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Geographic Variation in Toads of the debilis Group of Bufo

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In 1938, Taylor (1938,513) for the first time pointed out the existence of two distinct forms of toads in the assemblage previously referred to *Bufo debilis*. These he designated as the species *Bufo insidior* Girard and *Bufo debilis* Girard. Since then much confusion has reigned, especially with respect to the range and status of the southeasterly form regarded as *B. debilis*. Bogert & Oliver (1945,410) suggested the probability of subspecific relationship of the two, and probable inclusion of Oklahoma and Kansas within the range of the form then regarded as *B. debilis*. Brown (1950,46-7) reiterated the probability of subspecific relationship, and restricted the range of the western species, *B. insidior*, to Trans-Pecos Texas. Wright & Wright (1949,172-84) retained the specific status of these toads, as have Bragg & Smith (1943,296) and Bragg (*e.g.* 1950a,21), who recognize only *B. insidior* in Oklahoma. Still other authors have treated one or both forms, but none has altered their taxonomic status, except Smith (1950,75) who lists them as subspecies but without evidence. The problem of relationship has not up to the present time been critically studied by any author.

A good series of specimens from Mexico, Texas, Arizona, New Mexico, Oklahoma and Kansas has enabled us to contribute to the solution of this problem. We find evidence of intergradation between *debilis* and *insidior*, and a new character by which the two subspecies may be separated. We find a correlation between elevation and the ranges of the two forms and thus a possible explanation of their heretofore puzzling distribution. In addition, we here describe a new subspecies of the group and reconsider the status of *Bufo kelloggi* Taylor.

[1]Contribution from the Southwestern Biological Supply Co., Dallas, Texas; and Department of Zoology and Museum of Natural History, University of Illinois, Urbana, Illinois.

A total of 150 specimens has been examined. We express our appreciation for their loan from the University of Illinois Museum of Natural History through Dr. D. F. Hoffmeister; the University of Kansas Museum of Natural History through Dr. E. H. Taylor; the University of Oklahoma Museum of Zoology through Dr. A. N. Bragg; and Texas Christian University Zoological Collection through Dr. John Forsyth. The specimens in these collections are listed herein with the following abbreviations, respectively: UI, UK, UO, TCU. The collection of the senior author is indicated by the letter S.

Bufo debilis Girard

Diagnosis. — A small species, maximum snout-vent length 54 mm. (39 mm. in the United States); head and body flattened; supraorbital crest merely a rim about orbit, or absent; other cranial crests variable; a very large parotoid gland, as large as or larger than side of head, not in contact with eyelid, colored like body; head and body tubercular, without enlarged glands other than the parotoid.

Range. — Southwestern Kansas and southeastern Colorado to central Texas and northern Tamaulipas westward through Sonora and southern Arizona, southward to central Zacatecas.

Bufo debilis debilis Girard

Plate I

Bufo debilis Girard, Proc. Acad. Nat. Sci. Philadelphia, 1854, p. 87 (type locality in "lower part" of the Rio Grande and in Tamaulipas, Mexico).
Bufo debilis debilis Smith, Misc. Publ. Univ. Kans. Mus. Nat. Hist., no. 1, 1950, p. 75.

Diagnosis. — A subloreal crest present and other cranial crests relatively well-developed; thenar tubercle absent or weakly developed; pattern of disconnected round dots.

Range. — Southwestern Kansas between 101° and 98° W., southward through western Oklahoma (excluding the western Panhandle), Texas east to a line from Dallas to Atascosa Co., and westward to about 101° 30′ W. longitude, southeastward through eastern Tamaulipas, Mexico.

Specimens Examined. — Sixty-six, as follows. *Oklahoma*: 3 mi. W Emerson, 980 ft. elevation, Cotton Co. (UO 21494); N. Mangum, 1580 ft., Greer Co. (UO 21852-3); Elm Fork, Red River, 1500 ft., Harmon Co. (UO 25831-2); Duke, 1600 ft., Jackson Co. (UO 21496-7). *Texas:* Benton, 745 ft., Atascosa Co. (UI 1268, UK 11524-7); 7 mi. NW Westover, 1291

ft., Baylor Co. (S 1508-11); Brownsville, 57 ft., Cameron Co. (UI 3 spec.); Comanche, 1358 ft., Comanche Co. (TCU 1028-9); 5 mi. NW Carrollton, 600 ft., Denton Co. (S 1303-7); Chalk Mountain, 1200 ft., Erath Co. (S 1067); 6 mi. SW Junction, 2180 ft., Kimble Co. (S 1426); Brady, 1670 ft., McCulloch Co. (S 1411-4); Waco, 427 ft., McLennan Co. (UI 1436); 11 mi. NW Mason, 1834 ft., Mason Co. (S 1422-4); 2 mi. S Goldthwaite, 1580 ft., Mills Co. (TCU 789-90); 8 mi. E Aspermont, 1773 ft., Stonewall Co. (S 1540); Ft. Worth (and 5 mi. S of), 670 ft., Tarrant Co. (UK 2774-6, TCU 727, 972-3); Decatur, 1097 ft., Wise Co. (S 1068-78). *Nuevo León:* Sabinas Hidalgo (UI 21722-5). *Tamaulipas:* 6 mi. SW Jiménez (UI 3305-10). Intergrades, *B. d. debilis* and *B. d. insidior,* 7 mi. E Post, Garza Co., Texas, 2590 ft. (S 1512-5).

