1954, p. 96) gives the following account: "Ground color above light purplish gray or brown more or less clouded with cream (guanistic pigment?), often most abundantly across head from anterior portion of one eyelid to and centrally on back and on dorsal surfaces of limbs; head, back, and limbs spotted and blotched with dark brown; no greenish pigment; iris dark brown grading to dull gold in upper portion, conspicuous against lighter head color; below unmarked white with pinkish or purplish cast, especially on undersides of limbs and posteriorly on body (animals from Texas)."

A half-grown individual is described by Wright and Wright (1949, p. 370): "General color of snout region, area across shoulders, and rear of back is deep mouse gray heavily spotted with large spots of dark

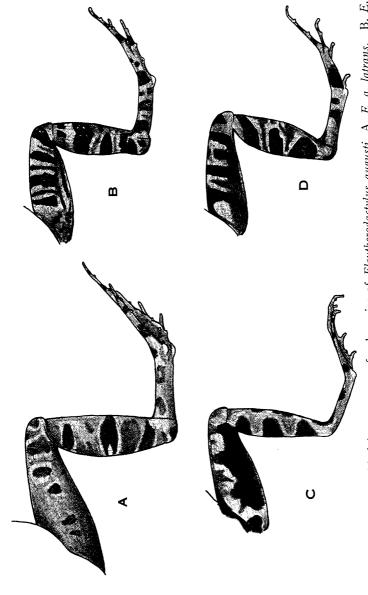


Fig. 5. Typical hind leg patterns of subspecies of Eleutherodactylus augusti. A. E. a. latrans. B. E. a. cactorum. C. E. a. fuscofemora. D. E. a. augusti.

quaker drab. The area between the eyes is vinaceous-fawn with 3 or 4 prominent black spots. Across the middle back is a light area of fawn with no spots."

The young individual from New Mexico is described by Koster (1946) as follows: "... most of dorsum greenish, darkest on head and neck; venter plain white; upper jaw whitish with vertical green bars... body with numerous dark green spots, the more posterior ones faintly outlined with whitish... hind limbs lighter green than the back with darker green bars, these more or less outlined with lighter." These notes were taken shortly after the frog had been preserved in formalin. According to Koster (letter quoted by Wright and Wright, 1949, p. 376), "It was strikingly green and ivory or white when first captured...."

Specimens from Coahuila: In color and pattern, these frogs resemble those from Texas except for the femoral region. In all seven specimens, the posterior half of the dorsal surface of the femur is very dark brown, and the bars are only very faintly indicated on the anterior half. (In specimens from Texas, the rear of the femur is almost as light as the general ground color, lighter than the bars on the legs.) The pattern of the femur alone will serve to distinguish the Coahuila frogs from all others examined (fig. 5C).

Specimens from Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo: In contrast to the frogs from Texas and Coahuila, which in general have a light brown aspect in preservative, the frogs of the present group have a darker, purplish brown appearance. The difference is sufficiently consistent that in a mixed lot of well-preserved specimens, the vast majority could properly be allocated to one of the two geographic groups merely on color alone. The dorsal body pattern is similar in the two groups, except that in the southern frogs there is a tendency for the individual blotches to be larger. However, much variation occurs. The greater intensity of pigmentation in the southern frogs is reflected particularly in the pattern of the hind legs. The femur usually has three, and often four, distinct dark bars. The secondary bars of ground color are sometimes as dark as the primary bars, especially on the tibia (fig. 5D).

Specimens from Guerrero, Oaxaca, México, Morelos, Puebla, Jalisco, Nayarit, and Sinaloa: In so far as can be determined from preserved specimens, the frogs from these regions are closely similar to those from Tamaulipas and associated states. In all Mexican frogs except those from Coahuila, the bars of the hind limbs are more regular and distinct than in the Texas frogs. The light edges separating the primary and secondary bars of the tibia are sometimes very pale and distinct (fig. 5B).

Color in Life: Taylor (1942, p. 393) gives the following account of the color of frogs from Puebla, based on type material of *E. cactorum*: "Ground color gray to brownish-cream with an irregular pattern of large purplish to lavender blotches, less distinct on sides; arms and legs banded with dirty cream and lavender; fingers and palm of hand cream; ventral surfaces cream with slight pigmentation on outer edges of jaws; heel and sole dim lavender; toes generally cream; posterior part of femur lavender with some darker mottling."

Specimens from Sonora and Arizona: The dorsal coloration of the three specimens is more like that of Texas specimens than like that of specimens from southern and eastern Mexico—lighter brown with spots less distinct. However, each has three dark bars on the femur, resembling in number but not intensity those of the other specimens from Mexico (excluding Coahuila).

ACCOUNTS OF SPECIES AND SUBSPECIES

With the foregoing accounts of variation in proportions, color, and pattern as a basis, the taxonomic relationships of the various populations may be inferred. It is necessary first to define the species group. Firschein (1951, pp. 271–272) has given the following definition: "... an intertympanic transverse fold (except in *E. tarahumaraensis*), bufonid habitus, a strongly defined ventral disc, large supernumerary tubercles on soles and palms, tips of fingers and toes bulbous with no transverse grooves present at tips, canthus rostralis rounded, and dorsal color pattern consisting of a series of light-bordered dark blotches." My only modifications of this definition are to note that the distinctness of the ventral disc is subject to individual variation (perhaps an artifact of preservation), and the dorsal blotches are not always light bordered.

