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A taxonomic revision of the *Phrynosoma douglasii* species complex (Squamata: Phrynosomatidae)

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Abstract

Short-horned lizards (*Phrynosoma douglasii* species complex) occur throughout the inter-montane West and Great Plains of western North America. The comparative morphology and color pattern variation of short-horned lizards was studied in 3,174 specimens. Multivariate analyses of 20 morphological and color-pattern characters were applied to 977 specimens, and univariate statistics were summarized for 52 samples totaling 1,134 specimens. The results of the morphological data analyses support the recognition of *P. douglasii* (Bell 1828) as a distinct species, and the resurrection of *P. brevirostris* Girard 1858a and *P. ornatissimum* Girard 1858a as species distinct from *P. hernandesi* Girard 1858a. Two new species allied to *P. brevirostris* are described: *P. bauri* **sp. nov.** from the eastern plains of Colorado and northeastern New Mexico, southeastern Wyoming and southwestern Nebraska south of the North Platte River, and *P. diminutum* **sp. nov.** endemic to the San Luis Valley of southern Colorado and northern New Mexico. The Mexican taxon *brachycercum* Smith 1942 is reassigned as a subspecies of *P. ornatissimum*, based on non-discrete character differences and overall morphometric similarity. The ranges of *P. hernandesi* and *P. ornatissimum* broadly overlap in central New Mexico, the former taxon occupying the coniferous forests of disjunct mountain ranges, the latter occuring in the surrounding desert grasslands. Principal components analysis has revealed morphological evidence of hybridization where the two taxa meet, generally within ecotones between montane forest associations and grasslands. Principal components analysis has also revealed a high level of morphological variability in populations occurring in the Colorado Plateau region of northeastern Arizona, northwestern New Mexico, extreme southwestern Colorado and adjacent Utah. The evidence suggests that these populations arose through past hybridization between the two species. The taxon *ornatum* Girard 1858b, although sharing several traits with *P. brevirostris*, is morphologically close to *P. hernandesi*. It is regarded as a stabilized population of hybrid origin, but treated taxonomically as a subspecies of *P. hernandesi*. The taxonomic arrangement in this study, with the exception of *P. douglasii*, is largely discordant with the proposed taxonomy from a previously published study based on mitochondrial DNA sequence data.

Key words: geographic variation, morphology, *Phrynosoma*, Phrynosomatidae, species delimitation, systematics, taxonomy

Introduction

As presently conceptualized, the *Phrynosoma douglasii* species complex consists of two species, *Phrynosoma douglasii* (Bell) and *Phrynosoma hernandesi* Girard, following Zamudio *et al*. (1997). The former species occurs along the Cascade Range in the Pacific Northwest region and the deserts as far east as southern Idaho (Stebbins, 1985; Nussbaum *et al*. 1983). The latter is widely distributed from the mixed grass prairies of southern Alberta and southwestern Saskatchewan (Powell & Russell, 1998) southward through the woodlands and grasslands of the Great Basin, Rocky Mountains, western Great Plains and eastern slopes of the Sierra Madre Occidental, reaching central Zacatecas, Mexico (Stebbins, 1985; Smith & Flores-Villela, 1994).

Phrynosoma douglasii was originally described as *Agama douglassii* [sic] by Thomas Bell (1828) on the basis of two specimens in the British Museum of Natural History collected by the British botanist and explorer, David Douglas. The species was transferred to the genus *Phrynosoma* by J. Wagler (1830) whose action was followed by J. E. Gray (1831). In 1858, Charles Girard (1858a, b) described several new species of short-horned lizards under the subgenus *Tapaya*: *T. brevirostris*, *T. hernandesi*, and *T. ornatissima*. In addition, the name *Phrynosoma ornatum* appeared as a caption in plate 21 of Girard's (1858b) atlas that accompanied his text (Girard, 1858a); however, in the text it was treated as a synonym of *Tapaya douglassii* [sic]. As explained by Stejneger (1919), Girard was uncertain as to the validity of *Phrynosoma ornatum* and while his text was in press, he decided to place the name in the synonymy of *T. douglasii*. However, Girard's decision came too late to alter the caption for the illustrations in his atlas. Stejneger (1919) regarded the name and associated illustrations as a valid description. In considering the status of *ornatum*, it was Stejneger's opinion that this taxon was not related to *P. hernandesi*, but was sufficiently distinct from *P. douglasii* to be treated as a subspecies. Therefore, he revived the name and applied it to the populations inhabiting the Salt Lake Valley of Utah. Smith (1946) and Reeve (1952) followed Stejneger's suggested treatment. Prior to Reeve's (1952) monograph on the genus, all of Girard's species were relegated to subspecies of *Phrynosoma douglasii* as follows: *P. d. ornatissimum* by H. C. Yarrow (1875); *P. d. hernandesi* by E. D. Cope (1900); *P. d. ornatum* by Stejneger (1919), and *P. d. brevirostre* by H. M. Smith (1946). Reeve (1952) continued with the accepted taxonomy at that time, and did not elevate any of Girard's taxa to full species.

Smith (1946:58) recognized that unresolved questions surrounded the status and validity of Girard's species, and commented (p. 301) …"the *douglassii* [sic] 'complex' of the horned lizards is seriously in need of careful study; probably this is the outstanding problem remaining to be studied in the systematics of the United States lizards."

The taxonomic difficulties presented by this group of lizards have their origin in the species descriptions published by Girard (1858a). Girard did not prepare separate descriptions and diagnoses, although the information in each account under the heading "SPEC. CHAR." could be assumed to constitute a diagnosis. More problematic, Girard did not designate type specimens in his species accounts. Type designations can be found as penciled annotations in the ledger entries at the Smithsonian Institution (USNM), but it is not known when, or by whom, these designations were made. It is suspected that Leonhard Stejneger may have made some of the type designations decades later (S. Gotte, personal communication). In some cases, discrepancies between Girard's original descriptions and the designated type material have been found. Adding to these difficulties, Girard's descriptive accounts are brief, and in most cases, incomplete. Consequently, confusion and disagreement concerning the validity and appropriate rank of the proposed short-horned lizard taxa emerged at the very beginning and have persisted to the present.

A seemingly intractable problem has been the question of the status of *P. d. ornatissimum* as a species distinct from *P. d. hernandesi*. Stejneger (1890) regarded the two taxa as separate species and provided detailed descriptions of their differences. But contrary to Girard's original statement that *P. ornatissimum* inhabits the mountainous region of New Mexico, Stejneger reported that *P. hernandesi* occurs in the forested parts of Arizona, Colorado, Utah, and New Mexico, whereas *P. ornatissimum* occupies the deserts of those regions. Cope (1900) treated the two taxa as subspecies of *P. douglassii* [sic], but he apparently lacked any clear concept of their diagnostic character differences or ecological relationships, in some cases assigning specimens to both taxa from the same localities in Arizona and New Mexico. Van Denburgh (1922) designated specimens from the mountains and plateaus of southeastern and central Arizona, New Mexico, Texas and Sonora as *P. d. hernandesi*, and assigned specimens from Idaho, Nevada, Utah, northeastern Arizona, Colorado, and northern New Mexico to *P. d. ornatissimum.* He considered *ornatissimum* as doubtfully distinguishable from the nominate subspecies but reached no definitive conclusion, citing a lack of sufficient material. Smith (1946) provided a cursory comparison of the two taxa and essentially followed Van Denburgh in delineating their respective distributions.

Reeve (1952) recognized *P. douglasii* as a polytypic species consisting of six subspecies and provided a detailed account for each, including a synonymy, diagnosis, description and summary of distribution. According to Reeve, the range of *P. d. hernandesi* included Arizona (exclusive of the northeastern area), most of Utah (exclusive of the Great Salt Lake Valley), northeastern Sonora and northern Chihuahua. He assigned all of New Mexico (with the exception of extreme southern Hidalgo County), northeastern Arizona, southern Colorado, and west Texas to the range of *P. d. ornatissimum*. Hence it can be inferred, based on these conjectural range limits, that Reeve's concept of the habitat preferences of *ornatissimum* included montane coniferous forests as well as desert grasslands.

In 1965, Gehlbach published a study of the herpetofauna of the Zuni Mountains region of New Mexico. Therein he reported on a series of short-horned lizards (which he regarded as topotypes of *ornatissimum*), and using Reeve's (1952) diagnostic characters, concluded that the series displayed an admixture of traits of the two taxa. He thought that both ontogenetic and environmental factors influenced the character variation and viewed *ornatissimum* and *hernandesi* merely as products of environmental gradients. He therefore relegated *ornatissimum* to the synonymy of *P. d. hernandesi*. Gehlbach (op. cit.) also stated erroneously that Durham (1956:222) described both "subspecies" from the Grand Canyon. In fact, Durham (op. cit.) regarded the Grand Canyon material as *hernandesi*, but mentioned that a single specimen from Flagstaff bore resemblance to *ornatissimum* in several traits. Degenhardt *et al*. (1996) re-emphasized Smith's (1946) opinion that the group was badly in need of revision, and raised the question whether two distinct taxa occurred on the New Mexico landscape.

Zamudio *et al*. (1997) analyzed mitochondrial DNA sequence data to determine species limits in the short-horned lizards. The authors detected high levels of nucleotide variation among population samples and discovered spatial distributions of mtDNA haplotype lineages that coincided with geographic regions. Their phylogenetic analyses revealed three major groups: a Pacific Northwest group to which they applied the name *P. douglasi* [sic]; a Great Basin—Colorado Plateau group, and a group from south and east of the Rocky Mountains. The authors applied the name *P. hernandezi* [sic] to the latter two groups. The earlier taxonomy of Reeve (1952) based on morphology was found to be seriously discordant with the authors' proposed classification based on molecular data from mtDNA sequence analysis.

In 1978 I initiated a preliminary comparative morphological study of material from New Mexico which revealed the possible existence of at least two distinct taxa. My research was eventually extended to all parts of the geographic range of the short-horned lizard species complex in order to undertake a complete taxonomic review. In addition to empirical morphological comparisons, multivariate and univariate statistical analyses were employed to discover discrete, non-overlapping character differences and correlated patterns of character variation that would facilitate objective delineation of species-level boundaries in this widespread complex.

Materials and methods

Morphological and color pattern data were collected from fluid-preserved specimens (see Appendix I). A total of 3,174 specimens was examined from throughout the range of the *Phrynosoma douglasii* species complex. Multivariate analyses were applied to 977 specimens, and univariate statistical analyses were applied to 52 samples totaling 1,134 specimens.

Statistical analyses

The characters recorded from specimens included meristic, morphometric and qualitative (shape, color pattern) traits. Linear measurements were taken from the head, cephalic horns, and tail and expressed as a proportion of head length. Statistics of dispersion (mean, standard error, standard deviation, and observed limits) were calculated for all quantitative characters. The coefficient of variation (CV) was calculated only for the meristic character FRS for comparisons among selected taxa. In some univariate analyses of quantitative characters the coefficient of difference (CD) was calculated to determine the percent of mutual non-overlap between samples. Due to gender-based differences for some characters, males and females were analyzed separately. An analysis of variance (ANOVA) was performed to determine which continuous, quantitative characters displayed greater variation between, than within, samples. The significance of difference among sample means was tested using the SAS system GLM procedure *t*-tests and tabulated for a subset of characters found to be taxonomically informative and useful.

Principal Components (PC) analysis (SAS Institute, 1990) was used to discover patterns of covariation among characters in the male and female data sets. Input data for the PC analyses consisted of character states drawn from individual specimens, including morphometric ratios from mensural characters and qualitative characters (shape, color pattern); qualitative traits were numerically encoded as binary or multi-state variables. Only adult specimens were used in the multivariate analyses to minimize ontogenetic differences in morphometry. Due to the different kinds of variables in the data sets, PC analysis was performed on the correlation matrices. The original taxonomic identity of each specimen was included *a posteriori* to determine whether the resulting clusters in multivariate space corresponded to previously recognized taxa.

Characters

Morphometric, meristic and qualitative characters are described below; with the exception of new characters, terminology follows Smith (1946) and Reeve (1952) (Fig. 1). Snout-vent length and tail length were taken with a metric ruler to an accuracy of 1 mm; all other measurements were taken with dial calipers to an accuracy of 0.1 mm. Gender was determined by noting presence or absence of hemipeneal bulges in the tail base and presence or absence of enlarged postcloacal scales (male and female, respectively).

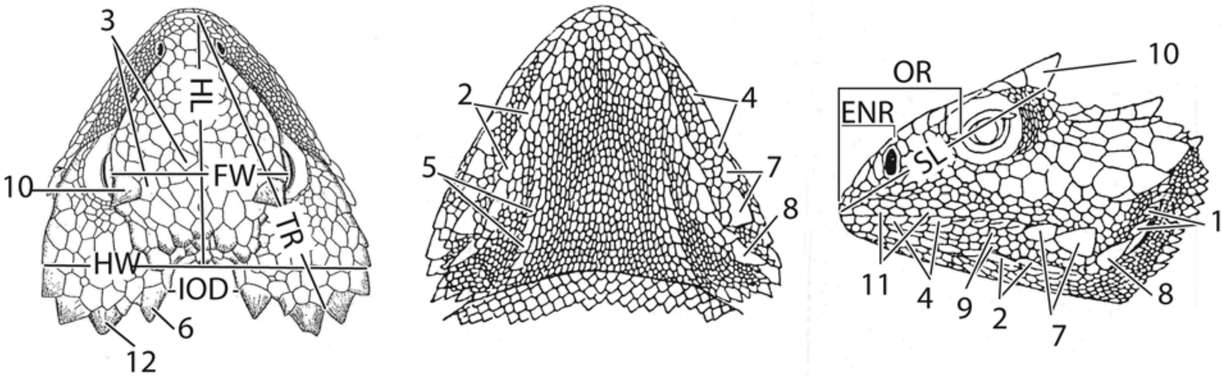

FIGURE 1. Dorsal, ventral, and lateral aspects of the head of *Phrynosoma hernandesi* (after Cope, 1900) showing measurements and terminology used in this study. Measurements are: frontal width (FW), head length (HL), head width (HW), interoccipital distance (IOD), snout length (SL), external naris-rostral scale distance (ENR), orbital-rostral scale distance (OR), and temporal-rostral scale distance (TR). Terminology includes: 1. auricular scales, 2 chinshields, 3. frontal rim scales, 4. infralabials, 5. longitudinal gular fold, 6. occipital horn, 7. postlabial scales, 8. postrictal spine, 9. sublabials, 10. superciliary spine, 11. supralabials, and 12. third temporal horn.