Additional Records.—Bogert & Oliver (1945, 410) record *B. debilis* (=*B. d. debilis*) from Archer Co., Texas; Brown (1950, 46) confirms this identification. Presumably referable to this race are Bragg's (1950a, 21) records for Beckham and Garvin cos., and the Murray-Carter Co. line, Oklahoma; Brown's (1950, 46) for Archer, Bexar, Bosque, Brown, Burnet, Cooke, Dallas, Duval, Gillespie, Hays, Hidalgo, Jim Wells, La Salle, Palo Pinto, Parker, Scurry, Tom Green, Webb, Wilbarger and Young cos., Texas; Strecker's (1908, 51; 1930, 6) for Refugio and Travis cos., Texas; Cope's (1880, 29) for Tom Green Co. (Ft. Concho), Texas; Bragg & Smith's (1943, 296) for Kiowa and Tillman cos., Oklahoma; Kellogg's (1932, 52) for Matamoros, Tamaulipas; and Bragg's (1941, 51-52) for Comanche Co., Oklahoma. Cragin (1894, 39) records the species for "the western part of Barber County, Kansas." This area has an elevation of less than 2000 feet. On the basis of elevation (a reliable indicator, as discussed in the following), we are confident that if the species occurs in Barber County, it is there represented by *B. d. debilis.* Occurrence of this race in Kansas cannot now be confirmed, as no specimens are known at the present time from areas east of the two western tiers of counties. Altitudes exceed 3000 feet in all other counties in Kansas from which specimens are known, as is to be expected for *B. d. insidior.*

The Pecos River of Texas lies in a deeply dissected valley which at least in its lower parts maintains an elevation of less than 2500 feet almost to the New Mexico border. Probably *B.d. debilis* occurs farther west in this valley, and likewise in the valley of the Rio Grande, than elsewhere, perhaps even reaching 103° W.

Bufo debilis insidior Girard

Plate II

Bufo insidior Girard, Proc. Acad. Nat. Sci. Philadelphia, 1854, p. 88 (type locality Chihuahua, Chihuahua).
Bufo debilis insidior Smith, Misc. Publ. Univ. Kans. Mus. Nat. Hist., no. 2, 1950, p. 75.

Diagnosis. — No subloreal crest, and other cranial crests absent or reduced; thenar tubercle relatively well-developed; pattern of short lines (linulate) presumably equivalent to

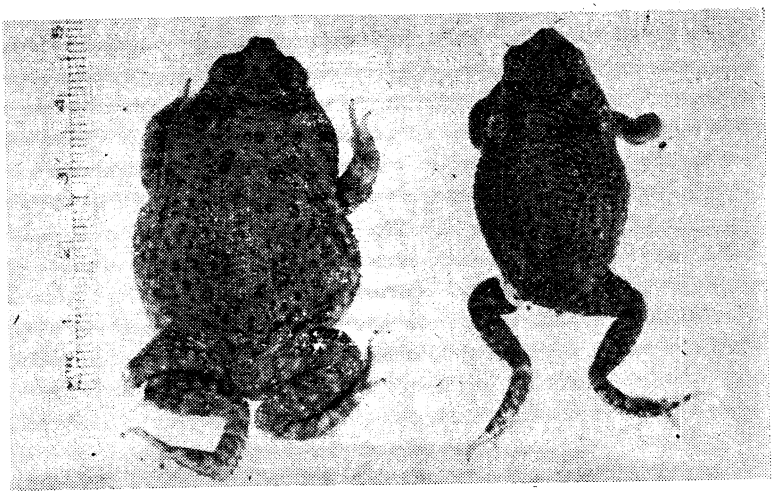

PLATE I. *Bufo d. debilis*. Left, UI 3305, 6 mi. SW Jimenez, Tamaulipas. Right, S 1424, 11 mi. NW Mason, Mason Co., Texas. (Photograph by Ruth M. Sanders)

PLATE II. *Bufo d. insidior*. Left, UI 123, 15 mi. S Zacatecas, Zacatecas. Right, UI 6052, 15 mi. S Ft. Huachuca, Cochise Co., Arizona. (Photograph by Ruth M. Sanders)

interconnected dots.

Range. — Southeastern Colorado and southwestern Kansas southward through northwestern Oklahoma; Texas west of about 101° 30′ W. longitude; eastern and southern New Mexico; southeastern Arizona; extreme western Sonora, central Coahuila and central Zacatecas, Mexico.

Specimens Examined. — Sixty-two, as follows. *Kansas:* 18 mi. N Elkhart, 3000-3500 ft., Morton Co. (UK 5646-9). *Oklahoma:* 3000-3500 ft., Cimarron Co. (UO 24028). *Texas:* Alpine, 4481 ft., Brewster Co. (UK 11549-72); 3 mi. SW Slaton, 3085 ft., Lubbock Co. (S 1507). *New Mexico:* 10 mi. N Florida, 4000-5000 ft., Luna Co. (UK 11541-5); *Arizona:* 15 mi. S Ft. Huachuca, 4000-6000 ft., Cochise Co. (UI 6052-4). *Coahuila:* La Rosa, 3000-4000 ft. (UI, 1 spec.). *Durango:* 5 mi. N Conejos, 3725 ft. (UI, 2 spec.). *Zacatecas:* 2 mi. S Majoma, 6000-7000 ft. (UI, 2 spec.); 10 mi. N Villa de Cos, 6000-7000 ft. (UI, 8 spec.); La Colorada, 6240 ft. (UI, 1 spec.); 15 mi. S Zacatecas, 2200 ft. (UI, 1 spec.). Intergrades, *B. d. debilis* and *B. d. insidior,* 7 mi. E Post, Garza Co., Texas, 2590 ft. (S 1512-5).