Eleutherodactylus augusti

Description: Frogs of this species usually present a toad-like aspect, owing to the broad head, chunky body, and short limbs. The head is broader than long and sometimes in larger individuals tends to flare out along the margins of the upper jaw. The nostrils are much closer to the end of the snout than to the eye. The canthus rostralis is rounded and the loreal region oblique. The snout is longer than the orbit, and the width of the upper eyelid slightly more to slightly less than the interorbital distance. The tympanum is distinct and smooth, with its upper rear quadrant sometimes partly overlapped by the supratympanic fold. This fold, when distinct, terminates above the insertion of the fore limb, behind the ear. A fold along the side of the body is more or less distinct and extends from the supratympanic fold to the groin. Except for an intertympanic

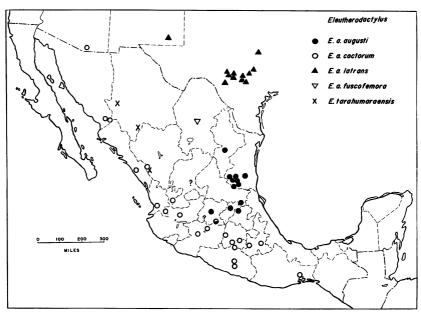


Fig. 6. Geographic distribution of forms of the *Eleutherodactylus augusti* group. Question marks indicate literature records not definitely assignable to subspecies. Half-filled circle indicates locality of intergradation between *E. a. augusti* and *E. a cactorum*.

fold which may be broken medially, the dorsal body surface is otherwise minutely pustulose or almost smooth. The ventral surface of the body is smooth, with an abdominal disc usually distinct.

The fingers and toes are unwebbed, the tips slightly expanded. Prominent subarticular tubercles are present on both front and hind feet, as are thenar and plantar tubercles. The inner metatarsal tubercle is large, the outer no larger than the subarticular tubercles.

The vomerine teeth are in two small patches located between and on a line with, or slightly posterior to, the internal nares.

The male possesses a subgular vocal sac, with a pair of slit-like openings located in the floor of the mouth.

Eleutherodactylus augusti augusti Dugès

Figure 7

Hylodes augusti Dugès, in Brocchi, 1879, p. 21. Smith and Necker, 1943, pp. 201–203, pl. 1, fig. 1.

Eleutherodactylus augusti, Kellogg, 1932, p. 100 (in part).

Eleutherodactylus latrans, TAYLOR AND SMITH, 1945, p. 63 (in part). MARTIN, 1955, p. 173.



Fig. 7. Eleutherodactylus augusti augusti, U.M.M.Z. No. 101184, adult male, 5 miles north of Antigua Morelos, Tampaulipas, \times 1.

Type: According to Smith and Necker (1943, p. 201), "The original description was apparently based upon three cotypes, none of them now extant in Guanajuato [the Alfredo Dugès Museum at the College of the State of Guanajuato]." These authors designate another (unnumbered) specimen in that collection as the neotype. The type locality is Guanajuato, Guanajuato.

The problem of which geographic population to associate with this name is not at present amenable to a clear-cut decision. It will be recalled that the population centering in Tamaulipas is characterized by relatively long legs (in the males) and relatively large ears (in both sexes). The more southern populations have shorter-legged males (Oaxaca an exception), and smaller ears in both sexes. Guanajuato lies between these two regions. I have not seen topotypic specimens of augusti. The individual studied by me from nearest the type locality is one from 4 miles west of Acámbaro, Guanajuato, a locality about 70 miles south-southeast of the city of Guanajuato. The next closest specimen is from Amoles, Querétaro, about 100 miles west of Guanajuato.

Smith and Necker (1943) have provided a description and photograph of the neotype of *augusti*, but there is no assurance that their measurements (however precise) were made in exactly the same manner as I have used, hence direct comparisons may not be valid. The Guanajuato specimen available to me is a female, hence not of much use in a comparison of leg lengths. However, it is worth noting that the foot of this individual is somewhat longer than that of southern females in the same general size range. The tympanum diameter/head width ratio is 0.17, thus at once equaling the lower limit of the range of the northern sample, and the upper limit of the southern, but is nearer the mean for the northern females. The specimen from Querétaro, an adult male, has a tympanum diameter/head width ratio of 0.18, thereby more closely resembling the Tamaulipas population, and also is closer to that group in leg length.

If the specimen from southern Guanajuato is considered an intermediate between northern and southern types, the frogs from the region of the city of Guanajuato to the north are probably also intermediate, possibly closer in characteristics to the northern population. With this possibility in mind, I have decided to apply the subspecific name *augusti* to that northern population, while recognizing that such action is most tentative owing to the paucity of data.

DIAGNOSIS: Distinguished from other subspecies of *augusti* by the following combination of characters: coloration usually dark purplish gray in preservative; femur with three or four dark bars; tympanum large, tympanum diameter/head width averages 0.192 ± 0.005 (0.17–0.22) in 10 adult males, and 0.180 (0.17–0.19) in four females; hind limbs of males relatively long, especially in smaller adults.

Geographic Distribution: Known from south-central Nuevo León through southern Tamaulipas and eastern San Luis Potosí to northern Querétaro and northern Hidalgo. Intergradation with *E. a. cactorum* presumably occurs in Guanajuato, as based on a specimen from 4 miles west of Acámbaro (U.I.M.N.H. No. 15827). Specimens of *E. a. augusti* have been examined from the following localities: *Nuevo León*: Ojo de Agua, near Galeana (C.N.H.M. No. 30647). *Tamaulipas*: Acuña, Sierra de Tamaulipas, 800 meters (U.M.M.Z. No. 95238); La Joya de Salas, 5500 feet (U.M.M.Z. Nos. 101182 [three specimens], 101183, 110690); 5 miles north of Antigua Morelos (U.M.M.Z. Nos. 101184 [two specimens], 102854, 110688); 24 miles north of Tula on the road to Jaumave, 1440 meters (U.M.M.Z. No. 110689); 10 kilometers northeast of Chamal (U.M.M.Z. No. 111256); 4 kilometers west of El Carrizo, slopes of Sierra Gorda, 1700 feet (U.M.M.Z. No. 111257). *San Luis Potosi*: Cave

near road between Pan American Highway and Xilitla (U.M.M.Z. No. 105501); 10 miles west of Naranjos (U.I.M.N.H. No. 15906). *Querétaro*: Amoles, 2000 meters (U.M.M.Z. No. 105427). *Hidalgo*: Puerto de la Zorra, 6 miles northeast of Jacala, 6000 feet (T.C.W.M. No. 10986).