Snout-vent length (SVL) was measured from the tip of the snout to the vent of the cloaca, to the nearest millimeter. Maximum snout-vent length is given for each taxon under the description.

Tail length (TL) was measured from vent to tail tip and expressed as a ratio of head length (HL). Experimental error was found to be smaller for head length than for snout-vent length, thereby improving the precision of the resulting proportional measurement. There are significant differences in proportional tail length between males and females.

Head length (HL) was measured from the rostral scale to the interoccipital margin of the head. Head length was used as an independent variable to generate ratios for other head measurements, e.g. snout length and head width.

Snout length (SL) was measured from the rostral scale to the posterior margin of the vertical postorbital bone and expressed as a ratio of head length (HL).

Snout length (ENR) was also measured from the external naris to the rostral scale, and expressed as a percentage of the distance from the anterior corner of the ocular orbit to the rostral scale (OR). Descriptive differences in snout length and head length are to be found in Girard (1858a), Yarrow (1882a), Stejneger (1890) and Cope (1900), thus suggesting the potential taxonomic importance of these morphometric characters.

Temporal-rostral distance (TR) was measured from the rostral scale to the posterior margin of the temporal shelf between the second and third (last) temporal horns and expressed as a ratio of head length (HL).

Length of the temporal shelf (TRE) was calculated by subtracting head length from the temporal-rostral distance and expressing the difference as a percentage of head length. The posterolateral development of the temporal shelf varies among previously recognized short-horned lizard taxa as indicated by descriptions in Cope (1900) and Reeve (1952) which suggest possible taxonomic significance. Cope (1900), noted that the degree of posterior expansion of the temporal shelf determines the depth of the occipital emargination.

Temporal shelf surface (TSS) varies from relatively flat to slightly convex to quite rounded among samples subjected to comparative study. Reeve (1952) described the convex surface of the temporal shelf in *P. d. brevirostre* [sic], and also drew comparisons between *P. d. ornatum* and *P. d. hernandesi.* TSS of was not used for data analysis but descriptions of the temporal shelf are presented in the diagnoses for the taxa.

Head diameter (HW) was measured at a level just anterior to the first temporal horns. Head diameter was then divided by head length (HL) and expressed as a ratio. Reeve (1952:819, 950–51) took this measurement at the angles of the lower jaws, and provided a quantitative summary of head width data for his recognized taxa of short-horned lizards.

Frontal width (FW) was taken from the outer edges of the left and right orbits just anterior to superciliary spine and expressed as a ratio of head length (HL). Reeve (1952:819) calculated the frontal width as a percentage of head width.

Interoccipital distance (IOD) was measured between the interior edges of the base of the left and right occipital horns and expressed as a ratio of head length (HL). Cope (1900), Van Denburgh (1922), and Smith (1946) did not evaluate this character. Reeve (1952) expressed the interoccipital distance in terms of the basal diameter of one occipital spine.

Occipital horn length (OH) was measured from the base to the tip of the occipital horn and expressed as a proportion of head length (HL).

Temporal horn length (TH) was measured from the base to the tip of the third (last) temporal horn and expressed as a proportion of head length (HL).

Superciliary spine length (SUP) was measured from the base to the tip of the superciliary spine along its dorsal surface and expressed as a proportion of head length (HL).

Occipital tubercles (TUB) are enlarged, convex scales situated on the dorsal surface of the occipital shelf, between the interparietal scale and the posterior margin of the shelf. Montanucci (2004) used the term "preoccipital tubercles", but the currently used term seems preferable. There are usually two or four tubercles and they vary in morphology, from low and rounded to elevated and pointed. The number and/or shape of the tubercles are mentioned in the descriptions of taxa.

The shape of the tympanum (TYMPS) is typically elliptic or oval with the vertical diameter exceeding the horizontal diameter. The anterior margin of the tympanum tends to be curvilinear, whereas the posterior margin may be slightly curvilinear to linear. The dorsal curvature of the tympanum may be equal to, or somewhat broader, than the ventral curvature. The tympanum is considered "moderately broad" if the horizontal diameter is 45 to 55% of the vertical diameter, and "broad" if the horizontal diameter is even greater. In *P. douglasii* the horizontal diameter is typically narrow, being about 33% or less of the vertical diameter. The encroachment of scales may cause a further reduction of the horizontal diameter of the tympanum, producing a very narrow ellipse. In extreme examples of reduction, the vertical and horizontal diameters are both greatly diminished, resulting in a small, rounded tympanic disc.

The surface of the tympanum (TYMPSU) is typically exposed or naked in members of the short-horned lizard species complex. But for the species *P. douglasii*, there is variation among populations within this taxon. The tympanum may be partly or entirely concealed by granular scales. In cases of partial concealment, the encroachment of scales may occur anywhere along the border of the tympanum, although the anterior, posterior, and ventral margins seem most affected.

Auricular scales (AUR) are located along the anterior margin of the ear opening and show variation in size and shape among the short-horned lizard taxa (Girard. 1858a). Subsequent authors, including Cope (1900), Van Denburgh (1922), Smith (1946), and Reeve (1952) gave no consideration to the potential taxonomic value of this character. Examination of the auricular scales indicates that they vary from slightly enlarged and rounded to elongated and tapered. The size and shape of the scales along the anterior border of the ear opening were not used in the data analysis, but recorded in the taxonomic descriptions.

Postrictal spine length (POST). The postrictal scale is a long, conical scale at the anteroventral corner of the ear opening (Reeve, 1952). The postrictal is considered to be the most posterior postlabial, if distinguished from the more anterior postlabials and from the subrictal; it occurs in the *P. coronatum* and *P. douglasii* species complexes (Smith, 1946; Reeve, 1952; Montanucci, 2004). In the short-horned lizards, it is usually present and differentiated from the postlabials situated anteriorly but in rare instances it is absent. The length of the postrictal was expressed as a proportion of head length (HL).

Postlabial scale number (PLAB). The postlabial scales are a series of several enlarged, flattened scales that are continuous with the infralabials. As the infralabials increase in size posteriorly and begin to develop a flattened edge, distinguishing the last infralabial from the first postlabial can be less than straightforward. Establishing the true angle of the mouth (*rictus oris*) is helpful in this regard (see Smith, 1946:25).

Orientation of occipital horns (OO) was recorded as nearly horizontal (0), directed upward at an angle, ca. 45°(1), or directed vertically or nearly so (2).

Orientation of temporal horns (OT) was recorded as nearly horizontal (0), directed upward at an angle, ca. 45°(1), or directed vertically or nearly so (2).

Rostrofrontal profile (RF) is the lateral profile of the head region, especially the slope of the snout and frontal area. Descriptions of short-horned lizard taxa can be found in Girard (1858a), Stejneger (1890) and Cope (1900), which suggest potential taxonomic utility of this character. In some taxa, the frontal area and snout have a rounded profile, the muzzle being described as short; in others the snout is "protruding" and the lateral profile of the head is flat with a gradual slope toward the snout. Rostrofrontal profile was recorded as gradually sloping (0), or rounded or angular, with a steep incline (1).

Frontal rim (FR), first noted by Richardson (1915), marks the posterior edge of the frontal area; it is well developed when the frontal area is elevated above the level of the occipital shelf. If the frontal and occipital areas are more or less at the same level, the rim is weakly developed and scarcely evident. A series of enlarged, convex scales runs along the rim; if the rim is well elevated above the occipital shelf, the posterior side of each scale will be oriented vertically or nearly so. In neonates of all short-horned lizard taxa, the frontal and occipital areas of the head are at the same level, but in some taxa, the frontal area becomes elevated above the occipital shelf as the lizard grows. The frontal rim was subjectively recorded in adults as not elevated (0), slightly elevated (1), elevated (2) or well elevated above the occipital shelf (3).

Frontal rim scales (FRS) form a series of enlarged, convex scales along the frontal rim between the left and right superciliary spines. The enlarged scales may meet at the midline of the head or contact one or more smaller cephalic scales. In taxa with a well developed frontal rim, the enlarged scales are strongly convex, and their posterior sides are oriented vertically or nearly so, forming an elevated rim. In some taxa, the enlarged scales nearest the superciliary spines are strongly convex with vertical posterior sides, but the enlarged scales toward the midline have more gradually sloping, less vertical, posterior sides. Thus, the frontal rim is well elevated near the superciliary spines, becoming less elevated closer to the midline. In some cases, there may be only one enlarged scale medial to, and contacting, the superciliary spine; the posterior side of the enlarged scale may be oriented at a shallow angle or nearly horizontal, such that there is little indication of an elevated rim demarcating the frontal and occipital areas; or the enlarged scales may be completely absent. The number of enlarged frontal rim scales on the left/right sides of the head was recorded for the diagnoses of taxa.

Longitudinal gular folds (GUL) are weakly developed, ephemeral folds oriented longitudinally on the left and right sides of the gular area, just medial to the chinshields. The folds are easily obscured in museum specimens that have been distended slightly with preserving fluid. Toward the posterior end of each fold, the scales may become slightly enlarged and pointed (see Cope 1900, fig. 70) The longitudinal gular folds were recorded as absent (0), weakly developed without enlarged scales (1), or present with enlarged, pointed scales (2).

Dorsal spots (DS) show variability in size and shape among population samples, suggesting potential taxonomic significance. Previous authors, e.g. Cope (1900), Van Denburgh (1922), Smith (1946), and Reeve (1952) described various characteristics of the dorsal pattern of short-horned lizards, but little taxonomic emphasis was given to the size and shape of the dorsal spots. The dorsal spots were recorded as absent (0), small and wedge-shaped (1), transverse bands (2), small, rounded (3), or large, rounded (4).

Light-colored borders of dorsal spots (EM) are described and evaluated to some extent in all previous taxonomic studies of short-horned lizards. Whether the light border is confined to the posterior edge of the dorsal spot or also extends along the medial edge was recognized by Reeve (1952) as taxonomically useful. Other features of the light borders, such as whether they are discrete or diffuse and merging into the dorsal field, and whether they are relatively narrow or broad shows variation within and between population samples, and appears to be of taxonomic value in some cases. The light border was recorded as follows: confined to posterior edges of dorsal spots (1), occurs on medial and posterior edges of dorsal spots (2), nearly encircles dorsal spots (3).

Dorsolateral white spots (WS) are present or absent among short-horned lizard populations, and thus show potential taxonomic significance. However, this character has not been used for diagnostic purposes in previous taxonomic studies. Dorsolateral white spots were recorded as absent (0) or present (1).

Frontal pattern (FP) of the head may show variation within and between populations. The frontal region of the head was recorded as uniform (0), with whitish specks and/or lines outlining the frontal scales (1), or with one to several dark transverse bands with or without whitish borders (2).

Gular pattern (GP) was scored in specimens preserved while in the melanin-dispersed phase (i.e. the physiological “dark phase”). Specimens in intermediate stages of melanin dispersion presented faint or ambiguous patterns that in some cases were difficult to score. Gular patterns, although variable within populations, displayed characteristics associated with geographically defined populations and previously recognized taxa and thus were considered taxonomically informative. The following states were identified: gray suffusion (0), scattered spots with or without suffusion (1), spots and vermiculations (2), series of chevrons or irregular (wavy) transverse bands (3).

Abdominal pattern (ABD) was evaluated in specimens preserved while in the melanin-dispersed phase (i.e. “dark phase”). Specimens in intermediate stages of melanin dispersion presented faint or ambiguous patterns that in some cases were difficult to score. Abdominal patterns displayed characteristics associated with geographically defined populations and previously recognized taxa and thus were considered taxonomically informative. The following states were identified: large melanistic spots (0), scattered flecks and patches of melanin (1), gray suffusion (2).

Subcaudal bands (SCB), are a series of melanistic bands, usually interrupted medially along the underside of the tail. The character was evaluated in specimens preserved in the melanin-dispersed phase (i.e. “dark phase”). The following states were identified: interrupted bands proximally and complete bands distally under tail (0), only interrupted bands present (1), subcaudal bands absent (2).

Species concept

The general lineage concept of species (de Queiroz, 1998, 1999), which is considered an extension of the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978; Frost & Hillis, 1990) is followed in this taxonomic study of the short-horned lizards. Species delimitation is character-based in this study. Groups with discrete, non-overlapping differences in one or more morphological and/or color pattern characters are classified as distinct species. The diagnostic characters may include those inferred to be fixed or invariant within the putative species. If the quantitative characters are variable, they must be non-overlapping between putative species. In the case of qualitative polymorphic characters, to be diagnostic, none of the character states can be shared between the presumptive species. In some cases, multivariate analysis may distinguish species; in other cases, population samples may overlap in multivariate space, but nonetheless, they are regarded as separate species if discrete character differences are discovered through other comparative methods.