Additional Records.—Records from other counties in the United States and other localities in Mexico are: Dona Ana Co. (23 mi. N Las Cruces and Haystack Tanks in Tularosa Basin), New Mexico (Little & Keller, 1937, 219 and Lewis, 1950, 5, respectively); Guadalupe (Cuervo) and ?Grant (Hatchet Ranch) cos., New Mexico (Van Denburgh, 1924, 1920); Las Animas Co. (Trinidad), Colorado (Rodeck, 1943, 5); Pecos and Reeves cos., Texas (Brown, 1950, 47); Grant, Greeley, Hamilton and Logan cos., Kansas (Smith, 1950, 74); Villa Ahumada and Río Santa María near Progreso in Chihuahua and Músquiz, Sierra de Santa Rosa, Hermanas and 20 miles east of Torreón in Coahuila, Mexico (Smith & Taylor, 1948, 42). Unfortunately no definite locality data have been published for the specimens Cope observed (1892, 332) between Clarendon, Donley Co., and Big Spring, Howard Co., Texas; these would have represented intergrades or close approaches thereto. Campbell (1934, 3) has recorded the species from Miller Canyon, Huachuca Mts., and Kauffeld (1943, 343) cites it from a locality 30 miles south of Cochise, Cochise Co., Arizona.

Comparisons. — In four more or less objective characters the two forms, *B. d. debilis* and *B. d. insidior* differ: (a) size of cranial crests (absent or reduced in *insidior,* relatively well-developed in *debilis*); (b) pattern (tendency to be linulate or reticulate in *insidior,* dotted in *debilis*); (c) thenar tubercle (absent or weakly developed in *debilis,* better developed in *insidior*); (d) presence or absence of a subloreal crest (absent in *insidior,* present in *debilis*). The subloreal crest is a ridge extending forward from the subocular crest (present in both forms), parallel with and near the lip, to tip of snout below naris. Heretofore unnoticed, the character

provides, at least for all the material we have examined, infallible and ready means of separation of individuals of the two subspecies. The subloreal ridge together with the subocular ridge forms the dorsal margin of a sunken area which is bounded ventrally by a labial ridge along the upper jaw and which we designate as the *supralabial sulcus*. This sulcus, usually completely outlined in *Bufo d. debilis*, is modified in *B. d. insidior*, due to the absence of the subloreal crest and a reduction of the labial ridge anteriorly below the subloreal position. In no *B. d. insidior* does a detectable subloreal ridge exist; the loreal surface is flat except for isolated tubercles which may or may not be arranged in a linear series at the position that would be occupied by the subloreal ridge were that ridge present. In *B. d. debilis*, similar tubercles may exist, usually confined to the subloreal crest, but the critical feature is the presence of a pronounced ridge, well-elevated above the general level of the loreal surface. Our findings relative to the subloreal crest have been confirmed independently by Dr. John Forsyth and Mr. Louis Ramsey of Texas Christian University.

Other, less objective, differences exist between the two subspecies. Among the more obvious differences is the cranial tuberculation. To standardize comparisons as much as possible, the tip of the snout was selected as an area for examination of development of the granular rugosities or tubercles on the head. Both subspecies have these tubercles, but the larger and more elevated ones are found in *Bufo d. debilis*. The tendency in *B. d. insidior* is for such tubercles as are present to be smaller in size and regressive in character. None of the specimens examined of either subspecies was devoid of rugosities in this area.

B. d. insidior reaches a slightly larger size (males, 45 mm., females, 54 mm.) than *B. d. debilis* (males, 39 mm., females, 50 mm.). A north-south cline probably exists in this character, for Mexican specimens of both subspecies are larger than those from the United States (see discussion of geographic variation).

Intergradation. — The characters of *B. d. debilis* and *B. d. insidior* are intermingled in intergrading specimens from Post (Garza Co.), Texas. All of our specimens from there have the dotted dorsal pattern of *debilis* with only a few spots line-like; but in coloration (in preservative) they vary from

the light color associated with *B. d. insidior* to the darker color of *B. d. debilis*. One specimen which resembles *B. d. debilis* in coloration, pattern, and well-developed smooth cranial ridges, entirely lacks the subloreal ridge. Another light-colored specimen with very vestigial cranial ridges has a faint subloreal ridge. The other two specimens of the series are intermediate in development of cranial ridges between the above two extremes but one has a faint subloreal ridge and the other does not possess one. All of the above have a considerable number of granular rugosities or tubercles in the area occupied by the subloreal. *Bufo d. debilis* to the east (Stonewall County) lacks these rugosities and has smooth ridges and other features associated with *B. d. debilis*. A specimen from Lubbock Co., only 25 miles or so west of Garza Co., completely lacks interorbital, postorbital, and subloreal ridges, and is typical of *B. d. insidior* in these respects as well as in pattern, color, and other features.