Discussion: The general appearance of the frogs here assigned to the race augusti is closer to that of the frogs to the south, cactorum, than to the northern forms latrans and fuscofemora. The strong barring of the femur will serve to separate most augusti from most latrans (fig. 5) and when taken in conjunction with differences in size (none of 10 male augusti is as much as 70 mm. in body length; 16 of 35 male latrans are longer than 70 mm.) and color (light brown in latrans; darker purplish gray in augusti) nearly all specimens can be correctly assigned. The tympanum of the male augusti averages larger, but there is much overlap with latrans so that the difference, while statistically significant, is of limited use for purposes of practical taxonomy.

The race fuscofemora, known only from one locality in Coahuila, is adequately differentiated from augusti by the pattern of the femur (fig. 5). Too few specimens of fuscofemora are available to allow meaningful comparisons of proportions with augusti.

In pattern and color (of preserved material), augusti and cactorum are indistinguishable. Males of augusti, particularly the smaller adults, have longer legs than males of cactorum (excluding those from Oaxaca). But relative leg length is subject to ontogenetic change, so with the limited material available it has not been practical to express the differences by means of ratios. The differences are apparent in the scatter diagram (fig. 1). The difference in tympanum size seems less affected by ontogenetic change, at least among adults, so a proportional expression can be used to differentiate the subspecies. The minimum tympanum length/head width ratio for augusti (both males and females) is 0.17, while this figure represents the maximum ratio for cactorum of both sexes (fig. 4).

Eleutherodactylus augusti latrans Cope

Figure 8

Lithodytes latrans COPE, 1880, p. 25.

Eleutherodactylus latrans, Stejneger and Barbour, 1917, p. 34.

Type: (Cotypes) U.S.N.M. Nos. 10058, 10529, 10751, type locality Helotes, Bexar County, Texas.

DIAGNOSIS: A subspecies of *Eleutherodactylus augusti* differing from other races in the following combination of characters: coloration in pre-

servative usually light brown; two or three darker bars are present on the dorsal surface of the femur but are relatively weak and ill defined when contrasted to those seen in the races *augusti* and *cactorum*; rear of femur not very dark brown; adults of both sexes commonly attain a body length greater than 70 mm.

GEOGRAPHIC DISTRIBUTION: All localities in Texas from which specimens have been examined are in the region of the escarpment of the Edwards Plateau. A juvenile from southeastern New Mexico is tentatively assigned to this race, awaiting confirmation through the capture of adults. Presumably frogs of this species and possibly the race latrans occur in Trans-Pecos Texas, but the only record so far is that for a call, presumably of a barking frog, heard in Terrell County (Milstead, Mecham, and McClintock, 1950, p. 549). Records of other authors for latrans in Mexico are reassigned to the races augusti and fuscofemora. Specimens have been examined from the following localities: New Mexico: Twelve miles northwest of Carlsbad, Eddy County (U.N.M. No. 17). Texas: Real County, Prade Ranch, Río Frío (C.N.H.M. Nos. 55158-55159); Bexar County, Bulverde (T.N.H.C. No. 9591), Frieschhaun Ranch, 3 miles south of Bulverde (T.N.H.C. Nos. 9592–9595, 14089), Helotes (U.M.M.Z. No. 64047), Madler Ranch, 1 mile south of Helotes (U.I.M.N.H. No. 34327), 2 miles north of Helotes (T.C.W.M. Nos. 9036–9038), 2.5 miles north of Helotes (T.N.H.C. No. 11718); Bandera County, Sutton Ranch, 18 miles northwest of Medina (U.I.M.N.H. No. 28644, T.N.H.C. Nos. 1901, 2045–2056, 2075–2078, 7021–7027, 13406); Uvalde County, Ray Miller Ranch, 5 miles northwest of Montell (T.N.H.C. Nos. 2110-2114); Hays County, 2.7 miles southeast of Wimberly (T.N.H.C. No. 7028); Edwards County, Tanner Ranch near 700 Springs (T.N.H.C. Nos. 7029-7030); Kerr County, Hunt (T.C.W.C. No. 1101); Williamson County, Merrel's Cave, 2 miles west of McNeil (M.V.Z. No. 57727); Kendall County, 11 miles east of Boerne (A.M.N.H. Nos. 54663–54666). Brown (1950, p. 54) records this species from Bosque Hills, McLennan County, a locality about 100 miles north-northeast of the closest place from which I have seen a specimen.

DISCUSSION: This subspecies is compared with the race *augusti* in the account of that form. None of the Texas specimens approaches in color of the femur the specimens from Coahuila (*fuscofemora*). Greater size of *latrans*, different dorsal color, and larger ears all serve to differentiate this form from *cactorum*.