The purpose of classification is to reflect both phylogeny and biological diversity (Smith *et al*., 1997). This dual purpose of classification has long been recognized (e.g. Simpson, 1961:27–28). In some cases, population samples differ significantly (statistical significance of 0.05% or greater) for one or more quantitative characters, but the differences are not discrete, i.e. the observed limits of character variation overlap. Recognizing such groups as distinct species would not be justified because of the absence of discrete differences. However, recognizing these distinctive groups at the subspecies level may be warranted in some cases. Although the concept has been criticized by numerous authors (see references in Mayr, 1969), application of the subspecies concept can provide enhanced resolution of the patterns of character variation across populations, thereby fulfilling the purpose of accounting for biological diversity.

The so-called 75% rule, applicable to both quantitative and encoded qualitative characters, is ostensibly a requirement for the recognition of subspecies, although seldom followed (Mayr, 1969). In some cases it is also useful to calculate the extent of mutual non-overlap between two population samples. The coefficient of difference (CD) is a statistic that uses the sample mean and standard deviation to determine the percent joint non-overlap between two population samples for a quantitative character. However, application of the CD in taxonomic decisions is arbitrary because morphological divergence is theoretically a continuum from no differentiation to complete differentiation between any two populations. There are other considerations as well, such as the degree of geographic isolation between populations, and whether character variation is clinal and/or geographically discordant. Populations considered for subspecies recognition should occupy a geographical segment or subdivision of the species’ distribution and there should be morphological evidence of intergradation at the contiguous boundaries between subspecies. In my taxonomic study of the short-horned lizards, two cases emerge that, in my opinion, qualify for the use of the subspecies category (see below).

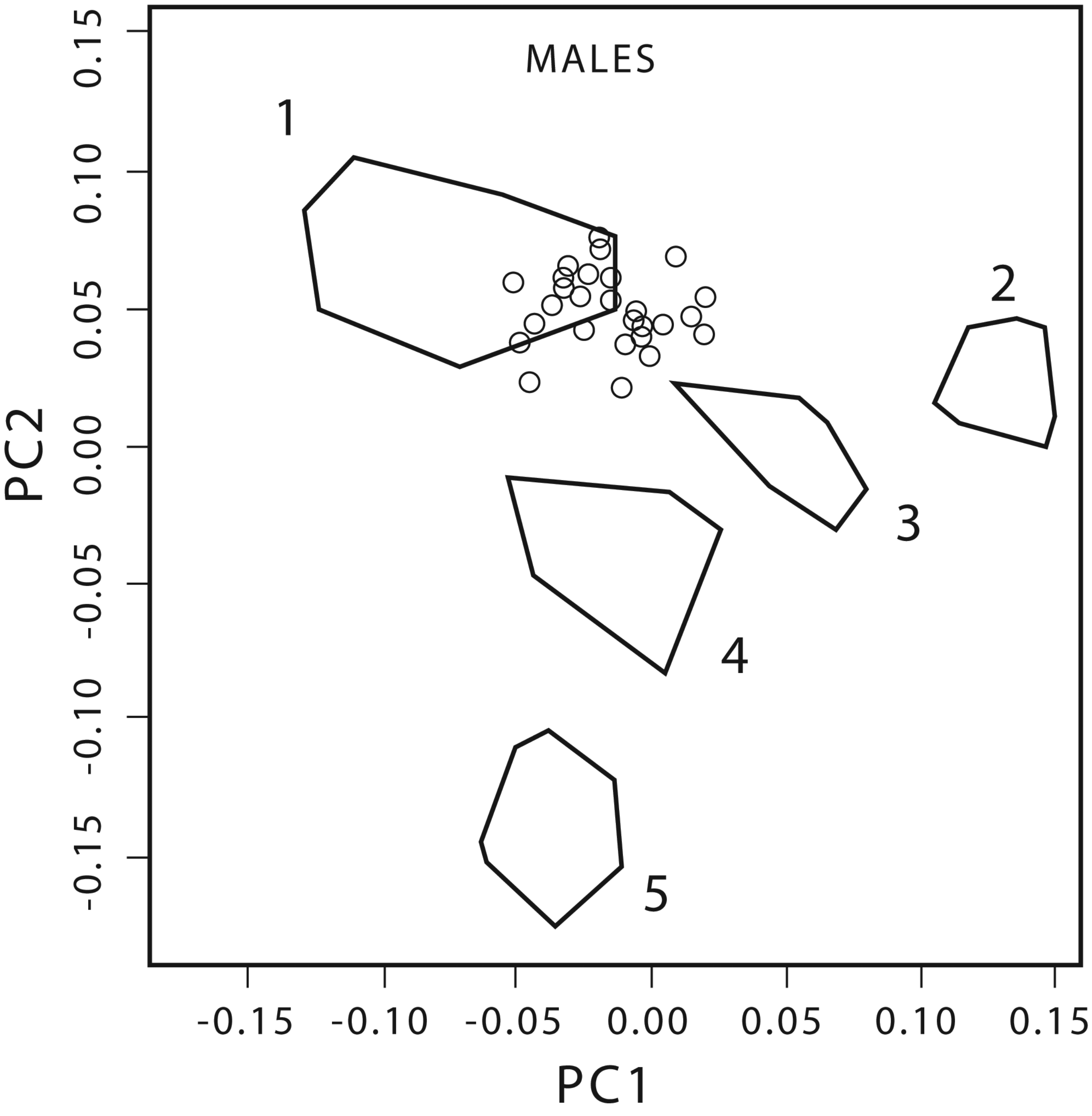

FIGURE 2. Projection of male samples (n = 216) of the *Phrynosoma douglasii* (species complex) on the first two principal components (PC1, PC2) of a 20-character correlation matrix. PC1 explains 36.7% and PC2 explains 23.8% of the total variance. Where taxa overlap, plots depicted as polygons and data points for the purpose of clarity. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are labeled as follows: 1. nominotypical *P. hernandesi,* 2. *P. douglasii,* 3. *P. brevirostris,* 4. *P. ornatissimum brachycercum,* 5. nominotypical *P. ornatissimum.* Open circles represent data points for *P. hernandesi ornatum.* See text for further discussion.

Results and discussion

Principal components analysis was applied to data sets comprised of nine morphometric ratios and eleven qualitative (categorical) characters. Bivariate scatterplots of PC1 vs. PC2 resulted in discrete clusters with interpretable patterns of morphological relationships. Scatterplots for the other PC axes (e.g. PC1 vs. PC3 or PC4, etc.) produced ambiguous patterns with considerable overlap among taxa. The plots (PC1 vs. PC2) of the male and the female data sets are similar (Figs. 2–3). The analyses reveal clusters corresponding to four previously described species: *P. brevirostris* Girard, *P. douglasii* (Bell), *P. hernandesi* Girard, and *P. ornatissimum* Girard. The taxon *ornatum* Girard (circles) overlaps with the *P. hernandesi* cluster and approaches the *P. brevirostris* cluster primarily along the PC 1 axis. The taxon *brachycercum* Smith forms another cluster situated between *P. hernandesi* and *P. ornatissimum* along the PC 2 axis, but it is close to *P. ornatissimum* along the PC 1 axis. Clusters representing two new species allied to *P. brevirostris* were also revealed by the principal components analysis, but they are depicted separately for the purpose of discussion (Figs. 4–5); see below.

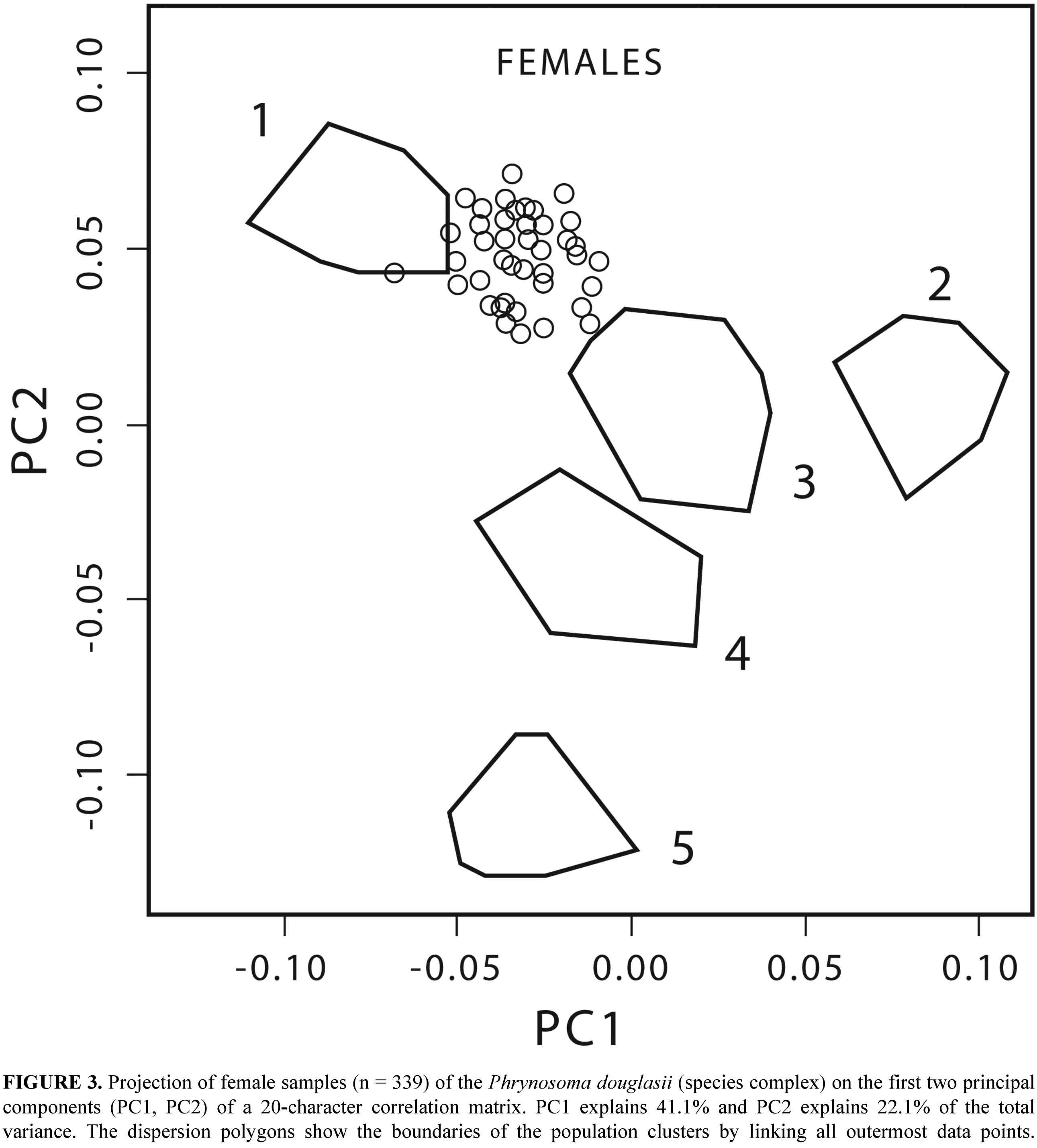

FIGURE 3. Projection of female samples (n = 339) of the *Phrynosoma douglasii* (species complex) on the first two principal components (PC1, PC2) of a 20-character correlation matrix. PC1 explains 41.1% and PC2 explains 22.1% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are labeled as follows: 1. nominotypical *P. hernandesi,* 2. *P. douglasii,* 3. *P. brevirostris,* 4. *P. ornatissimum brachycercum,* 5. nominotypical *P. ornatissimum.* Open circles represent *P. hernandesi ornatum.* See text for further discussion.

Characters with high loadings on PC1 are (in descending order): TR, TH, HW, SUP, GP, ABD, FR, and FP. Characters with high loadings on PC2 include (in descending order): EM, WS, OT, DS, OO, SCB, RF, and FR

(Table 1). Therefore, the short-horned lizard taxa are positioned along the PC1 axis according to head proportions (TR, HW), length of cephalic horns (TH, SUP), development of the frontal rim (FR), and the qualitative traits GP, ABD, and FP. *Phrynosoma hernandesi* is characterized by an expanded temporal shelf (both posteriorly and laterally), relatively long temporal horns, well developed superciliary spines, and an elevated frontal rim. *P. douglasii*, which is positioned at the opposite extreme of the PC1 axis, has a greatly reduced temporal shelf, short cephalic horns, and the frontal rim is weakly developed or absent. Several characters of the dorsal pattern (EM, WS, DS), the orientation of the cephalic horns (OT, OO), the rostrofrontal profile (RF), development of the frontal rim (FR), and the subcaudal pattern (SCB) determine the positions of taxa along the PC 2 axis. *Phrynosoma hernandesi, P. brevirostris, P. douglasii* are similar in having dorsal spots with posterior light borders (EM), wedge-shaped dorsal spots or transverse bands (DS), and lacking dorsolateral white spots (WS). *P. ornatissimum* differs from the aforementioned taxa in having large, rounded dorsal spots, discrete, narrow white or yellow borders along the medial and posterior edges of the dorsal spots, and conspicuous dorsolateral white spots.

TABLE 1. Character loadings from correlation matrices for the first and second principal components of the multivariate analyses of male and female data sets.