Zoogeography. — The zoogeographic significance of the distribution now apparent is of considerable interest. Strangely, the boundary between the two forms does not coincide with the most obvious physiographic barriers, except perhaps in northwestern Texas and northwestern Oklahoma, where the eastern edge of the High Plains and Llano Estacado (Loomis, 1938,215) apparently constitute a barrier. In southern Texas, the barrier appears to be more or less coincident with that between the Llano Estacado (where *Bufo d. insidior* occurs) and the Edwards Plateau (where *Bufo d. debilis* is found).

In searching for dissimilarities in areas occupied by the two subspecies, we have considered soils, rainfall, temperature and other ecological factors. Both subspecies have been taken in a variety of soil conditions and no separation appears indicated on this basis alone. There does appear to be a difference in rainfall in areas occupied by the two subspecies in the United States. *Bufo d. debilis* is found in the rainfall belt where the annual precipitation is 20 to 40 inches; *Bufo d. insidior* is in the 10- to 20-inch belt. There is no significant difference in the mean annual temperatures of the areas in Texas populated by the two, but because of a difference in elevation in the two areas, one of the subspecies *(B. d. insidior)* may experience more drastic temperature changes. Probably no single factor can totally limit the range of a

species but in this study one significant factor stands out as invariably bearing directly or indirectly on the distribution of the two forms. All of our specimens of *Bufo d. insidior* and all records available place it at an elevation at 2500 ft. and higher, while *Bufo d. debilis* is found from sea level to 2500 ft. Where the altitude ranges of the two forms meet, in the single series known to us at present, from Garza County,

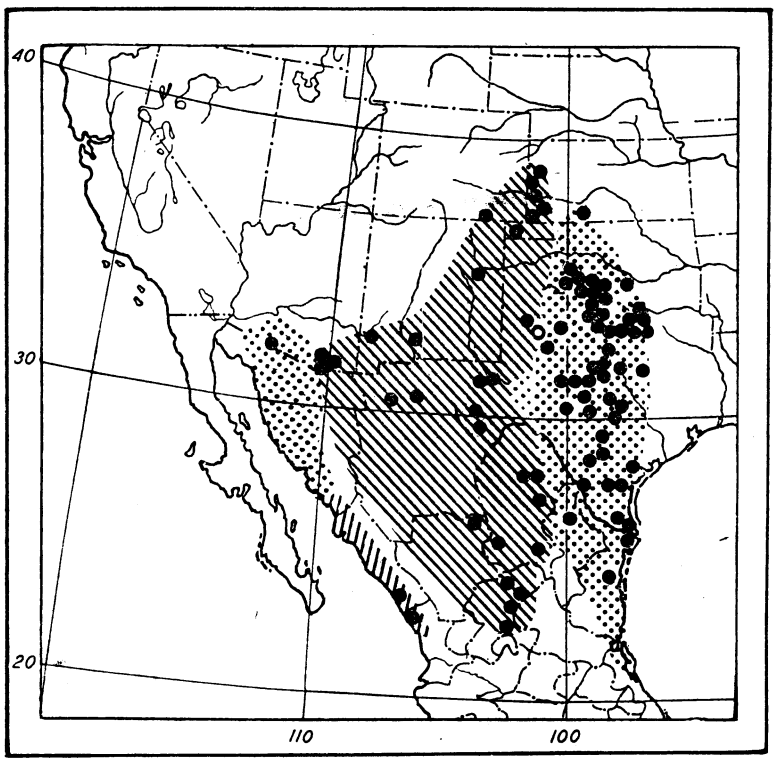

FIG. 1. Approximate ranges of forms of the *debilis* group of *Bufo*. Known locality records, including both literature records and specimens examined, indicated by solid dots; hollow dot, intergrades. Eastern stippled area, *B. d. debilis;* western stippled area, *B. d. retiformis;* diagonal lines, *B.d. insidior;* nearly vertical lines, *B. d. kelloggi.* (Map by Hobart M. Smith)

Texas, we have found the two subspecies intergrading.

We take elevation to be, of course, not a necessarily single factor in itself, but more probably a composite one including numerous ecological conditions which are correlated with vertical (as well as horizontal) factors. We believe the influence of such generally overlooked and obscure correlatives as atmospheric pressure and radiation may be greater than

that of the more conspicuous factors like temperature and rainfall. The relatively broad area over which altitudes appear to limit these forms is admittedly in contrast with the clear-cut situation usually recognized in altitudinal differentiation.

Examined on the basis of elevation, the ranges of the two forms appear more intelligible. *Bufo d. insidior* might be mapped as following the Central Plateau through Mexico at elevations of 2500 feet and higher from central Zacatecas, to southeastern Arizona, southern New Mexico and Trans-Pecos Texas in the United States. Upon entering the Great Plains and particularly the Llano Estacado from southeastern New Mexico, its elevation is maintained up through the High Plains of Texas, northwestern Oklahoma and southwestern Kansas. *Bufo d. debilis* is found in the lower areas to the east at altitudes less than 2500 feet. Whereas elevation would appear to be a factor separating the two subspecies, a different factor would appear to have a bearing on limiting the eastern range at low altitudes of *Bufo d. debilis*. In Texas, its eastern boundary appears to be on a line through Dallas County to Atascosa County and thence to the coastal plain. This north-south line closely approximates the edge of the 20- to 40-inch rain belt and it is significant that *Bufo d. debilis* has not been taken farther east in Texas where the precipitation is heavier.