While there is a strong suggestion of integradation between augusti and cactorum, there are as yet no specimens that may be classified as

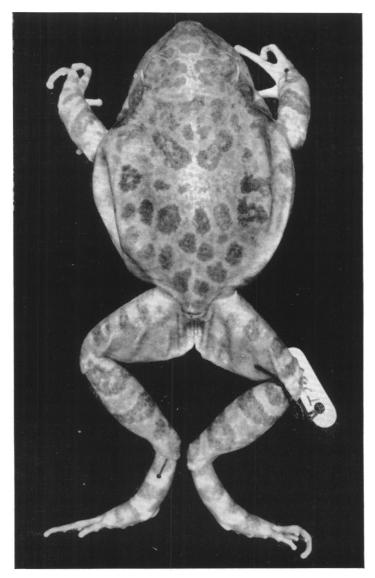


FIG. 8. Eleutherodactylus augusti latrans, T.N.H.C. No. 2055, adult male, 18 miles northwest of Medina, Bandera County, Texas, \times 1.

intergrades between *latrans* and either of the two geographically adjacent forms, *fuscofemora* and *augusti*. Distances of approximately 220 and 330 miles, respectively, separate the closest known stations for these subspecies and *latrans*. Of all four forms here considered as subspecies of

augusti, latrans has perhaps the strongest claim to specific status. Yet, with the possible exception of larger body size, the characters of latrans (but not the combination of characters) are closely approached or duplicated in the Mexican frogs. Thus the dorsal coloration is apparently similar in fuscofemora; average tympanum size of males is intermediate between the means of augusti and of cactorum; relative tibia lengths show considerable overlap; and the usual hind leg pattern of latrans is duplicated in occasional cactorum and augusti. Reference of all these forms to the same species has a practical aspect, too. If augusti and latrans were to be regarded as distinct species, the specific allocation of frogs in western Mexico and Coahuila would raise an additional problem.

It would be of great interest to know the characters of the frogs presumably inhabiting Trans-Pecos Texas and southeastern New Mexico. The only specimen from the region, the one from New Mexico, is a juvenile and of little use in racial allocation. Frogs of the Big Bend region might just as well be close to fuscofemora as to latrans.

Eleutherodactylus augusti cactorum Taylor

Figures 9 and 10

Eleutherodactylus cactorum Taylor, "1938" (1939), p. 391, fig. 2. Hylodes augusti, Mocquard, 1899, pp. 160–161. Eleutherodactylus augusti, Kellogg, 1932, p. 100 (in part). Eleutherodactylus bolivari Taylor, 1942, pp. 298–299, pl. 26, figs. 1–4.

Type: E.H.T.-H.M.S. No. 6383, female, collected 20 miles northwest of Tehuacán, Puebla, Mexico, on August 30, 1936, by E. H. Taylor.

DIAGNOSIS: The race *cactorum* differs from other subspecies in possessing the following combination of characters: tympanum diameter/head width ratio usually less than 0.17 in both males and females; adult males less than 70 mm. in body length; dorsal color (in preservative) dark purplish gray.

Geographic Distribution: Southern Mexico from the Isthmus of Tehuantepec to the southern edge of the plateau region, and north along the foothills of the Pacific coast to extreme southern Arizona. Specimens have been examined from the following localities: Oaxaca: Mixtequilla Mountain, "6 leagues" (approximately 18 miles) north of Tehuantepec (U.M.M.Z. No. 82155), Cerro San Pedro del Istmo, near Tehuantepec (U.I.M.N.H. Nos. 35499, 37274–37275), Quiengola (U.I.M.N.H. No. 15822). Guerrero: Agua del Obispo, 3300 feet (T.C.W.M. Nos. 8377, 8673, 10990, U.S.N.M. Nos. 116420–116421), Chilpancingo (U.I.M.N.H. Nos. 15823–15826), 3 miles west of Chilpancingo, 5000 feet (T.C.W.C. Nos.



FIG. 9. Eleutherodactylus augusti cactorum, T.C.W.M. No. 10074, adult male, 4 miles west of Chilpancingo, Guerrero, × 1.

10068-10069), 4 miles west of Chilpancingo, 5800 feet (T.C.W.C. Nos. 10070-10077), 8 kilometers north of Taxco, 5500 feet (T.C.W.C. No. 8376). Puebla: Two miles east of Raboso (U.I.M.N.H. No. 34879), 20 miles northwest of Tehuacán (U.S.N.M. No. 116489, topotype of cactorum). Morelos: Ten miles northeast of Cuernavaca (U.I.M.N.H. No. 15828). México: Ixtapan de la Sal, 5250 feet (A.M.N.H. No. 55212), Ixtapan del Oro (U.I.M.N.H. No. 15968, type of E. bolivari, formerly E.H.T.-H.M.S. No. 29564). Jalisco: Three miles north of Guadalajara. 5000 feet (U.K.M.N.H. Nos. 28093, 28134-28139), La Laguna (U.S.N.M. No. 46828). Navarit: One mile east of Ixtlán del Río, 3700 feet (U.K.M.N.H. No. 29776). Sinaloa: Thirty-six miles north of Mazatlán (F.A.S. No. 9225, U.I.M.N.H. No. 38992). Sonora: Agua Marin, 8.3 miles west-northwest of Alamos, 1800 feet (M.V.Z. No. 28777), 2 miles east of Guirocoba (M.V.Z. No. 28778). Arizona: Madera Canyon, Santa Rita Mountains, Santa Cruz County (C.A.S. No. 65891).

In addition to the localities in the previous paragraph, there are several records in the literature for specimens that possibly or probably belong to this subspecies. Smith and Taylor (1948, p. 64), in summarizing

records of E. augusti, list the following localities from which I have not seen specimens: Cerro San Juan, Nayarit; Ventanas, Durango; Tupátaro, Guanajuato; Zacatecas, Zacatecas; Lake Pátzcuaro (near Quiroga) and Uruapan, Michoacán. Specimens from Cerro San Juan, Nayarit, are described by Kellogg (1932, p. 101). From his description, it is evident that the species augusti is represented, and assignment of the race cactorum follows from the presence of that race to the southeast in Nayarit. Ventanas, Durango (on more recent maps as Villa Corona), is at an elevation of 620 meters in the barranca of the Río Presidio. Miss Alice Grandison of the British Museum (Natural History) kindly examined the three specimens from this locality for me and determined that they all possess an intertympanic fold. They are therefore properly referred to augusti. Their assignment to the race cactorum is on the basis of the presence of that race immediately to the west. The specimen from Tupátaro, Guanajuato, may be from the region of intergradation between augusti and cactorum. The Zacatecas locality is too isolated to permit a reasonable guess as to the identity of the population in that region. Presumably, frogs from Michoacán represent cactorum, though there is a slight possibility that augusti influence will show up in that region.