	Males		**Females**	
Character	**PC1**	**PC2**	**PC1**	**PC2**
FR	0.274581	0.256122	0.262564	0.269406
GP	0.289583	0.208180	0.283908	0.205801
OO	-0.142591	0.309959	-0.128050	0.288503
OT	-0.030763	0.331041	0.018097	0.308427
RF	-0.211550	0.298117	-0.210020	0.294463
DS	0.148185	0.318179	0.148827	0.332445
EM	0.074445	0.366840	0.079656	0.401157
WS	0.089292	0.349415	0.098998	0.366815
FP	-0.256213	0.045214	-0.267988	0.023403
ABD	-0.280548	0.134314	-0.286139	0.130435
SCB	-0.224318	0.308788	-0.223815	0.304107
TL	0.116675	-0.202267	0.189793	-0.227960
SL	0.184075	0.108867	0.218674	0.065405
FW	-0.032112	0.150055	0.015303	0.102240
HW	0.323470	0.076363	0.307377	0.030415
TR	0.338337	0.062594	0.319046	0.024677
IOD	0.014834	0.160602	0.050517	0.135487
OH	0.268451	0.030247	0.272985	0.048699
TH	0.328443	-0.072277	0.318912	-0.068335
SUP	0.311089	-0.078929	0.297355	-0.101620

Principal components analysis (Figs. 2 and 3) separated the taxon *brachycercum* (polygon 4) from *P. ornatissimum* (polygon 5) on the basis of several dorsal pattern characters including medial white borders of the dorsal spots (EM), dorsolateral white spots (WS), and shape of the dorsal spots (DS). However, these differences are not fully discrete. In 45 specimens of *brachycercum*, all lack the medial border, but in 145 specimens of *ornatissimum* about 2.8% lack the medial borders. The dorsolateral white spots are present in 14% (absent in 86%) of the *brachycercum* sample, whereas the spots are present in nearly all (98.6%) of the *ornatissimum* sample. The shape of the dorsal spots is polymorphic in *brachycercum,* varying from small, wedge-shaped, to large, rounded spots, or forming transverse bands. In *ornatissimum* the spots, although varying somewhat in size, are usually rounded. The two taxa are very similar in morphometric features of the head, length and orientation of cephalic horns, development of the frontal rim, and proportional tail length. There are no statistically significant differences in these characters, although the two taxa show a significant difference in the number of frontal rim scales, but for the left side only (Table 3). The taxon *brachycercum* occurs over a large region of northern Mexico. Whether it is allopatric or contiguous with populations of *P. ornatissimum* is unclear. The critical region in northern Chihuahua is virtually uncollected, but one specimen (photo voucher) from near Janos, Chihuahua, shows an admixture of traits from *P. ornatissimum* and the taxon *brachycercum.* Janos is only 35 km north of Rancho Ramos, the northernmost record for *brachycercum*, and if *P. ornatissimum* occurs near Janos, then it raises the possibility of intergradation with *brachycercum.* Pending more information from critical localities, *brachycercum* is provisionally treated as a subspecies of *P. ornatissimum*.

In the principal components plots (Figs. 2 and 3), the cluster (open circles) representing the taxon *ornatum* partially overlaps the polygon representing *P. hernandesi* (polygon 1), and is situated between the latter and *P. brevirostris* (polygon 3). The relative positions of these taxa fall primarily along the PC 1 axis. The taxon *ornatum* is characterized by having a somewhat reduced temporal shelf (TRE), a less protruding snout (ENR), a more obtusely rounded rostrofrontal profile (RF), slightly shorter cephalic horns (TH), a reduced or absent frontal rim (FR). It also has a lower mean number of enlarged frontal rim scales (FRS) and a slightly shorter tail (TL). Statistically significant differences between *P. hernandesi* and *ornatum* are noted for the characters TRE, ENR, TH, FRS and TL (Table 3). The coefficient of difference (or percent joint non-overlap) for these characters are: TRE (92.5%, males; 89%, females); ENR (53.3%); TH (81%); FRS (84% left, 81% right); TL (54.7%, males; 59.1%, females). The characters TRE, TH, and FRS are considered useful in distinguishing the two taxa at the subspecies level (see discussion below).

Principal components plots (Figs. 4 and 5) show substantial overlap between *P. brevirostris* (polygon 3) and the samples from the San Luis Valley of south-central Colorado (open circles). The partial separation of the two groups occurs primarily along PC 2. However, the San Luis Valley samples differ discretely from *P. brevirostris* in having melanistic spots on the abdomen and incomplete subcaudal bands (melanin-dispersed phase); both color pattern traits are absent in the latter taxon. The temporal shelf (TRE) is significantly shorter and more convex in the San Luis Valley samples than in *P. brevirostris*, and females of the former also have a significantly shorter tail than *P. brevirostris*, although both characters have overlapping limits (Table 3). The San Luis Valley population is allopatric with a broad geographic separation from *P. brevirostris*. Therefore, on the basis of discrete character differences and allopatry, the San Luis Valley population is regarded as a distinct species, herein named *Phrynosoma diminutum* **sp. nov.**

Population samples from the plains of eastern Colorado, southwestern Nebraska, southeastern Wyoming and northeastern New Mexico represent a morphologically distinct taxon which herein is named. *Phrynosoma.bauri* **sp. nov.** The cluster (triangles) representing this taxon is separated from *P. brevirostris* (polygon 3) and from *P. diminutum* **sp. nov.** (open circles) along both PC axes, especially PC 1 (Figs. 4 and 5). *P. bauri* **sp. nov.** differs discretely from *P. brevirostris* in having dorsolateral white spots (WS), and in the melanin-dispersed phase, melanistic abdominal spots (ABD). It is also essentially discretely distinct from *P. brevirostris* in having an elevated frontal rim (FR). The two taxa are similar in having an abrupt rostrofrontal profile and truncate snout (ENR), but have statistically significant differences for tail length (TL) in females, extent of the temporal shelf (TRE), number of frontal rim scales (FRS), and length of temporal horns (TH); see Table 3. *P. bauri* **sp. nov.** occurs south of the North Platte River and appears to be allopatric from *P. brevirostris*.

Phrynosoma bauri **sp. nov.** differs discretely from *P. diminutum* **sp. nov.** in having dorsolateral white spots (WS) and an elevated frontal rim (FR). Statistically significant differences between the two taxa are noted for the number of frontal rim scales (FRS), extent of the temporal shelf (TRE), length of the third temporal horn (TH), and tail length (TL) in females (Table 3). It also reaches a greater snout-vent length than *P. diminutum* **sp. nov.** (Table 5). *P. bauri* **sp. nov.** and *P. diminutum* **sp. nov.** appear to be parapatrically associated along the southeastern edge of the San Luis Valley (see **Taxonomic accounts**).

In Figs. 4 and 5, the clusters (triangles) representing *P. bauri* **sp. nov.** overlap extensively with *P. o. brachycercum* (polygon 4). This overlap is due to similarity between the two taxa in several characters with high loadings on PC 1 (TR, TH, SUP, and FP) and PC 2 (EM, OT, DS, OO, and RF). Nearly complete separation of the two taxa was noted in the scatterplots of PC 2 vs. PC 4 (not shown) where characters GP and TL have moderate to high loadings on PC 4. Comparisons of morphology and color pattern between the two taxa reveal that they are distinct and easily diagnosed by the characters GP, WS, ABD, and SCB; the taxa are also widely separated geographically (see **Taxonomic accounts**).

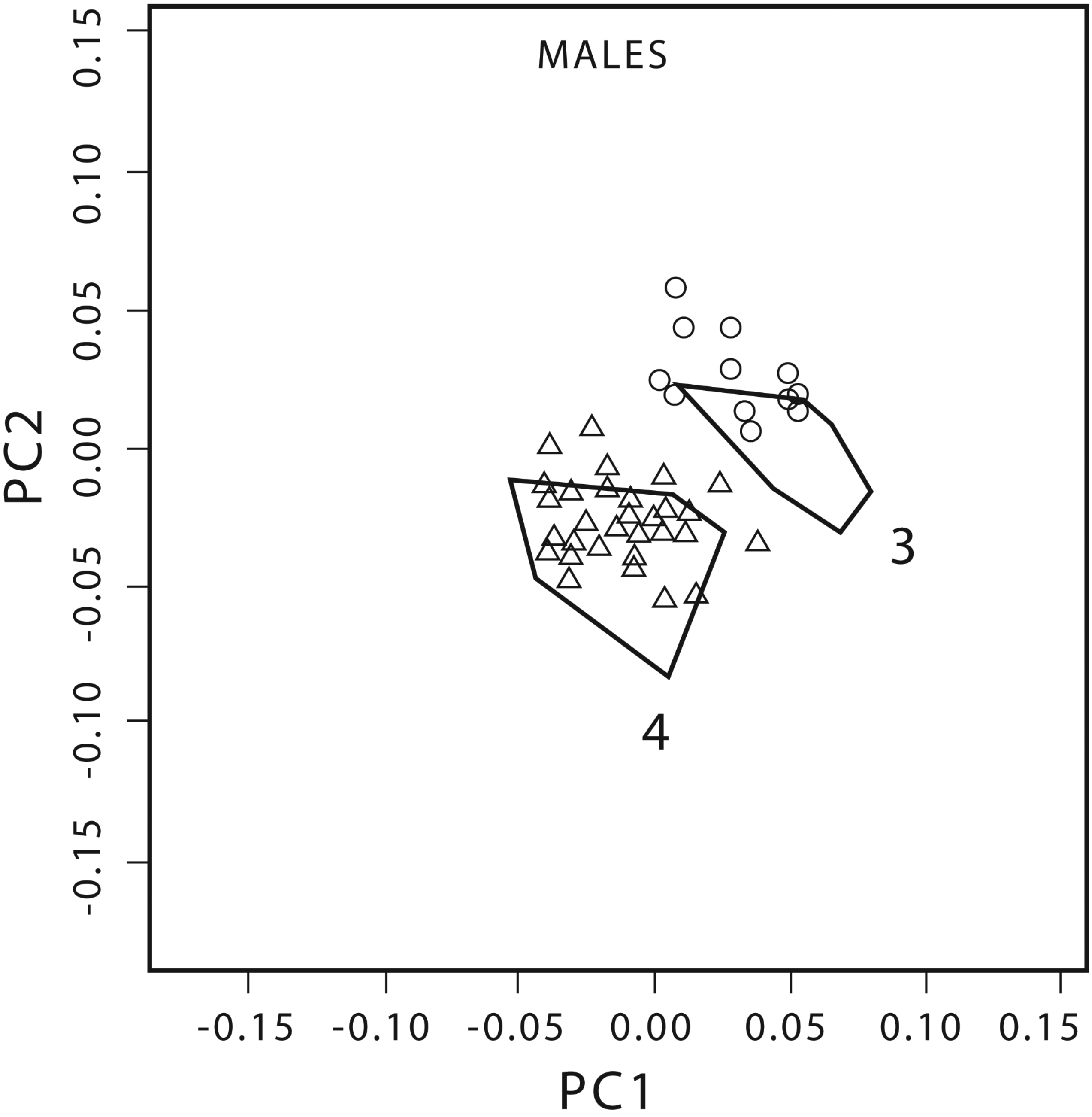

FIGURE 4. Projection of male samples (n = 79) of the *Phrynosoma douglasii* (species complex) on the first two principal components (PC1, PC2) of a 20-character correlation matrix. PC1 explains 36.7% and PC2 explains 23.8% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygon no. 3 represents *Phrynosoma brevirostris;* open circles represent *Phrynosoma diminutum* **sp. nov.**; triangles represent *Phrynosoma bauri* **sp. nov.** which overlaps with *Phrynosoma ornatissimum brachycercum* (dispersion polygon no. 4). See text for further discussion.

Inspection of the PCA plots did not reveal any evidence of clinal variation across taxa correlated with latitude. The results show that the polygons representing the different taxa do not correspond to the latitudinal positions of their respective geographic ranges. For example, the ranges of *P. douglasii* (polygon 2) and *P. brevirostris* (polygon 3) are situated mostly north of the range of *P. hernandesi* (polygon 1), whereas *P. o. brachycercum* (polygon 4) occurs south of the range of *P. ornatissiumum* (polygon 5). As these geographic relationships are not mirrored by the positions of the groups along the axes of PC 1 or PC 2, clinal variation across taxa correlated with latitude can be discounted in this species complex.