The failure of *B. d. debilis* and *B. d. insidior* to respect the arbitrary lines of demarcation between the recognized biotic provinces of Texas (Blair, 1950), leads us to add our support to the suggestion (Johnson, Bryant & Miller, 1948, 237) that the concept of "biotic" areas is somewhat misleading unless accepted with ample reservation. It is apparent that each and every species is limited in its distribution by its unique set of toleration limits (both minimal and maximal) to many ecological factors, together and separately. It is not to be expected that any two species can have precisely the same set of toleration limits; in fact this impossibility is a fundamental concept of speciation itself. Therefore any grouping of organisms according to range should be regarded as subject to grave limitations.

An error frequent in discussions of "biotic" provinces is the unrestricted use of the term "biotic." Most schemes are based upon the distribution of restricted groups of animals,

as the mammals (Blair, 1950) or the endotherm vertebrates (Goldman & Moore, 1945) or reptiles and amphibians (Smith, 1949) or salamanders (Stuart, 1943) or even a single genus of lizards (Smith, 1939), but in no such treatment is the term "biotic" justified. To be sure, these authors and others have given as much attention to topography, climate and vegetation as to the distribution of the groups primarily concerned, but the selection of a certain set of boundaries from the truly unlimitable number of possibilities is nevertheless guided by the distribution of limited groups. Boundaries that are respected by one group are not necessarily equally important in the life processes of other groups. The areas mapped should be labelled what they are — mammalian provinces, or herpesian provinces, etc. — not biotic. That any geographic areas can be regarded as truly biotic — implying that all plants and animals are influenced — is questionable. If so, they must be the very largest and most distinct areas.

Any feature such as elevation — and perhaps only elevation — which has correlated with its variation a comparably great variation in a relatively large number of other features such as rainfall, temperature, solar radiation, etc. — is obviously destined to influence the distribution of a greater percentage of organisms in a given area than other, less extensively reflected, features. No distributional province (as most "biotic" provinces more appropriately may be termed) can, of course, be expected to be reflected in the distribution of all species within that province. What percentage must be involved to warrant reference to the province as a "distributional" one is an arbitrary point yet to be determined. The biogeographic regions are justifiably recognized, and perhaps the sub-regions as well. The lesser subdivisions are all highly questionable, however, on a "biotic" basis. It is obvious that only those areas whose limits are clearly definable in terms of elevation (or water or distance barriers) merit any consideration whatsoever as "biotic" areas. Any boundary established on other bases obviously will have many exceptions in the form of species that are not affected at that boundary; such lines scarcely merit thought as "biotic," although they may mark barriers significant in the distribution of limited groups.

We thus conclude that, as sometimes interpreted in recent

years, "biotic" provinces are not actually the blocks of which the commonly-recognized zoogeographic subregions and regions are constructed. No such lesser subdivisions as distinct as the larger divisions can in reality exist. Each successively finer division of the very largest regions recognized is progressively more nebulous, ill-defined and impractical. The finer the division, the more limited its applicability. No barriers not obviously multiple in nature (as elevation, water or distance) should be considered as distributional boundaries of areas regarded as "biotic" in scope.

These limitations should be kept in mind by all proponents of distributional areas. Many of the areas already proposed no doubt merit retention; others definitely do not. At least some limitation, not generally practiced in the past, is imposed by these considerations.

It should be reiterated that the life zone and distributional area concepts are distinct and separately meritorious. Life zones are recognized vertical zones, established on the basis of conspicuous components (chiefly trees, shrubs, or other vegetation in the absence of these). Actually any number of life zones with boundaries at any number of points could be established with reason; the simplest, most widely accepted and most useful boundaries are those associated with conspicuous vegetation types. Essentially the same zones may be recognized the world over, any one zone occurring at scattered spots throughout. Distributional areas, on the other hand, are dependent upon two factors, not one: ecological distinction from adjacent areas (as also for life zones), and geographic isolation over a certain period of time. Any distinct distributional area to be recognized must have been isolated for a sufficient length of time from other areas to have been reflected in the distribution of the species within (and without). Johnson *et al.* (1948,237) suggest that endemism be used as a measure of isolation for such areas.

Decision is difficult as to the validity of recognizing as distributional areas geographic regions that satisfy all the requirements but are small. Correlated is the uncertainty of the degree of endemism required of any area for its recognition as a distributional area. Probably no rule-of-thumb can be adopted at present (Johnson *et al., l.c.*, are equally pessimistic). The limitations previously discussed should influence final decisions.

Geographic Variation. — It is a remarkable fact that specimens from the Edwards Plateau proper, where on zoogeographic grounds one might expect *B. d. insidior,* belong to *B. d. debilis,* the form which farther north is found only east of the Plateau. There are a few subjective and vague differences between specimens from the central Plateau and those from the lower areas to the east (Baylor, Stonewall and Erath counties, eastward) such as a greater development of tubercles on the body and head in the Plateau specimens; but a taxonomic distinction is not warranted at the present time.