DISCUSSION: *Eleutherodactylus augusti cactorum* is compared with the other three forms in the accounts of those races, so the comparisons are not repeated here.

As originally described (Taylor, "1938" [1939], pp. 391-394), cactorum, type locality 20 miles northwest of Tehuacán, Puebla, was considered specifically distinct from augusti to the west and south and latrans to the north. The main distinguishing character of cactorum was considered to be the shortness of the hind limbs. With only a single topotype of cactorum available to me, I have not been able to compare the Puebla population with others on a statistical basis, but comparisons that can be made seem to indicate that differences of the Puebla population are minimal, if present at all. In figure 1, the tibia length of the topotype of *cactorum* is compared with that of other Mexican males. It is seen that this individual fits very neatly into the pattern of variation of frogs from Guerrero. The tympanum diameter presents a similar picture (fig. 3), but, in the size group to which the Puebla specimen belongs, the several races are rather similar in ear size. The difference in eye size suggested by Taylor for the Puebla frogs (eyelid greater than interorbital space in "cactorum," less than interorbital space in "latrans" and "augusti") does not appear to be present. Many if not most augusti (sensu lato) from all parts of the range have the eyelid greater than the interorbital space. There is, then, little to recommend the continued recognition of a form of the augusti group in Puebla distinct from other augusti of southern Mexico.



FIG. 10. Eleutherodactylus augusti cactorum, A.M.N.H. No. 55212, adult female, Ixtapan de la Sal, México, from a Kodachrome by Charles M. Bogert.

Eleutherodactylus bolivari Taylor, 1942, type locality Ixtapan del Oro, México, was distinguished in the original description from other members of the species group in that it lacked a vocal sac. In the key to the species of Eleutherodactylus in the checklist of the Amphibia of Mexico (Smith and Taylor, 1948), the absence of the vocal sac is not mentioned, but the species is separated from augusti and latrans (sensu Smith and Taylor) in being slender and frog-like, rather than heavy and toad-like, and in having the ventral disc not strongly defined as opposed to strongly defined.

The absence of the vocal sac and openings apparently reflects only the age of the specimen. It is small (body length 40 mm.), and the vocal sac openings in *augusti* apparently do not make their appearance until the frog is in the region of 45 to 50 mm. in body length. I have examined several individuals in this general size range in which only one sac opening was present. The body shape and distinctness of the ventral disc depend largely on the state of preservation of the specimen, on whether the animal was gravid, and on the presence or absence of a full stomach. *Eleutherodactylus tarahumaraensis* was similarly considered to be a slender, frog-like form, but all adult specimens taken subsequent to the capture of the type specimen have proved to be considerably more rotund. *Eleutherodactylus bolivari* must be considered a synonym of *E. augusti cactorum*.

As presently defined, *cactorum* very probably contains within its rather wide geographic limits at least two other regional populations probably worthy of nomenclatural recognition. The only two adult specimens from Oaxaca, both males, are very long-legged (fig. 1), in striking contrast to the frogs of Guerrero and Puebla. Far size, too, may be larger, but the difference is not so great as to be convincingly demonstrable with only two specimens.

Probably if more specimens were available from Arizona and Sonora, this region, too, would prove to have its distinct subspecies. In fact, a strong case could be presented for referring the frogs of this region to latrans rather than to cactorum. The color of the preserved specimens is more similar to that of Texas frogs than to that of frogs of southern Mexico. This may indicate direct genetic relationship to latrans, or merely may reflect parallel adaptation to the more arid northern regions. The single female from Arizona is larger (body length 77 mm.) than any of the Mexican specimens, resembling the Texas frogs in this respect, but has a relatively small ear, the tympanum length/head width ratio (0.16) being closer to the mean for southern cactorum (0.149 ± 0.002) than to that computed for female latrans (0.184±0.005). Unfortunately, both Sonoran specimens (males) are small and hence of little use in proportional comparisons. The banding of the femur in all three Arizona and Sonoran frogs appears to me to be more similar to that seen to the south in cactorum rather than to that seen in latrans. Several kinds of animals associated with augusti to the south range northward through Sonora, barely crossing the border into southern Arizona. For the present, I prefer to ally these northwestern *Eleutherodactylus* with the frogs to the south, rather than with *latrans* to the east, but it should be clear that such a decision is highly tentative in view of the shortage of material. Two individuals from southern Sinaloa are more like the frogs to the south than like the Sonoran specimens.

Eleutherodactylus augusti fuscofemora, new subspecies

Figure 11

Eleutherodactylus latrans, Schmidt and Owens, 1944, pp. 99–100.

Type: C.N.H.M. No. 48132, collected on August 21, 1939, at Sacaton, 5 miles south of Cuatro Ciénegas, Coahuila, Mexico, by Edward G. Marsh.

PARATYPES: Six specimens, C.N.H.M. Nos. 48133–48138, collected at the same time and place as the type specimen by Marsh.