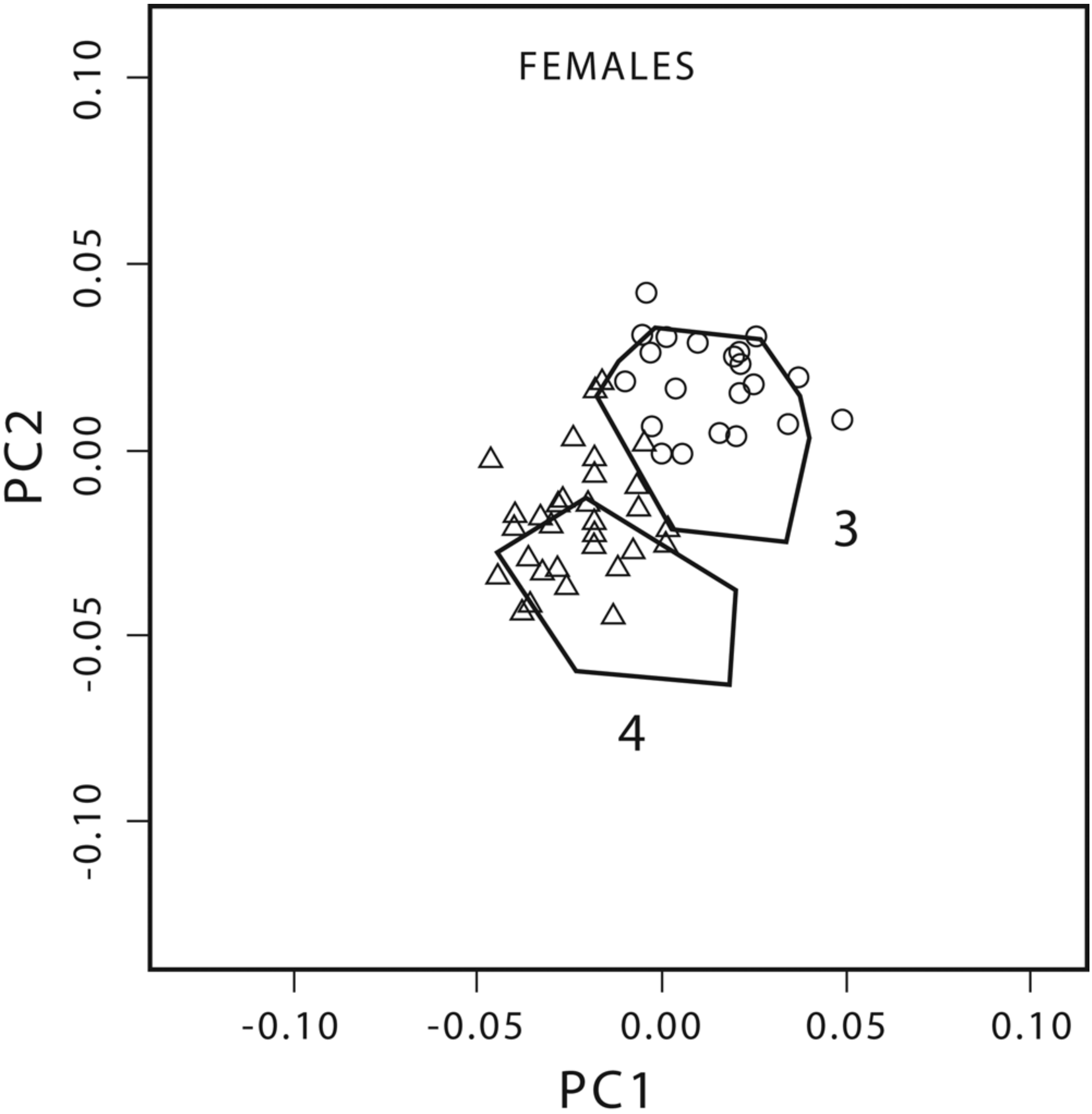

FIGURE 5. Projection of female samples (n = 112) of the *Phrynosoma douglasii* (species complex) on the first two principal components (PC1, PC2) of a 20-character correlation matrix. PC1 explains 41.1% and PC2 explains 22.1% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygon no. 3 represents *Phrynosoma brevirostris;* open circles represent *Phrynosoma diminutum* **sp. nov.**; triangles represent *Phrynosoma bauri* **sp. nov.** which overlaps with *Phrynosoma ornatissimum brachycercum* (dispersion polygon no. 4). See text for further discussion.

Principal components analysis was also applied to the study of hybridization between *P. hernandesi* and *P. ornatissimum.* Neff & Smith (1979) demonstrated the usefulness of this multivariate method for detecting hybridization between taxa, and the advantages of the method over linear discriminant function analysis. The results of my analyses of hybridization are presented following the **Taxonomic accounts**.

The statistics of dispersion for the nine morphometric ratios used in the multivariate analyses are summarized for selected geographic segments or local population samples (52 samples; 1,134 specimens) representing each taxon (Table 2).

TABLE 2. Measurement ratios for male and female samples from selected localities for taxa of the *Phrynosoma douglasii* species complex. Mean ± standard deviation followed by observed limits in parentheses. All ratios were obtained by dividing by head length (HL). UCRB = Upper Colorado and Green River basins

Taxon/Locality	n	TL	SL	FW	HW	TR	IOD	OH	TH	SUP
P. brevirostris										
Canada (male)	7	2.27 ± 0.11 (2.12 – 2.41)	0.88 ± 0.01 (0.86 – 0.91)	0.73 ± 0.02 (0.69 – 0.76)	1.16 ± 0.05 (1.09 – 1.23)	1.10 ± 0.02 (1.07 – 1.13)	0.40 ± 0.02 (0.36 – 0.42)	0.09 ± 0.01 (0.07 – 0.11)	0.09 ± 0.01 (0.07 – 0.11)	0.08 ± 0.01 (0.07 – 0.10)
Canada (female)	14	1.90 ± 0.13 (1.72 – 2.13)	0.88 ± 0.01 (0.86 – 0.89)	0.72 ± 0.02 (0.69 – 0.75)	1.21 ± 0.03 (1.15 – 1.25)	1.15 ± 0.02 (1.12 – 1.21)	0.37 ± 0.03 (0.31 – 0.43)	0.09 ± 0.01 (0.07 – 0.12)	0.11 ± 0.01 (0.08 – 0.14)	0.09 ± 0.01 (0.07 – 0.13)
Colorado, W. (male)	9	2.19 ± 0.31 (1.68 – 2.77)	0.88 ± 0.01 (0.86 – 0.90)	0.72 ± 0.01 (0.70 – 0.74)	1.22 ± 0.04 (1.15 – 1.31)	1.15 ± 0.04 (1.10 – 1.22)	0.35 ± 0.01 (0.32 – 0.37)	0.11 ± 0.02 (0.08 – 0.14)	0.11 ± 0.01 (0.08 – 0.14)	0.09 ± 0.01 (0.08 – 0.11)
Colorado, W. (female)	19	1.85 ± 0.18 (1.44 – 2.26)	0.88 ± 0.01 (0.85 – 0.90)	0.73 ± 0.01 (0.70 – 0.77)	1.27 ± 0.04 (1.18 – 1.33)	1.19 ± 0.03 (1.09 – 1.24)	0.34 ± 0.02 (0.29 – 0.38)	0.11 ± 0.02 (0.05 – 0.14)	0.12 ± 0.02 (0.08 – 0.16)	0.10 ± 0.01 (0.08 – 0.12)
Montana (male)	16	2.15 ± 0.21 (1.76 – 2.43)	0.87 ± 0.02 (0.81 – 0.90)	0.73 ± 0.02 (0.70 – 0.76)	1.18 ± 0.04 (1.11 – 1.24)	1.12 ± 0.02 (1.05 – 1.16)	0.37 ± 0.01 (0.33 – 0.41)	0.09 ± 0.01 (0.06 – 0.11)	0.09 ± 0.01 (0.07 – 0.11)	0.08 ± 0.01 (0.07 – 0.10)
Montana (female)	20	1.95 ± 0.19 (1.55 – 2.30)	0.88 ± 0.01 (0.85 – 0.91)	0.72 ± 0.02 (0.67 – 0.77)	1.26 ± 0.04 (1.16 – 1.34)	1.17 ± 0.03 (1.13 – 1.23)	0.37 ± 0.01 (0.33 – 0.40)	0.10 ± 0.01 (0.06 – 0.13)	0.11 ± 0.01 (0.08 – 0.15)	0.09 ± 0.01 (0.07 – 0.12)
Nebraska, NW. (male)	14	2.15 ± 0.13 (1.91 – 2.32)	0.88 ± 0.01 (0.86 – 0.91)	0.75 ± 0.03 (0.71 – 0.82)	1.20 ± 0.04 (1.12 – 1.26)	1.14 ± 0.02 (1.11 – 1.17)	0.35 ± 0.02 (0.30 – 0.41)	0.09 ± 0.01 (0.07 – 0.14)	0.10 ± 0.01 (0.07 – 0.13)	0.09 ± 0.01 (0.06 – 0.11)
Nebraska, NW. (female)	17	1.95 ± 0.15 (1.64 – 2.24)	0.88 ± 0.01 (0.85 – 0.89)	0.74 ± 0.02 (0.70 – 0.79)	1.25 ± 0.03 (1.19 – 1.32)	1.18 ± 0.03 (1.13 – 1.25)	0.35 ± 0.01 (0.31 – 0.38)	0.10 ± 0.02 (0.08 – 0.16)	0.11 ± 0.02 (0.07 – 0.16)	0.09 ± 0.01 (0.07 – 0.11)
Utah: UCRB (male)	22	2.14 ± 0.18 (1.93 – 2.51)	0.88 ± 0.01 (0.85 – 0.91)	0.74 ± 0.02 (0.68 – 0.79)	1.23 ± 0.04 (1.13 – 1.31)	1.15 ± 0.04 (1.04 – 1.23)	0.34 ± 0.02 (0.31 – 0.38)	0.09 ± 0.01 (0.06 – 0.14)	0.10 ± 0.01 (0.08 – 0.12)	0.09 ± 0.01 (0.07 – 0.11)
Utah: UCRB (female)	29	1.90 ± 0.18 (1.57 – 2.29)	0.88 ± 0.01 (0.85 – 0.90)	0.73 ± 0.02 (0.69 – 0.78)	1.29 ± 0.05 (1.20 – 1.41)	1.20 ± 0.04 (1.11 – 1.28)	0.35 ± 0.03 (0.28 – 0.41)	0.10 ± 0.02 (0.06 – 0.18)	0.11 ± 0.02 (0.08 – 0.15)	0.10 ± 0.01 (0.07 – 0.12)
Wyoming (male)	24	2.24 ± 0.22 (1.88 – 2.76)	0.88 ± 0.01 (0.86 – 0.91)	0.75 ± 0.02 (0.72 – 0.79)	1.20 ± 0.04 (1.11 – 1.28)	1.13 ± 0.02 (1.09 – 1.18)	0.36 ± 0.02 (0.32 – 0.39)	0.09 ± 0.01 (0.06 – 0.15)	0.09 ± 0.02 (0.07 – 0.16)	0.09 ± 0.01 (0.07 – 0.12)
Wyoming (female)	48	1.87 ± 0.15 (1.55 – 2.27)	0.88 ± 0.01 (0.85 – 0.91)	0.73 ± 0.02 (0.68 – 0.78)	1.23 ± 0.04 (1.14 – 1.34)	1.16 ± 0.03 (1.09 – 1.23)	0.36 ± 0.02 (0.30 – 0.43)	0.10 ± 0.01 (0.07 – 0.13)	0.11 ± 0.01 (0.08 – 0.14)	0.10 ± 0.01 (0.08 – 0.12)
P. bauri **sp. nov.**										
Colorado, NE (male)	36	2.27 ± 0.22 (1.69 – 2.79)	0.88 ± 0.02 (0.84 – 0.92)	0.76 ± 0.02 (0.71 – 0.80)	1.23 ± 0.04 (1.15 – 1.31)	1.16 ± 0.03 (1.11 – 1.21)	0.36 ± 0.03 (0.28 – 0.43)	0.14 ± 0.02 (0.10 – 0.17)	0.14 ± 0.02 (0.10 – 0.17)	0.10 ± 0.01 (0.08 – 0.12)
Colorado, NE (female)	34	2.00 ± 0.13 (1.80 – 2.35)	0.88 ± 0.01 (0.85 – 0.91)	0.75 ± 0.02 (0.70 – 0.79)	1.23 ± 0.04 (1.06 – 1.33)	1.17 ± 0.02 (1.13 – 122)	0.36 ± 0.02 (0.32 – 0.42)	0.14 ± 0.01 (0.10 – 0.18)	0.14 ± 0.01 (0.11 – 0.18)	0.11 ± 0.01 (0.09 – 0.14)
P. diminutum **sp. nov.**										
CO: San Luis Valley (male)	12	2.15 ± 0.19 (1.80 – 2.38)	0.88 ± 0.01 (0.84 – 0.93)	0.74 ± 0.01 (0.72 – 0.75)	1.17 ± 0.02 (1.14 – 1.21)	1.10 ± 0.01 (1.07 – 1.13)	0.36 ± 0.04 (0.30 – 0.44)	0.10 ± 0.02 (0.07 – 0.16)	0.10 ± 0.01 (0.08 – 0.13)	0.09 ± 0.01 (0.08 – 0.10)
CO: San Luis Valley (female)	23	1.79 ± 0.12 (1.59 – 2.09)	0.87 ± 0.01 (0.84 – 0.89)	0.74 ± 0.03 (0.69 – 0.79)	1.21 ± 0.04 (1.14 – 1.27)	1.11 ± 0.02 (1.06 – 1.15)	0.36 ± 0.02 (0.31 – 0.42)	0.10 ± 0.02 (0.06 – 0.13)	0.10 ± 0.02 (0.06 – 0.13)	0.09 ± 0.01 (0.06 – 0.11)
P. douglasii										
ID: Snake River Plain (male)	7	2.24 ± 0.16 (1.95 – 2.43)	0.87 ± 0.02 (0.85 – 0.90)	0.75 ± 0.03 (0.68 – 0.78)	1.15 ± 0.06 (1.04 – 1.23)	1.12 ± 0.04 (1.04 – 1.16)	0.29 ± 0.03 (0.25 – 0.33)	0.09 ± 0.02 (0.06 – 0.12)	0.08 ± 0.02 (0.05 – 0.11)	0.07 ± 0.01 (0.05 – 0.08)
ID: Snake River Plain (female)	12	1.93 ± 0.17 (1.57 – 2.21)	0.86 ± 0.01 (0.84 – 0.88)	0.72 ± 0.02 (0.68 – 0.76)	1.18 ± 0.05 (1.10 – 1.32)	1.13 ± 0.03 (1.10 – 1.21)	0.31 ± 0.02 (0.28 – 0.34)	0.10 ± 0.01 (0.08 – 0.14)	0.09 ± 0.01 (0.07 – 0.12)	0.07 ± 0.01 (0.06 – 0.09)
OR: Cabin Lake (female)	60	1.78 ± 0.14 (1.48 – 2.15)	0.86 ± 0.01 (0.84 – 0.90)	0.75 ± 0.02 (0.70 – 0.79)	1.18 ± 0.03 (1.09 – 1.29)	1.11 ± 0.02 (1.05 – 1.15)	0.34 ± 0.02 (0.29 – 0.39)	0.09 ± 0.01 (0.07 – 0.12)	0.08 ± 0.01 (0.06 – 0.10)	0.07 ± 0.01 (0.06 – 0.09)
OR: Hart Mtn. Refuge (female)	16	1.91 ± 0.09 (1.76 – 2.07)	0.87 ± 0.01 (0.85 – 0.90)	0.73 ± 0.01 (0.70 – 0.76)	1.19 ± 0.04 (1.14 – 1.26)	1.13 ± 0.02 (1.0 9 – 1.17)	0.30 ± 0.01 (0.27 – 0.32)	0.10 ± 0.01 (0.08 – 0.11)	0.08 ± 0.01 (0.07 – 0.10)	0.08 ± 0.003 (0.07 – 0.08)
OR: Lake Abert (male)	20	2.13 ± 0.16 (1.98 – 2.55)	0.87 ± 0.01 (0.85 – 0.90)	0.77 ± 0.02 (0.72 – 0.81)	1.18 ± 0.04 (1.09 – 1.25)	1.08 ± 0.02 (1.02 – 1.12)	0.35 ± 0.02 (0.31 – 0.40)	0.09 ± 0.01 (0.07 – 0.11)	0.08 ± 0.01 (0.05 – 0.10)	0.07 ± 0.006 (0.05 – 0.08)
OR: Lake Abert (female)	17	1.95 ± 0.13 (1.76 – 2.25)	0.87 ± 0.01 (0.85 – 0.91)	0.75 ± 0.02 (0.71 – 0.78)	1.19 ± 0.04 (1.12 – 1.29)	1.11 ± 0.03 (1.06 – 1.16)	0.34 ± 0.02 (0.31 – 0.38)	0.09 ± 0.01 (0.07 – 0.11)	0.08 ± 0.01 (0.06 – 0.10)	0.07 ± 0.01 (0.05 – 0.09)
OR: Santiam Jct. (male)	32	2.05 ± 0.13 (1.58 – 2.33)	0.85 ± 0.01 (0.83 – 0.89)	0.73 ± 0.02 (0.69 – 0.77)	1.09 ± 0.02 (1.03 – 1.15)	1.04 ± 0.01 (1.02 – 1.08)	0.32 ± 0.02 (0.28 – 0.37)	0.08 ± 0.01 (0.06 – 0.11)	0.07 ± 0.01 (0.04 – 0.09)	0.07 ± 0.01 (0.04 – 0.08)
OR: Santiam Jct. (female)	76	1.61 ± 0.14 (1.23 – 1.94)	0.85 ± 0.01 (0.81 – 0.90)	0.72 ± 0.02 (0.68 – 0.78)	1.13 ± 0.02 (1.07 – 1.25)	1.07 ± 0.02 (1.01 – 1.15)	0.32 ± 0.02 (0.27 – 0.37)	0.08 ± 0.01 (0.06 – 0.10)	0.07 ± 0.01 (0.05 – 0.10)	0.07 ± 0.01 (0.05 – 0.09)
Washington (female)	18	2.06 ± 0.20 (1.63 – 2.54)	0.88 ± 0.01 (0.85 – 0.91)	0.73 ± 0.02 (0.66 – 0.77)	1.19 ± 0.03 (1.10 – 1.24)	1.15 ± 0.03 (1.10 – 1.22)	0.31 ± 0.02 (0.27 – 0.35)	0.12 ± 0.01 (0.09 – 0.17)	0.09 ± 0.01 (0.07 – 0.12)	0.08 ± 0.01 (0.06 – 0.10)