Mexican specimens of both *B. d. debilis* and *B. d. insidior* are distinguishable from northern specimens in numerous respects. Especially noteworthy are differences in size, color and pattern.

The size differences are clearly portrayed by the accompanying figures (compare right and left figures of plates I and II). Mexican *B. d. insidior* of both sexes reach a much larger size. The adult males measure 40-45 mm., whereas in the United States they measure 33-38 mm. in snout-vent length; females measure 51-54 mm. in Mexico, 35-37 mm. in the United States. A larger series of both sexes of *B. d. insidior* from the United States is needed in order for us to form accurate conclusions, but we believe the size differences in our series are significant.

The same difference exists in our series of female *Bufo d. debilis* from Mexico and the United States: those from Mexico are much larger, measuring 44-50 mm. as opposed to 34-39 mm. in the United States. The males, however, are of similar size in both regions! Larger series may show that this apparent discrepancy does not exist.

Preserved specimens of *B. d. insidior* from Texas, Arizona, and Oklahoma (Kansas and New Mexico specimens not examined for this feature) appear much lighter in color than specimens of *B. d. debilis* from Texas. Mexican *B. d. insidior,* on the other hand, generally appear darker. When these are separated into color groups, many *B. d. insidior* from Mexico are as dark as the darkest *B. d. debilis* from Texas; and an equal proportion of the Texas *B. d. debilis* are as light-colored as the lightest Mexican *B. d. insidior.* Although the nature of preservative used and differences in handling of materials make such color comparisons sub-

ject to question, present observations indicate that color differences do exist between Mexican and United States specimens of this species.

The spots on the dorsum of *B. d. debilis* are characteristically dotted and those on *B. d. insidior* often linulate (of short isolated lines). No *B. d. debilis* have been found with linulate markings and all but two of our *B. d. insidior* from the United States are linulate. Such, however, is not the case in *B. d. insidior* from Mexico, as 43.4% (almost half) are dotted as in *B. d. debilis.*

In pointing out differences in size and pattern between specimens from Mexico and the United States, we do not feel justified in separating the groups on this basis. Rather we would say that, in spite of these variations which may be of nearly uninterrupted clinal nature and influenced by different habitats, the characters we have given for separation of the two subspecies (especially the subloreal ridge) and the factors for separation of their ranges (especially elevation) are borne out as having major significance.

In contrast, we have in our series of specimens one from Pima County, Arizona, in the Sonoran Desert section of the Basin and Range Province, which is entirely different from others. This toad is smooth-skinned and with a totally different dorsal pattern. It has well-developed interorbital and postorbital crests as in *B. d. debilis,* but is of larger size and lacks the subloreal ridge. It was found at a low elevation (1000-1500 ft.), contrary to examples of *B. d. insidior.* Although we have but a single specimen, the differences are so pronounced that we feel justified in designating it as the type of a new subspecies which we here name.

Bufo debilis retiformis subsp. nov.

Plate III

TYPE. — Univ. Ill. Mus. Nat. Hist. no. 5847, adult female from 14.4 mi. S.Ajo, Pima County, Arizona. Secured alive on a road at night following a heavy rain during the day of July 1, 1948, by Max Hensley and W. Leslie Burger.

Diagnosis. — Subloreal crest absent; interorbital and postorbital crests well-developed; tip of snout smooth; skin relatively smooth; pattern a coarse, continuous, dark network on back and limbs.

Description of type. — Interorbital crests smooth, well-developed as in *Bufo d. debilis* but closer together as in *B.*

kelloggi, semi-circular, closely bordering orbit, continuing anteriorly as prominent preorbital ridges; postorbital crests higher than preorbital, extending to anterior borders of tympana; a gap between postorbital and interorbital and from this point, on either side, a faint ridge running posteromedially; these join along posterior margin of frontals.

Ridges forming supralabial sulcus reduced; subocular and labial ridges much reduced, with faint tubercles occupying their position; no subloreal ridge; snout protruding but more rounded than in *B. d. debilis;* tip of snout smooth, without granular rugosities present in other subspecies of *B. debilis.*

Interorbital surface (5.5 mm. mid-orbitally) flat, smooth,

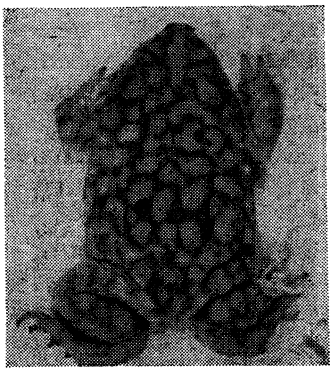

PLATE III. *Bufo d. retiformis,* holotype. [Snout-vent length 45 mm.] UI 5847, 14.4 mi. S Ajo, Pima Co., Arizona. (Photograph by Ruth M. Sanders)

without tubercles, continuing anteriorly to nares, as a broad depression; back of eyes this central area pitted; canthus rostralis faintly swollen, its ridge with a linear series of small rounded tubercles; nostrils large, distance between them 3 mm., slightly closer to orbit than to midpoint of upper jaw.