DIAGNOSIS: In this subspecies the rear part of the dorsal surface of

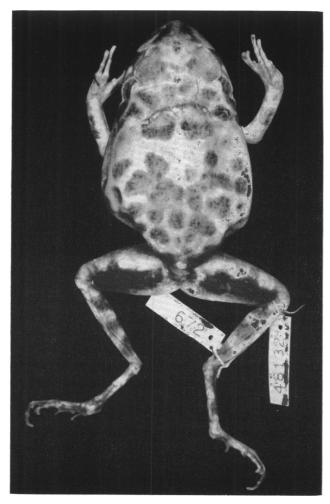


Fig. 11. Eleutherodactylus augusti fuscofemora, C.N.H.M. No. 48132, adult female, type specimen, 5 miles south of Cuatro Ciénegas, Coahuila, × 1.

the femur is dark (brown in preservative) and there is much of the same color in the groin. In the other races of augusti (augusti, latrans, and cactorum), the rear of the femur is never so conspicuously darker than the rest of the leg (fig. 5). Also in fuscofemora, the bars seen on the anterior part of the femur in other races are absent or only very faintly indicated.

Description of Type Specimen: Adult female, body length 67.8 mm., head width 28.9 mm., tibia length 26.9 mm., tympanum length 5.2

mm. Body form typical of the species (see p. 13). Orbit length 8.9 mm., interorbital distance approximately equal to the width of the upper eyelid.

The dorsal body ground color is light brown. On the back there are about 25 rounded darker brown spots ranging from 3 mm. to 10 mm. in diameter. An elongate blotch runs from the rear of the tympanum down towards the insertion of the fore limb, but does not reach that point. Two dark bands, the anterior twice the width of the posterior, run from the orbit to the upper lip. A dark blotch occupies much of the snout. The posterior half of the dorsal surface of the femur is dark brown. The same color is present in the groin. Two bars, only slightly darker than the ground color, are faintly visible on the anterior surface of the femur. Three dark bars are present on the tibia.

Variation: The paratypes agree in essentials with the type. In one individual, the rear of the femur is not so dark as in the others. Smaller specimens show less dorsal spotting and more of a tendency to the cross-banded condition of juveniles.

Discussion: The relatively pale ground color together with the indistinct banding of the anterior part of the femur allies this race with *latrans*, but none of the many *latrans* examined shows the darkening of the posterior part of the femur and groin that characterizes the Coahuila frogs. A specimen from near Galeana, Nuevo León, has the posterior part of the femur relatively dark, but this individual is dark in general and shows distinct bars on the femur. It is considered to be *augusti*.

There are too few specimens of fuscofemora to reveal much of variation in body proportions, but there is a suggestion that females have shorter feet than those of other races (p. 7). The ear size is probably similar to that of the other northern races, relatively large (tympanum length/head width ratio 0.19 in one small adult male), in contrast to the small-eared form, cactorum.

The type locality is the only place where this subspecies has been found.

Notes on the Habitat of Eleutherodactylus augusti

I have not personally observed this species in the field, but assemble here some notes pertaining to the various races as recorded by other persons.

Most authors dealing with E. a. latrans have stressed its restriction to rocky regions. It is usually found in caves, in fissures in canyon walls, or in similar holes and crevices associated with rocky areas. Koster's (1946) account of the capture of a juvenile in New Mexico is of interest in this respect: "The region for several hundred yards about the location

is a grassy plain with a scattering of shrubs." Perhaps juveniles tend to wander more widely than adults and thus disperse to the often discontinuous habitat characteristic of adults.

Schmidt and Owens (1944, p. 100) relate that all frogs in the series of E. a. fuscofemora were caught in mouse traps, apparently getting into the traps just before dawn. No other information is available regarding these frogs.

Dr. Paul Martin has kindly made available to me his manuscript dealing with the herpetology of the Gómez Farías region, Tamaulipas (Martin, MS), from which I quote the following notes on E. a. augusti: "Strictly saxicolous, latrans [= augusti] occupies all available rock habitats in southern Tamaulipas except Cloud Forest and possibly part of the humid Pine-Oak Forest . . . During the dry season a few individuals were found in damp caves (El Pachon, Sierra Gorda) with Syrrhophus latodactylus . . .

"In its local distibution in southwestern Tamaulipas *latrans* is virtually unique, ranging through both the treeless, xeric, *Yucca*-covered hills of the Tula district and into various forest habitats."

Published observations on *E. augusti cactorum* suggest that this form is not so limited to rocky situations as seems to be the case with other subspecies. In the original description of *Eleutherodactylus cactorum*, Taylor ("1938" [1939], p. 393) gives this information: "The three specimens of this species were collected in large mounds formed by a species of cactus. Often the mounds would have a circumference of thirty feet, a height of two or three feet, and would contain many hundreds of the thick plants. Usually the plants or stems grow so closely together that one can scarcely find an opening large enough to insert a pencil. Occasionally rodents burrow under or gnaw a passageway beneath the mound. In this way the amphibians apparently gain entrance." Smith and Van Gelder (1955, p. 147) record another specimen from Puebla as having been found "in cave at a spring 200 ft. from entrance."

Writing of *E. a. cactorum* in Guerrero, Taylor and Smith (1945, p. 574) note that two specimens were found "hopping on the ground in open pine forest at night, September 31, 1939." A large female captured by Archie F. Carr and Charles M. Bogert at Ixtapan de la Sal, México, on July 18, 1951, was found not long after nightfall in a limestone region with numerous small caves, sink holes, and occasional ponds. Its presence was disclosed by its eyeshine at a distance of approximately 70 feet. It did not move, but remained in the beam of light until it was seized (Bogert, personal communication).