… …*continued on the next page*

TABLE 2. (Continued)

Taxon/Locality	n	TL	SL	FW	HW	TR	IOD	OH	TH	SUP
P. hernandesi										
AZ: Chiricahua Mts. (female)	11	2.01 ± 0.16 (1.77 – 2.43)	0.89 ± 0.01 (0.86 – 0.91)	0.74 ± 0.03 (0.69 – 0.79)	1.40 ± 0.04 (1.32 – 1.46)	1.28 ± 0.02 (1.22 – 1.32)	0.34 ± 0.03 (0.27 – 0.39)	0.14 ± 0.02 (0.10 – 0.18)	0.19 ± 0.03 (0.15 – 0.23)	0.14 ± 0.01 (0.12 – 0.18)
AZ: Huachuca Mts. (female)	8	2.14 ± 0.12 (1.96 – 2.33)	0.88 ± 0.01 (0.86 – 0.89)	0.71 ± 0.02 (0.69 – 0.75)	1.38 ± 0.04 (1.30 – 1.45)	1.28 ± 0.03 (1.22 – 1.33)	0.31 ± 0.03 (0.26 – 0.35)	0.12 ± 0.01 (0.10 – 0.13)	0.18 ± 0.01 (0.15 – 0.20)	0.13 ± 0.01 (0.10 – 0.15)
AZ: Kaibab Plateau (female)	22	2.06 ± 0.17 (1.74 – 2.40)	0.87 ± 0.01 (0.85 – 0.90)	0.70 ± 0.02 (0.66 – 0.75)	1.26 ± 0.06 (1.11 – 1.40)	1.21 ± 0.04 (1.14 – 1.27)	0.32 ± 0.02 (0.25 – 0.38)	0.11 ± 0.01 (0.08 – 0.14)	0.13 ± 0.02 (0.10 – 0.18)	0.10 ± 0.01 (0.07 – 0.12)
AZ: San Francisco Peaks (male)	16	2.77 ± 0.18 (2.44 – 3.01)	0.87 ± 0.02 (0.84 – 0.92)	0.72 ± 0.02 (0.68 – 0.77)	1.30 ± 0.04 (1.20 – 1.40)	1.24 ± 0.02 (1.17 – 1.27)	0.32 ± 0.03 (0.27 – 0.38)	0.14 ± 0.02 (0.10 – 0.20)	0.18 ± 0.02 (0.13 – 0.21)	0.11 ± 0.01 (0.09 – 0.14)
AZ: San Francisco Peaks (female)	40	2.32 ± 0.17 (2.06 – 2.72)	0.87 ± 0.01 (0.83 – 0.91)	0.71 ± 0.02 (0.65 – 0.80)	1.29 ± 0.04 (1.22 – 1.40)	1.22 ± 0.03 (1.17 – 1.30)	0.33 ± 0.03 (0.25 – 0.39)	0.13 ± 0.01 (0.09 – 0.17)	0.16 ± 0.02 (0.11 – 0.23)	0.12 ± 0.01 (0.08 – 0.15)
AZ: Santa Catalina Mts. (male)	6	2.47 ± 0.13 (2.33 – 2.69)	0.88 ± 0.01 (0.86 – 0.90)	0.74 ± 0.03 (0.67 – 0.76)	1.35 ± 0.04 (1.29 – 1.40)	1.26 ± 0.02 (1.23 – 1.31)	0.36 ± 0.04 (0.32 – 0.43)	0.12 ± 0.02 (0.09 – 0.15)	0.18 ± 0.02 (0.15 – 0.20)	0.13 ± 0.01 (0.12 – 0.14)
AZ: Santa Catalina Mts. (female)	17	2.22 ± 0.18 (1.89 – 2.51)	0.88 ± 0.01 (0.85 – 0.91)	0.72 ± 0.02 (0.68 – 0.76)	1.34 ± 0.06 (1.21 – 1.48)	1.26 ± 0.03 (1.20 – 1.32)	0.34 ± 0.03 (0.25 – 0.40)	0.13 ± 0.01 (0.10 – 0.16)	0.19 ± 0.02 (0.15 – 0.22)	0.13 ± 0.01 (0.10 – 0.17)
MX: Sonora, N. (male)	19	2.25 ± 0.15 (1.87 – 2.60)	0.88 ± 0.01 (0.84 – 0.91)	0.72 ± 0.01 (0.69 – 0.74)	1.34 ± 0.06 (1.21 – 1.47)	1.25 ± 0.04 (1.18 – 1.32)	0.35 ± 0.03 (0.30 – 0.41)	0.12 ± 0.02 (0.09 – 0.16)	0.17 ± 0.02 (0.14 – 0.21)	0.13 ± 0.02 (0.09 – 0.18)
MX: Sonora, N. (female)	23	2.03 ± 0.16 (1.75 – 2.46)	0.88 ± 0.01 (0.84 – 0.92)	0.72 ± 0.02 (0.67 – 0.77)	1.36 ± 0.03 (1.27 – 1.43)	1.28 ± 0.03 (1.22 – 1.33)	0.31 ± 0.03 (0.26 – 0.38)	0.13 ± 0.01 (0.10 – 0.16)	0.19 ± 0.02 (0.14 – 0.22)	0.14 ± 0. 01 (0.10 – 0.18)
NM: Animas Valley (male)	7	2.21 ± 0.23 (1.86 – 2.53)	0.88 ± 0.01 (0.86 – 0.90)	0.74 ± 0.04 (0.69 – 0.81)	1.31 ± 0.07 (1.19 – 1.40)	1.22 ± 0.05 (1.13 – 1.30)	0.34 ± 0.02 (0.30 – 0.37)	0.13 ± 0.03 (0.10 – 0.17)	0.16 ± 0.04 (0.12 – 0.23)	0.11 ± 0.02 (0.08 – 0.15)
NM: Catron Co. (female)	15	2.23 ± 0.13 (2.00 – 2.47)	0.87 ± 0.02 (0.84 – 0.90)	0.68 ± 0.02 (0.63 – 0.71)	1.29 ± 0.06 (1.17 – 1.40)	1.22 ± 0.04 (1.15 – 1.28)	0.32 ± 0.03 (0.26 – 0.40)	0.13 ± 0.03 (0.07 – 0.17)	0.16 ± 0.03 (0.10 – 0.22)	0.11 ± 0.02 (0.07 – 0.14)
NM: Grant Co. (male)	18	2.50 ± 0.23 (1.95 – 2.80)	0.88 ± 0.01 (0.86 – 0.91)	0.71 ± 0.02 (0.64 – 0.75)	1.32 ± 0.06 (1.17 – 1.43)	1.25 ± 0.04 (1.12 – 1.34)	0.29 ± 0.04 (0.21 – 0.35)	0.13 ± 0.02 (0.09 – 0.17)	0.17 ± 0.03 (0.11 – 0.23)	0.12 ± 0.01 (0.09 – 0.15)
NM: Grant Co. (female)	14	2.15 ± 0.16 (1.87 – 2.47)	0.88 ± 0.01 (0.86 – 0.91)	0.71 ± 0.02 (0.67 – 0.78)	1.35 ± 0.05 (1.26 – 1.43)	1.27 ± 0.03 (1.22 – 1.35)	0.29 ± 0.02 (0.24 – 0.33)	0.14 ± 0.02 (0.10 – 0.17)	0.18 ± 0.02 (0.15 – 0.24)	0.14 ± 0.02 (0.10 – 0.17)
NM: Sacramento Mts. (male)	13	2.29 ± 0.15 (2.08 – 2.48)	0.88 ± 0.01 (0.85 – 0.90)	0.70 ± 0.02 (0.66 – 0.73)	1.25 ± 0.04 (1.19 – 1.35)	1.21 ± 0.03 (1.13 – 1.25)	0.30 ± 0.03 (0.26 – 0.37)	0.13 ± 0.02 (0.09 – 0.16)	0.15 ± 0.03 (0.09 – 0.20)	0.10 ± 0.01 (0.08 – 0.13)
NM: Sacramento Mts. (female)	56	2.16 ± 0.18 (1.78 – 2.50)	0.88 ± 0.01 (0.85 – 0.91)	0.68 ± 0.02 (0.63 – 0.73)	1.26 ± 0.04 (1.14 – 1.38)	1.24 ± 0.03 (1.15 – 1.29)	0.28 ± 0.03 (0.22 – 0.37)	0.14 ± 0.02 (0.08 – 0.20)	0.16 ± 0.03 (0.10 – 0.25)	0.12 ± 0.01 (0.08 – 0.16)
NM: Sandia–Manzano Mts. (male)	10	2.36 ± 0.11 (2.13 – 2.48)	0.88 ± 0.02 (0.83 – 0.90)	0.72 ± 0.02 (0.69 – 0.75)	1.25 ± 0.03 (1.18 – 1.30)	1.22 ± 0.04 (1.15 – 1.31)	0.32 ± 0.02 (0.29 – 0.36)	0.14 ± 0.02 (0.08 – 0.16)	0.16 ± 0.03 (0.12 – 0.20)	0.10 ± 0.01 (0.08 – 0.13)
NM: Sandia–Manzano Mts. (female)	22	2.07 ± 0.18 (1.74 – 2.46)	0.88 ± 0.01 (0.86 – 0.90)	0.72 ± 0.02 (0.67 – 0.78)	1.26 ± 0.04 (1.16 – 1.33)	1.21 ± 0.04 (1.11 – 1.28)	0.31 ± 0.03 (0.22 – 0.37)	0.14 ± 0.02 (0.10 – 0.21)	0.17 ± 0.02 (0.13 – 0.23)	0.11 ± 0.02 (0.08 – 0.16)
P. h. ornatum										
Nevada, NE. (male)	13	2.36 ± 0.21 (1.93 – 2.71)	0.88 ± 0.01 (0.85 – 0.92)	0.74 ± 0.01 (0.72 – 0.76)	1.24 ± 0.05 (1.17 – 1.36)	1.16 ± 0.03 (1.09 – 1.21)	0.34 ± 0.03 (0.29 – 0.40)	0.11 ± 0.01 (0.09 – 0.13)	0.13 ± 0.02 (0.09 – 0.17)	0.10 ± 0.01 (0.08 – 0.12)
Nevada, NE (female)	27	2.12 ± 0.12 (1.89 – 2.35)	0.88 ± 0.02 (0.84 – 0.93)	0.73 ± 0.03 (0.67 – 0.81)	1.31 ± 0.05 (1.21 – 1.46)	1.18 ± 0.03 (1.12 – 1.27)	0.34 ± 0.02 (0.27 – 0.39)	0.12 ± 0.01 (0.09 – 0.17)	0.14 ± 0.02 (0.09 – 0.21)	0.11 ± 0.01 (0.08 – 0.14)
UT: Great Salt Lake Valley (male)	28	2.17 ± 0.17 (1.88 – 2.58)	0.87 ± 0.01 (0.83 – 0.90)	0.71 ± 0.02 (0.67 – 0.76)	1.23 ± 0.04 (1.16 – 1.28)	1.16 ± 0.03 (1.10 – 1.22)	0.35 ± 0.02 (0.31 – 0.40)	0.12 ± 0.02 (0.08 – 0.16)	0.13 ± 0.02 (0.08 – 0.16)	0.10 ± 0.01 (0.07 – 0.14)
UT: Great Salt Lake Valley (female)	44	1.92 ± 0.14 (1.61 – 2.20)	0.87 ± 0.01 (0.83 – 0.92)	0.70 ± 0.02 (0.66 – 0.74)	1.27 ± 0.04 (1.15 – 1.35)	1.19 ± 0.03 (1.11 – 1.25)	0.34 ± 0.02 (0.26 – 0.38)	0.13 ± 0.01 (0.09 – 0.17)	0.14 ± 0.02 (0.09 – 0.19)	0.11 ± 0.02 (0.09 – 0.18)
P. ornatissimum										
NM: Albuquerque (male)	23	1.95 ± 0.15 (1.67 – 2.22)	0.89 ± 0.01 (0.87 – 0.91)	0.74 ± 0.02 (0.68 – 0.80)	1.32 ± 0.04 (1.25 – 1.42)	1.23 ± 0.02 (1.16 – 1.28)	0.35 ± 0.02 (0.32 – 0.39)	0.13 ± 0.01 (0.10 – 0.16)	0.13 ± 0.01 (0.10 – 0.16)	0.10 ± 0.01 (0.07 – 0.13)
NM: Albuquerque (female)	31	1.62 ± 0.11 (1.39 – 1.81)	0.88 ± 0.01 (0.85 – 0.90)	0.73 ± 0.02 (0.67 – 0.77)	1.34 ± 0.04 (1.23 – 1.44)	1.24 ± 0.02 (1.18 – 1.30)	0.35 ± 0.02 (0.31 – 0.40)	0.13 ± 0.01 (0.09 – 0.16)	0.14 ± 0.01 (0.11 – 0.18)	0.10 ± 0.01 (0.08 – 0.15)
NM: Torrance Co. (male)	6	2.00 ± 0.14 (1.76 – 2.14)	0.88 ± 0.02 (0.85 – 0.91)	0.73 ± 0.02 (0.69 – 0.75)	1.27 ± 0.01 (1.25 – 1.29)	1.22 ± 0.02 (1.18 – 1.26)	0.36 ± 0.03 (0.33 – 0.41)	0.12 ± 0.01 (0.10 – 0.14)	0.12 ± 0.02 (0.09 – 0.15)	0.09 ± 0.01 (0.08 – 0.11)
NM: Torrance Co. (female)	17	1.64 ± 0.15 (1.33 – 1.96)	0.88 ± 0.01 (0.84 – 0.91)	0.73 ± 0.02 (0.68 – 0.77)	1.28 ± 0.04 (1.21 – 1.35)	1.21 ± 0.03 (1.10 – 1.26)	0.35 ± 0.03 (0.27 – 0.41)	0.12 ± 0.01 (0.08 – 0.15)	0.12 ± 0.01 (0.09 – 0.14)	0.09 ± 0.01 (0.07 – 0.12)
P. o. brachycercum										
MX: Chihuahua (male)	13	1.86 ± 0.25 (1.49 – 2.38)	0.88 ± 0.02 (0.84 – 0.91)	0.73 ± 0.02 (0.69 – 0.78)	1.32 ± 0.05 (1.20 – 1.39)	1.22 ± 0.04 (1.15 – 1.29)	0.36 ± 0.03 (0.31 – 0.42)	0.10 ± 0.01 (0.08 – 0.12)	0.12 ± 0.02 (0.08 – 0.16)	0.09 ± 0.01 (0.06 – 0.11)
MX: Chihuahua (female)	13	1.55 ± 0.12 (1.32 – 1.74)	0.88 ± 0.02 (0.84 – 0.91)	0.74 ± 0.03 (0.68 – 0.78)	1.33 ± 0.07 (1.22 – 1.42)	1.21 ± 0.04 (1.14 – 1.27)	0.33 ± 0.03 (0.27 – 0.39)	0.12 ± 0.01 (0.10 – 0.16)	0.13 ± 0.02 (0.07 – 0.17)	0.09 ± 0.01 (0.06 – 0.12)