Parotoid glands large, relatively smooth, somewhat the shape of a truncated pyramid with its apex an obtuse angle extending laterally to level of inferior border of tympanum, closest together near their anterior ends (8.5 mm.), divergent posteriorly (17.5 mm.), not quite twice as long as wide at their greatest extremities (10.2 mm. x 5.7 mm.; 9.3 mm. x 6.5 mm.), separated from post-orbital crest by a series of tubercles.

Tympanum longer than wide (3 mm. x 2.5 mm.), about half diameter of eyelid (5.5 mm.), and placed vertically on

a line with angle of jaws; anterior edge of tympanum elevated over its posterior, which dorsally is in close approximation to parotoid.

Fingers faintly webbed, of approximately same size, except third which is only slightly longer; a large palmar tubercle and a well developed thenar; toes about one-half webbed; two well developed metatarsal tubercles; skin smooth.

Dorsum (of preserved specimen) a light yellowish gray, more yellow toward sides; entire surface of dorsum crossed with a network of broad brownish-black bands joined together as in a net; this pattern continuous over parotoid and dorsal surface of arms and legs; a dark band over each eyelid, running to interorbital space, then backward to join network; the interorbital space unmarked aside from this band, smooth, and bony. Warts of the dorsum of two colors, dark in dark-colored bands and light yellow outside of these bands; warts of medium size, only faintly spiny, scattered over the entire dorsum but nowhere occurring in the profusion seen in other races of *B. debilis*. Skin much smoother to the touch and particularly so on legs, which are almost as smooth as those of a Ranid; a cluster of large light-colored tubercles just back of angle of jaw, and a linear series of large light-colored tubercles, not spiny, running laterally along side of body from posterior end of parotoid down three-fourths of length of body; banded dorsal pattern continues onto legs and noticeable on tibia; between these bands more intense yellowish-brown patches which may, in life, have been brightly colored. Rear of femur light-colored, unmarked posteriorly but mottled near anus with a continuation of dorsal color. If color existed in the groin of the live specimen, it has faded in the preservative, as this area is clear and not mottled.

Venter unspotted; throat tinged with bluish gray; "sitting spot" a discolored bluish tone which extends over most of under-surface of femur; granulations of abdomen extending onto throat as in other races of *B. debilis;* lower jaw rimmed by light color.

Measurements as follows: snout-vent, 45 mm.; tibio-fibular portion of leg (knee to heel), 15.5 mm.; tarsus and foot to tip of 4th toe, 19.5 mm.; tip of 4th toe reaching anterior border of orbit when leg is flexed; head width (at inside angle of jaws) 14 mm.; head length (from tip of snout

between nares to angle of jaw) 11 mm.

Range. — Although now known only from southwestern Arizona, on the basis of known altitude preferences of other forms of this group, and the distributional patterns of other reptiles and amphibians, we believe it probable that this race extends southward through most of western Sonora.

Bufo debilis kelloggi Taylor

Bufo kelloggi Taylor, Univ. Kansas Sci. Bull., vol. 24, 1936 (1938), pp. 510-514 (type locality 2 miles east of Mazatlan, Sinaloa).

Diagnosis. — Like *B. d. debilis* except dark markings more extensive, of broad bands; parotoid gland less prominent, base craniad instead of medial; tubercles more spiny; cranial crests higher, thinner, sharper.

Range. — Northern Nayarit probably to southern Sonora. Recorded only from the type locality and Acaponeta, Nayarit. We conjecture a range to southern Sonora on the basis of distributional patterns of other reptiles and amphibians (Smith, 1949,226).

Specimens Examined. — Thirteen, including 12 alcoholic paratypes and one skeleton (UIMNH).

Remarks. — *Bufo debilis kelloggi* is similar in size (30-42 mm.) to *Bufo d. debilis* from Texas and is also similar in structure. Both forms possess a subloreal ridge, a well outlined supralabial sulcus, well-developed cranial crests (more developed in *B. d. kelloggi*) and a flat-headed skull structure as described below. Both have granular rugosities on the tip of the snout.

In dorsal pattern, they are entirely different. The markings of *B. d. kelloggi* are variable but, in general, have the appearance of broad bands, tending to give the toad a longitudinally striped appearance. These bands frequently join or fuse to make a partial network. There is a lateral dark band along the sides, apparently absent in *B. d. debilis* and, in some specimens, large dark-colored tubercles with several apices are noticeable. This spininess varies, however, in the material examined from one extreme to the other. In *B. d. debilis* from Texas there is a tendency for the tubercles to be rounded, particularly at their bases, giving the dorsum a beaded appearance.

The tympanum is placed similarly in both forms. The parotoid glands in *B. d. kelloggi* are much obscured by skin, usually not as elevated as in *B. d. debilis* and in some cases it is practically impossible to determine their outline. Where

observable, the glands, although triangular in shape, appear to differ from those of usual *B. d. debilis* in having the base of the triangle at the anterior end of the gland rather than dorsally, and very wide. Particularly noticeable are the thin, high, sharp cranial crests, usually tuberculated, of *B. d. kelloggi*. The preorbital ridge in particular is high and sharp.