The field notes of Léon Diguet, as quoted by Mocquard (1899, p. 160)

and translated by Kellogg (1932, p. 102), provide interesting information on the habits of *cactorum* in Nayarit: "This batrachian is encountered in the territory of Tepic in damp ravines at the commencement of the rainy season; that is, the end of June and July. Its voice is resounding and can be heard at a distance after sunset. At this time it is found attached upon certain smooth-barked trees, such as Burseras, the color of which is the same as that of the animal." This record of arboreal habits marks the greatest divergence from the recorded habits of the subspecies *latrans* and *augusti*. Mocquard suggests that the ventral disc of this species is an adhesive organ, an adaptation to maintaining the animal's position on trees or rocks. Specimens from Durango were reported "from a mine 1000 feet deep" (Günther, 1885–1902, p. 235), but the position of the frogs in the mine with respect to depth was not recorded.

The only published information on the habitat of E. augusti in Arizona is furnished by Stebbins (1951, p. 221). He notes that one individual found in Madera Canyon, Santa Rita Mountains, Arizona, by Charles Vorhies and John Hendrickson, was discovered under a large boulder where there was much rock and little soil (this is not the individual from Madera Canyon that I examined, which so far as I know is the only one from Arizona to reach a scientific collection). Dr. Loye Holmes Miller has kindly furnished me with this account (in litt.) of his encounter with what probably was E. augusti in the Santa Rita Mountains: "Yes, I found what must have been the Barking Frog in Santa Rita Mts. though no specimen was collected. Date was April 25, 1931 and locality Florida Canyon (just north of Madera Canyon). There had been rain and snow the night before—snow but slightly higher elevation. The site was about 1/4 mile up canyon from the present Ranger Station in the canyon. Weather had been fairly dry before this storm. Numbers of the frogs were seen and the peculiar appearance and voice attracted my attention (early morning before sun in canyon bottom) . . .

"I've never seen anything like it before or since though I've repeatedly been at the exact site in Florida Canyon. The season and atmospheric conditions have not coincided to favor *Eleutherodactylus* and me (it was cold down in that canyon)."

The Sonoran specimens were found one in a well 12 feet deep (Stebbins, 1951, p. 221), and the other caught in a mouse trap under a rock near water (Stebbins, *loc. cit.*; Bogert and Oliver, 1945, p. 405).

Eleutherodactylus tarahumaraensis Taylor

Figures 12 and 14

Eleutherodactylus tarahumaraensis Taylor, 1940, pp. 250–253, fig. 1. Eleutherodactylus augusti, Bogert and Oliver, 1945, pp. 405–406.

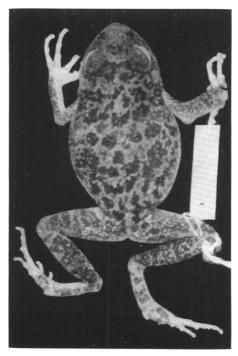


Fig. 12. Eleutherodactylus tarahumaraensis, M.V.Z. No. 58797, adult female, 7 miles southwest of El Vergel (Lagunita), Chihuahua, \times 1.

Type: U.I.M.N.H. No. 15955 (formerly E.H.T.-H.M.S. No. 23008), female, collected at Mojaráchi[c], Chihuahua, Mexico, 6900 feet, by Irving Knobloch.

DIAGNOSIS: A species of the *augusti* group differing from the other species of that group, *augusti*, in lacking an intertympanic fold and in being of smaller adult size; the largest specimen, a gravid female, is 52.7 mm. in body length.

GEOGRAPHIC DISTRIBUTION: Known only from high elevations in the Sierra Madre Occidental of Chihuahua and Durango, Mexico (fig. 6). Specimens have been examined from the following localities: *Chihuahua*: Mojaráchi[c], 6900 feet (U.I.M.N.H. No. 15955, type specimen), 7 miles southwest of El Vergel (Lagunita), 7800 feet (M.V.Z. Nos. 58795–58800). *Durango*: Ten miles northwest of Las Adjuntas (M.V.Z. No. 58364), 6 miles west-southwest of Las Adjuntas, 8500 feet (M.V.Z. No. 58801).

The specimens from Durango extend the known range of this species slightly more than 300 miles to the south-southeast of the only previously known station, the type locality, and the specimens from El Vergel in

extreme southern Chihuahua provide an intermediate locality. Smith and Taylor (1948, p. 64) suggests that sight records for Magdalena, Jalisco, and Ixtlán, Nayarit, may pertain to this species. All Jalisco and Nayarit specimens seen to date are *augusti*, but *tarahumaraensis* may very well range south into the high mountain regions of Nayarit and Jalisco, as well as north into Sonora. Its occurrence along the eastern border of Sinaloa is likewise to be expected.

Description: The habitus is like that of *augusti*—toad-like, with a relatively chunky body and short limbs. A ventral dermal disc is present but is not at all distinct. The male possesses a subgular vocal pouch and paired, slit-like openings in the floor of the mouth. The dorsal body surface is minutely pustulose, the venter more nearly smooth. The intertympanic fold seen in *augusti* is consistently absent. A diagonally placed fold of skin passes over and behind the tympanum. Tympanum diameter is variable; the tympanum length/head width ratio ranges from 0.14 to 0.19, mean 0.163 in six adult males, and is 0.16 and 0.20 in two females. Inner and outer metatarsal tubercles, plantar and palmar, and all subarticular tubercles are well developed.

The body pattern consists of numerous closely spaced spots that sometimes fuse together to give a mottled appearance. These spots may be indistinctly outlined in a shade lighter than the ground color. The tibia is barred, but the pattern of the femur tends more towards a mottled condition rather than bars. The single young specimen shows the cross-banded juvenile pattern seen also in *augusti*.

The dorsal ground color in life is green, often quite bright; the darker spots are gray. The iris is green.