TABLE 3. Selected morphometric and meristic characters for the taxa belonging to the *Phrynosoma douglasii* (species complex). Values are the mean ± two standard errors, the observed limits in parentheses, and the sample size. A different superscript letter indicates that sample means are significantly different ($P < 0.05$).

Character	*P. brevirostris*	*P. bauri* **sp. nov.**	*P. diminutum* **sp. nov.**	*P. douglasii*	*P. hernandesi*	*P. h. ornatum*	*P. ornatissimum*	*P. o. brachycercum*
ENR	42.9 ± 0.96^{a} (34.9–50) n = 44	44.3 ± 0.99^{a} (38.4–50) n = 31	45 ± 1.87^{a} (38.8–50) n = 16	44.6 ± 1.04^{a} (36.6–49) n = 33	49.4 ± 1.56^{b} (42.5–57.3) n = 31	45.3 ± 1.62^{a} (39.2–54.2) n = 27	43.8 ± 1.39^{a} (35.2–50) n = 29	45.4 ± 2.15^{a} (40.8–50) n = 10
FRS (L)	1.14 ± 0.12^{a} (1–2) n = 35	2.84 ± 0.23^{b,e} (1–4) n = 43	1.63 ± 0.23^{c} (0–3) n = 35	0.66 ± 0.21^{d} (0–2) n = 59	2.96 ± 0.15^{b,e} (2–4) n = 31	1.64 ± 0.28^{c} (0–3) n = 44	3.20 ± 0.16^{b} (2–4) n = 34	2.75 ± 0.22^{e} (2–3) n = 16
FRS (R)	1.14 ± 0.12^{a} (1–2) n = 35	2.65 ± 0.25^{b,e} (1–4) n = 43	1.60 ± 0.22^{c} (0–3) n = 35	0.73 ± 0.20^{d} (0–2) n = 59	2.93 ± 0.13^{b,e} (2–4) n = 31	1.77 ± 0.29^{c} (0–3) n = 44	3.21 ± 0.21^{b} (2–4) n = 33	2.82 ± 0.26^{b} (2–4) n = 17
TRE (male)	12.9 ± 0.67^{a} (5.4–17.8) n = 62	16.8 ± 0.90^{b} (11.1–24.2) n = 45	10.1 ± 0.95^{c} (7.1–13) n = 12	7.4 ± 0.86^{d} (2–19.5) n = 71	25.7 ± 0.96^{e} (18.9–32.3) n = 48	17.3 ± 0.83^{b} (13.2–22.6) n = 35	22.9 ± 0.98^{f} (16.7–28.4) n = 30	20.9 ± 2.31^{f} (15.1–26.8) n = 13
TRE (female)	16.4 ± 0.64^{a} (9.5–25.4) n = 96	18.1 ± 0.82^{b} (12.9–23) n = 42	11.7 ± 0.99^{c} (6.2–15.8) n = 23	10.3 ± 0.66^{c} (1.9–17.5) n = 93	26.1 ± 0.79^{d} (17.2–36.2) n = 107	19.8 ± 0.73^{e} (11.8–27) n = 71	23.1 ± 0.68^{f} (17.9–30) n = 58	22.6 ± 1.39^{f} (14.7–32) n = 31
TH	10.3 ± 0.48^{a} (6.6–16.7) n = 71	13.7 ± 0.38^{b} (8–18.5) n = 87	10.4 ± 0.57^{a} (6.7–13.5) n = 35	8.0 ± 0.13^{c} (4.6–10.6) n = 268	18.2 ± 0.46^{d} (10.3–24.1) n = 129	13.9 ± 0.38^{b} (8.8–21) n = 136	13.9 ± 0.41^{b} (10.5–16.7) n = 56	12.7 ± 0.72^{b} (7.3–18.2) n = 44
TL (male)	220 ± 4.81^{a} (176–276) n = 62	226 ± 6.20^{a} (169–279) n = 49	215 ± 11.04^{a} (180–238) n = 12	214 ± 5.36^{a} (158–255) n = 52	247 ± 8.87^{b} (187–301) n = 46	222 ± 6.41^{a} (188–271) n = 41	193 ± 4.51^{c} (139–224) n = 57	189 ± 14.47^{c} (149–238) n = 14
TL (female)	190 ± 3.48^{a} (155–230) n = 95	199 ± 4.47^{b} (158–235) n = 47	179 ± 4.94^{c} (159–209) n = 24	167 ± 4.14^{d} (123–225) n = 91	219 ± 4.84^{e} (175–272) n = 76	199 ± 3.66^{b} (161–235) n = 81	160 ± 3.16^{d} (118–196) n = 79	153 ± 5.50^{d} (117–193) n = 33

Univariate comparisons reveal that among the members of the *P. douglasii* species complex, there are statistically significant differences for some meristic and morphometric characters, as noted above in several cases. The quantitative characters found to be taxonomically informative and useful are summarized in Table 3. Some quantitative characters also show possible clinal patterns of variation or differ significantly between local population samples within taxa. See **Variation** under **Taxonomic accounts** for further information. A description of general patterns across taxa based on univariate comparisons follows.

Snout length (ENR, external naris to rostral scale distance) is significantly greater in *Phrynosoma hernandesi* than in the other members of the species complex. This species typically has a protruding snout and its rostrofrontal profile is more or less flat and gradually sloping. *P. brevirostris* and *P. ornatissimum*, in contrast, have a short snout and the rostrofrontal profile is more or less rounded or angular with a steep incline. The number of enlarged frontal rim scales (FRS) shows significant divergence across taxa. The lowest mean values for this character are noted in *P. douglasii* and *P. brevirostris*. The highest mean values are noted in *P. bauri* **sp. nov.**, *P. h. hernandesi*, *P. o. ornatissimum*, and *P. o. brachycercum.* Mean values falling between these two groups are noted in *P. diminutum* **sp. nov.** and *P. h. ornatum.* The high number of enlarged frontal rim scales is correlated with the development of an elevated frontal rim especially as observed in *P. h. hernandesi*, *P. o. ornatissimum*, and *P. o. brachycercum*. Conversely, taxa in which the frontal rim is absent or weakly elevated have a low number of enlarged frontal rim scales, e.g. *P. brevirostris* and *P. douglasii.* The temporal shelf (TRE) is most extensive in *P. h. hernandesi* and somewhat less developed in *P. o. ornatissimum* and *P. o. brachycercum.* The taxa with small body size, e.g. *P. brevirostris*, *P. diminutum* **sp. nov.** and *P. douglasii* have a short, rather more convex or rounded temporal shelf. Taxa with a more or less intermediate development of the temporal shelf include *P. bauri* **sp. nov.** and *P. h. ornatum*. The third temporal horn (TH) is longest in *P. h. hernandesi* and shortest in *P. douglasii*. The other taxa have mean values falling more or less in between these two extremes. Taxa with mean values somewhat less than *P. h. hernandesi* include *P. bauri* **sp. nov.,** *P. h. ornatum*, *P. o. ornatissimum* and *P. o. brachycercum*. Those with values somewhat greater than *P. douglasii* include *P. brevirostris* and *P. diminutum* **sp. nov.** Relative length of the third temporal horn is correlated with the length of the other cephalic horns, e.g. occipital and superciliary horns. Also, in taxa with short temporal horns, there is a tendency for the horns to project upward, especially in *P. douglasii*. Tail length (TL) is greatest in *P. h. hernandesi* and shortest in *P. o. ornatissimum* and *P. o. brachycercum*. The remaining taxa have mean values falling in between these extremes, but most are closer to *P. h. hernandesi* than to the short-tailed *P. ornatissimum.* Possible clinal patterns in proportional tail length are noted across some populations of *P. h. hernandesi* and *P. douglasii* and are described under the appropriate taxonomic account.

Selected color pattern characters of taxonomic importance are summarized in Table 4, and as indicated in the foregoing discussions are diagnostic for some comparisons. The ventral surfaces of the short-horned lizard taxa show differences in melanin pigmentation patterns that are useful for diagnostic purposes. Unfortunately, these pattern characters are not evident in specimens preserved in the "light phase", when the melanin is strongly aggregated. Specimens preserved in the "dark phase" or some intermediate stage between "light" and "dark" phases, however, provided useful information for describing diagnostic pattern differences.

Phrynosoma ornatissimum and *P. o. brachycercum* uniquely share a gular pattern of chevrons or wavy transverse bands. At intermediate stages between the "light" and "dark" phases, the pattern is usually fragmented into small spots or short lines, but the chevron pattern is usually still evident from these remnants. *P. douglasii* has a pale gray to charcoal suffusion over the gular surfaces. At intermediate stages of melanin dispersion, there may be only scattered flecks of melanin in the gular area. In *P. brevirostris*, the typical pattern consists of small, rounded spots scattered over the gular surfaces. Less commonly, there may be vermiculations with or without gray suffusion. The taxa *P. bauri* **sp. nov.,** *P. diminutum* **sp. nov.**, *P. h. hernandesi* and *P. h. ornatum* usually have vermiculations, relatively few spots, and varying amounts of gray suffusion.