The relationship between *B. d. debilis* and *B. d. kelloggi* is close in structural features. It is significant also that *B. d. kelloggi* with a well-developed subloreal ridge is found at a low altitude as is the eastern counterpart, *B. d. debilis*. Nevertheless the characters distinguishing the two forms provide complete separation (so far as now known) and we regard them at least of equal if not greater significance than the characters distinguishing the other races of *B. debilis*. A decision regarding the specific status of *kelloggi* involves, however, not only its distinguishing characters but also the lack of geographically intermediate specimens between it and other races of *debilis*. *Bufo d. retiformis* may effect a contact, for its pattern more closely approaches that of *B. d. kelloggi* than of *B. d. insidior*.

Aside from dorsal pattern (a factor involved as well in a separation of *B. d. debilis* and *B. d. insidior*) the structural differences between *B. d. kelloggi* Taylor and *B. d. debilis* Girard appear to be primarily those of degree of development rather than dissimilarity, and on this basis we feel justified in regarding *kelloggi* as a subspecies of *Bufo debilis*.

Group Considerations

Phylogeny of Members. The approximate course of phylogeny of the four forms involved in this group seems apparent. *B. d. insidior* is the most primitive, and all three of the others are probably derived from it. *B. d. retiformis* appears to be a northwestward offshoot of *B. d. insidior*.

Origin of Group. — We cannot at the present time conjecture the origin of the group. Obviously a certain similarity to *B. punctatus* exists, but relationships with other groups are obscure.

Skeletal Characters. — Of some significance in consideration of the origin of the group is the skeleton, which appears to be unusual in a number of respects. We have examined one skeleton each of *Bufo d. debilis* and *Bufo d. kelloggi*, and find them unusual in seven features: (1) flat parasphenoid,

(2) flat prootic, (3) very broad, flat frontals, (4) dentiform serrations on a palatal process of palatine bone, (5) hypertrophy of transverse processes of 4th vertebra, (6) presence of a sternal fontanelle, and (7) absence of neural spines on any vertebrae. The orbits are relatively large, and the pterygoids accordingly are concealed in ventral view, along most of their lateral extent, below the lower jaw; this condition may be expected, however, in any small species.

In contrast to these features, in most *Bufo* the parasphenoid has a strongly convex surface on the midventral part between the orbits; the dorsal surface of the prootic bone is curved, with the anterior edge raised; the frontals are relatively narrow, concave, and with prominent ridges on either side; the palatal process is usually weakly developed and lacks serrations; the transverse processes of the 4th vertebra are little expanded, narrower than those of the 3rd vertebra, which are the largest of any vertebra; a sternal fontanelle immediately posterior to the coracoids is absent; and most if not all vertebrae possess some evidence of a neural spine.

In the skeletons of *B. d. debilis* and *B. d. kelloggi*, the interorbital arm of the parasphenoid is flat, and the dorsal surfaces of the prootic bones are flat and in virtually the same plane as the frontals; both of these features, and especially the latter, are correlated with the flattened skull. The width of the frontals between the orbits is but little less than half the length of the skull, whereas in *B. americanus* and others it is less than one-third the length of skull. The palatal process of the palatine bone is a nearly vertical ridge which is very prominent in these forms, and usually bears from one to three pronounced, tooth-like serrations that are evident on the surface of the palate even of fluid-preserved specimens. The ridges are probably present in most if not all individuals, but the serrations are variable, visible in one-half to nearly all specimens, depending upon locality. The transverse processes of the 4th vertebra are somewhat wider than those of the third vertebra, whereas in other species those of the 3rd are much larger; in some manner this is correlated with development of the scapular muscles, but whether it indicates a caudal shift of the girdle is uncertain. The sternum is broad, although perhaps no broader in proportion than in other *Bufo;* the peculiar fea-

ture is, however, the presence of an uncalcified central area near the proximal end of the sternum. This may be a juvenile feature, although both individuals are adults, and thus may be characteristic of immature specimens of any species, or even adults of smaller species, in which calcification simply is incomplete. Correlated with the flattened head and body are the strongly flattened vertebrae, which are peculiar chiefly in lacking neural spines. The dorsal surfaces are, instead, broadly flattened above, with a slight ridge at the lateral edges of these surfaces where they more or less abruptly drop off to the lower levels of the neural arch.

Our comparative skeletal material unfortunately is limited, including only 12 species: *B. fowleri woodhousei* (2), *B. terrestris americanus* (2), *B. horribilis* (4), *B. compactilis speciosus* (3), *B. simus* (1), *B. alvarius* (1), *B. cognatus* (3), *B. gemmifer* (1), *B. valliceps* (7), *B. marmoreus* (5), and *B. coccifer* (2). None of these possesses notable similarities to the *B. debilis* group. In all, the parasphenoid is convex, except in one *B. valliceps* in which it is nearly flat at the anterior end just posterior to the sphenethmoid; the prootic is concave, although it approaches flatness in one *B. marmoreus*. The frontals vary considerably in interorbital width, but in none are they so broad as to equal one-half the length of the skull. Palatal processes are present in all, are roughened in several individuals, and have 6-8 tooth-like serrations in *B. coccifer*, 2-3 in one *B. t. americanus*. In none is the transverse process of the 4th vertebra as wide as, or wider than, that of the 3rd vertebra. In one individual of *B. valliceps* the neural spines were very low and virtually nonexistent. The sternal fontanelle is absent in all.

Skeletal comparisons confirm the distinctness of the *B. debilis* group, but fail to shed positive light upon relationships.

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