Discussion: Using Taylor's original description (1940) as a basis, Bogert and Oliver (1945, pp. 405-406) suggested that tarahumaraensis should be regarded as a synonym of augusti. Smith and Taylor (1948, p. 64) countered this suggestion with the statement that "These two species are the most widely different of the entire group of Eleutherodactylus to which they belong." According to the view adopted in this paper, they are the only two species in the group. The action of Bogert and Oliver was reasonable, as the truly diagnostic characters of tarahumaraensis, small size and absence of the intertympanic fold, were not given emphasis by Taylor. Instead, the species was differentiated from other members of the augusti group on the basis of having "longer, slenderer legs, and a slender, rather than a toad-like body" (Taylor, 1940, p. 253). Leg length proves to be highly variable, both ontogenetically and geographically, in the populations of augusti, and the range of variation within tarahumaraensis is included within that of augusti. The shape of the body depends on a number of factors: young individuals tend to be slimmer, and males

tend to be slimmer than females. State of preservation also affects this character. All specimens of *tarahumaraensis* taken subsequent to the type specimen, with the exception of one small juvenile, have been considerably more "toad-like" in shape than the type.

However, the specific distinctness of *E. tarahumaraensis* has been verified by the constancy of the diagnostic characters in the additional specimens captured since 1940. None shows an intertympanic fold, while this structure is constantly present in *augusti*, though sometimes incomplete medially. The largest of the two female specimens is gravid, and measures 52.7 mm. in body length. Six adult males (all attracted attention by calling) measure from 37.3 to 43.6 mm., while *augusti* males apparently do not approach maturity until about 45 or 50 mm. in length, and attain a length of well over 60 mm. The two species *augusti* and *tarahumaraensis* have not been captured at the same locality, but have been taken within a few miles of each other. *Eleutherodactylus augusti cactorum* occurs at Ventanas (= Villa Corona) in the barranca of the Río Presidio on the western edge of Durango at an elevation of about 1900 feet, while *tarahumaraensis* has been taken an air-line distance of 17 miles away near Las Adjuntas at an elevation of 8500 feet.

ECOLOGICAL NOTES: Our campsite at 7 miles southwest of El Vergel,



Fig. 13. Rock-littered and partly logged hillside, habitat of *Eleutherodactylus tarahumaraensis*, 6 miles west-southwest of Las Adjuntas, 8500 feet, Durango, July 9, 1953.

7800 feet, Chihuahua, was in a rather open pine forest from which many of the larger trees had been removed by loggers. We arrived at the end of the dry season (June 28, 1953) when there was little undergrowth, the area having a rather arid aspect. A little rain evidently had fallen shortly before our arrival, and while it seemed to have done little more to the landscape than stir up the dust, it evidently stimulated a single Eleutherodactylus, which on the evening of June 29 gave a few desultory calls from a rock outcrop near camp. (The frog may have called on the evening of our arrival, the 28th, but if so its voice was drowned out by the voices of a group of Mexican and Tarahumara loggers who entertained us musically that evening.) The following afternoon was marked by a fairly heavy shower, and in the evening the frog (presumably the same individual) called regularly and was captured. The call is a monosyllabic "quack," very reminiscent of the call of Hyla "arenicolor" in California (not to be confused with Hyla arenicolor in Arizona, which trills), and carries for several hundred yards. I have not heard augusti call in the field, but through the courtesy of Mr. David Pettus I have heard a tape recording of E. a. latrans. As well as memory can compare the two, the calls are qualitatively similar, but that of the smaller species lacks the loudness and explosive quality of the barking frog.



FIG. 14. Eleutherodactylus tarahumaraensis, showing similarity of color pattern to appearance of lichen-encrusted rock on which the frog lives.

What was probably the first heavy rain of the season fell on the afternoon of July 2 and apparently provided the stimulus for calling, for after sundown at least 10 individuals that had not previously been heard began calling from along several hundred yards of rocky outcrops. Three individuals were collected, one a gravid female found hopping towards a male a few feet away. Collecting these frogs was possible only after much tedious and time-consuming stalking and listening. These and other individuals collected subsequently were found either in crevices in rocky outcrops or exposed on boulders, all after dark. The green color of the frogs matches the lichen-encrusted rocks closely (fig. 14). The only other species of frog found in the same habitat at El Vergel was Hyla eximia, a single individual of which was taken in a rock crevice. This Hyla is found in a variety of habitat situations. A juvenile tarahumaraensis found 10 miles northwest of Las Adjuntas, Durango, by Mr. S. Weitzman on July 4, 1952, was collected on an outcrop with an adult Hyla arenicolor. These two species bear a considerable resemblance to each other.

When Riemer and I arrived at 6 miles west-southwest of Las Adjuntas, 8500 feet, on July 7, 1953, the rainy season had evidently been in progress for some time at this high altitude. The logged clearings and the understory of the pine-oak-madrone forest were very lush and green, and rain fell on each of the three and one-half days of our stay. Calling of *Eleutherodactylus* here was weak and sporadic, suggesting that the main period of breeding possibly had passed. Only a single individual was captured, at night on a rock on a rock-strewn hillside that had been partly cleared by logging (fig. 13).

SUMMARY

The augusti species group of the genus Eleutherodactylus is composed of two species, E. tarahumaraensis and E. augusti. Eleutherodactylus tarahumaraensis inhabits high regions of the Sierra Madre Occidental in Chihuahua and Durango, Mexico. Eleutherodactylus augusti is a polytypic species ranging from Arizona, New Mexico, and Texas to the Isthmus of Tehuantepec. Four races of augusti are recognized: augusti, latrans, cactorum, and fuscofemora, the last-named described as new in this paper. The races differ from one another in maximum size attained, color and pattern, tympanum size, and leg length. Eleutherodactylus augusti, latrans, and cactorum were formerly considered to be distinct species, along with E. bolivari Taylor which is treated as a synonym of E. a. cactorum.

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