The melanin pattern of the abdominal area displays differences among the short-horned lizard taxa. *P. brevirostris*, *P. ornatissimum* and *P. o. brachycercum* have scattered flecks and patches of melanin pigment during the "dark" phase; there are no well defined spots. *P. douglasii* has a pale gray suffusion, with some scattered flecks over the abdominal surfaces. The remaining taxa, including *P. h. hernandesi*, most *P. h. ornatum*, *P. bauri* **sp. nov.**, and *P. diminutum* **sp. nov.**, have melanistic spots, usually arranged more or less in transverse rows. In some specimens of *P. h. hernandesi* and *P. h. ornatum*, the spots are irregular in form and produce a "mottled" pattern. In some *P. h. ornatum* the abdomen has sparsely scattered or densely scattered flecks. In some specimens of *P. diminutum* **sp. nov.** and *P. h. hernandesi* the entire undersurface is suffused with dark gray or black pigment. Dark suffusion has not been noted in *P. h. ornatum.*

TABLE 4. Selected color and pattern characters for the taxa belonging to the *Phrynosoma douglasii* species complex. See text for additional information concerning color pattern variation within and among taxa.

Character	**Gular pattern**	**Abdominal pattern**	**Subcaudal bands**	**Dorsolateral white spots**	**Margins of dorsal spots**
P. brevirostris	scattered spots, ± suffusion ± vermiculations	scattered gray flecks & patches, no spots	absent	absent	posterior pale margin
P. bauri **sp. nov.**	scattered spots, vermiculations	melanistic spots	± interrupted bands distally	present	posterior pale margin
P. diminutum **sp. nov.**	scattered spots, &/or vermiculations	melanistic spots, or dark suffusion	± interrupted bands distally	± scattered white dots and flecks	posterior pale margin
P. douglasii	gray suffusion, or flecks	gray suffusion, flecks	absent	absent	posterior pale margin
P. hernandesi	vermiculations, spots ± gray suffusion	melanistic spots, or dark suffusion	interrupted &/or complete bands	absent	posterior pale margin
P. h. ornatum	vermiculations, spots ± gray suffusion	melanistic spots ± gray suffusion, or gray flecks	interrupted &/or complete bands	absent	posterior pale margin
P. ornatissimum	chevrons or wavy bands	scattered flecks, gray patches	absent	present	medial & posterior pale margins
P. o. brachycercum	chevrons or wavy bands	scattered flecks, gray patches	absent	generally absent, present in few	posterior pale margin

The subcaudal surfaces show differences in pigment patterns among the taxa. In *P. brevirostris*, *P. douglasii*, *P. ornatissimum* and *P. o. brachycercum* the underside of the tail is immaculate and lacks any pattern. In *P. h. hernandesi* and *P. h. ornatum*, the subcaudal surfaces have interrupted bands on the proximal portion of the tail and interrupted or complete bands near the distal end. In *P. bauri* **sp. nov.** and *P. diminutum* **sp. nov.** the subcaudal pattern is variable; interrupted bands may or may not be present distally on the tail.

The presence or absence of dorsolateral white spots is another taxonomically useful character. In the nominotypical *P. ornatissimum* and *P. bauri* **sp. nov.** the dorsolateral surfaces of the body have conspicuous white, rounded spots. The other taxa lack these spots, although they are present in some specimens of *P. o. brachycercum*. Specimens of *P. diminutum* **sp. nov.**, especially populations occurring on sandy soils, may have numerous small white dots and flecks scattered over the dorsolateral surfaces.

The dark dorsal spots typically have light-colored borders in all short-horned lizard taxa. In nominotypical *P. ornatissimum*, the borders are white and/or yellow, narrow and discrete, and extend along the posterior and medial edges of the dorsal spots; the medial border is unique to this species. All other taxa have light colored borders along the posterior edges of the dorsal spots. The color of the light borders is variable in *P. h. hernandesi*, including white, yellow, orange-yellow, red, and coral pink. The remaining taxa typically have white or yellow borders.

Relationships and taxonomic status of Phrynosoma ornatum

Stejneger (1919) held the opinion that *ornatum* bears no close relationship to *P. hernandesi*, but is sufficiently distinct to be regarded as a subspecies of the typical *P. douglasii*. He reached this conclusion after examining a series of specimens collected by Herbert J. Pack near the western limits of Salt Lake City. Richardson (1915:424), after comparing five specimens collected from Deeth, Elko County, Nevada, with samples of *P. douglasii* from Oregon and *P. hernandesi* from Arizona and New Mexico, considered the Nevada specimens to be nearly intermediate between the two taxa. However, in view of their larger size and longer head spines, Richardson thought they more closely resembled the "southern form", i.e. *P. hernandesi*. Reeve (1952:932) stated that *ornatum* is "intermediate" between *hernandesi* and *douglasii*, but that it is more closely related to the former taxon than the latter. Presumably its "intermediate" position was based on what Reeve perceived to be a "more moderate development of the temporal area and spines".

Morphological evidence supports the hypothesis that *ornatum* is of hybrid origin, with one parent clearly being *P. hernandesi*. Traits from this parental species include red pigmentation on the temporal and occipital horns, which extends onto the temporal shelf in some specimens, a red border above the lateral fringe row, large melanistic spots on the abdomen and partial or complete subcaudal bands during the melanin-dispersed phase.

Reeve (1952) explicitly implicated *douglasii* (the Pacific Northwest subspecies according to his taxonomy) as the other parent in the origin of *ornatum*. This seems improbable as body size differences between *P. douglasii* and *P. hernandesi* would likely preclude successful matings. More likely, interspecific hybridization in the past involved male *P. hernandesi* with female *P. brevirostris* because *P. brevirostris* is a larger species that potentially could mate with *P . hernandesi*. Males of *P. hernandesi* reach sexual maturity at about 60 mm snout-vent, an appropriate body size for sexually mature female *P. brevirostris*.

Evidence from comparative morphology supports the idea that *P. brevirostris* was involved in the origin of *ornatum*. The general morphology of the head and associated lepidosis of *ornatum* agrees more closely with that of *P. brevirostris* than with that of *P. douglasii*. The frontal rim is virtually lacking in *P. douglasii* but in some specimens of *P. brevirostris* and *ornatum* it is weakly developed and slightly elevated above the occipital shelf. The temporal shelf is flat to slightly convex in both *P. brevirostris* and *ornatum*, but it is convex to strongly rounded in *P. douglasii*. The surfaces of the cephalic scales have numerous granulations in *P. brevirostris*, *P. hernandesi* and *ornatum*. In contrast, the scale surfaces in *P. douglasii* have rugosities formed by narrow, irregular ridges, with few, if any, granulations.

The average number of enlarged frontal rim scales in *ornatum* is more or less intermediate between that of *P. hernandesi* and *P. brevirostris* (Table 3). Also, *ornatum* displays greater variability than either of the putative parental taxa for this character. The coefficients of variation are: *P. brevirostris* (23.58% and 34.61%) for two samples from Niobrara County, Wyoming; *P. hernandesi* (12.99% and 19.73%) for Arizona and New Mexico samples respectively, and *ornatum* (49.64% and 52.97%) for Nevada and Utah samples respectively. The taxon *ornatum* also displays considerable morphological variability in lepidosis within local populations. Some specimens have a bristly appearance with longer and more numerous dorsal spinous scales, whereas others have fewer, shorter spines on the dorsum. The difference in appearance is easily detectable, especially by comparing the length of the lateral fringe row spines. Also, the rostrofrontal profile varies from nearly flat and gradually sloping to more rounded or angular.

The color pattern of the abdomen is polymorphic in the taxon *ornatum*. Some specimens have large melanistic spots and these may be interconnected to form a mottled pattern. In other specimens, the central abdomen is devoid of spots and instead, it has gray flecks, and spots occur only laterally. In relatively few specimens, the abdomen is completely devoid of spots and there are scattered gray flecks which may be sparsely or densely scattered. Sixtyone adult specimens in the melanin-dispersed phase were scored for abdominal color pattern. Forty-seven lizards (77%) had large melanistic spots (as in *P. h. hernandesi*); in seven specimens (11.5%) the spots were more or less confined to the lateral areas of the abdomen and the central area had gray flecks or was unmarked; in six lizards (ca. 10%), the abdomen had scattered gray flecks (as in *P. brevirostris*), with one specimen being very densely flecked, and another nearly immaculate.

The variability in morphology and color pattern noted in *ornatum* seems indicative of the postulated mixed ancestry of this form. It is generally accepted that introgressive hybridization is an important source of genetic variability for adaptive evolution. The past hybridization and introgression suspected between *P. hernandesi* and *P. brevirostris* appears to have enhanced the adaptive potential of *ornatum*, resulting in a genotype capable of tolerating the more thermally extreme and arid conditions of the Bonneville Basin as compared with the more moderate montane environment of the Wasatch Range inhabited by *P. hernandesi.* Furthermore, as an introgressant and stabilized form, *ornatum* appears to have a broad ecological tolerance, with locally adapted populations occupying a range of habitats throughout the Great Basin region (see **Distribution and habitat** for this taxon).

The taxonomic status of *ornatum* seems problematic because of this taxon's generally intermediate morphology. The morphological characters distinguishing *ornatum* from *P. hernandesi* are statistically significant and overlapping. But the two taxa show mutual non-overlap ranging between 81% and 92.5% for the characters TRE, TH, and FRS (see discussion above). The geographic distribution of *ornatum* is large, encompassing thousands of kilometers. Evidence of intergradation with *P. hernandesi* is limited due to a dearth of specimens from the western slopes of the Wasatch Range, but there is little doubt that the two forms exchange genes. Hence, recognizing *ornatum* as a subspecies of *P. hernandesi*, while acknowledging that it is a stabilized entity of probable hybrid origin, seems to be the best course of action.

Molecular vs. morphological data

Zamudio *et al.* (1997) analyzed mitochondrial DNA sequence data to determine species limits in the *Phrynosoma douglasii* species complex, which at that time was recognized as a single, polytypic species according to Reeve's (1952) taxonomy. The authors obtained sequence data from 64 individuals representing 38 localities from throughout the western United States. However, their study lacked sample representation for the Mexican taxon *brachycercum* and the short-horned lizards endemic to the San Luis Valley of Colorado and New Mexico.

Their phylogenetic analyses were performed using aligned sequences for all gene regions combined (a total of 783 base pairs). Two methods of phylogenetic reconstruction were used—maximum likelihood and parsimony, in combination with various weighting schemes. The following phylogenetic trees were presented: two maximum likelihood trees, one with all codon positions equally weighted and transition:transversion weighting of 1:5, and another weighted by codon position (figs. 4a & 4b in Zamudio *et al.* 1997); two alternative maximum likelihood trees with transition:transversion weighting of 1:10 (figs. 5a & 5b in Zamudio *et al.* 1997); two strict consensus trees, a consensus of 10 most parsimonious trees with equal weighting of all substitutions, and another consensus of 18 most parsimonious trees with codon position weighting (figs. 6a & 6b in Zamudio *et al.* 1997); two strict consensus trees, a consensus of 10 most parsimonious trees with 1:5 transition:transversion weighting, and another consensus of five most parsimonious trees with 1:10 transition:transversion weighting (figs. 7a & 7b in Zamudio *et al*. 1997).

The topologies of these phylogenetic trees differed slightly, but all trees revealed a division of the short-horned lizard populations into three major clades: 1) a Pacific Northwest group (PNW) which the authors recognized as a distinct species and applied the name *P. douglasi* [sic]; 2) a Great Basin-Colorado Plateau group (GB/CP), and 3) a group from south and east of the Rocky Mountains (SER). The name *P. hernandezi* [sic] was applied to the latter two groups. The molecular analysis also supported a close relationship between *Phrynosoma ditmarsi* Stejneger and *P. hernandesi*. However, the precise placement of *P. ditmarsi* was ambiguous; it was either the sister species of *P. hernandesi* or nested within *P. hernandesi*. The maximum likelihood tree with all codon positions weighted equally and transition:transversion weighting of 1:5 was presented as the preferred hypothesis for the short-horned lizard species complex (figs. 4a & 9 in Zamudio *et al.* 1997). The subspecific taxonomy of Reeve (1952) was superimposed on the preferred phylogeny, revealing considerable discordance between the two studies, the only exception being the PNW clade which in Reeve's (1952) taxonomic work was recognized as a separate subspecies.

Zamudio *et al.* (1997) used mtDNA sequence data in a tree-based approach to delimit species. Although the authors stated that the species *P. ditmarsi*, *P. douglasii* and *P. hernandesi* were all morphologically distinct, there was no attempt to include detailed morphological data, especially pertaining to *P. hernandesi*. Their analysis essentially rested on mtDNA sequence data alone. An obvious difficulty in their analysis was determining the hierarchical level of divergence at which species should be recognized. Their analytical results revealed that the GB/CP and SER clades within *P. hernandesi* were separated by a relatively deep divergence, but they did not distinguish the two clades from one another taxonomically. They acknowledged that their proposed taxonomic arrangement was conservative, recognizing only "basal and well-supported" clades. But the GB/CP and SER clades were well-supported, being resolved in every separate analysis. Other workers might have interpreted the two clades within their taxon *P. hernandesi* as divergence at the species level. Hence the taxonomic decision of Zamudio *et al.* (1997) seemed both subjective and arbitrary.

The relatively deep divergence between the GB/CP clade and the SER clade in *Phrynosoma hernandesi* is discordant with the results of my morphological analysis. There is no morphological evidence for a division within this taxon concordant with the two geographical regions represented by these clades. Instead, my analyses reveal several morphologically distinct species subsumed under their concept of *Phrynosoma hernandesi.* Zamudio *et al.* (1997, fig. 9) classified the mtDNA haplotype lineages (numbers 10 to 43) as *Phrynosoma hernandesi*. In my proposed taxonomy, these lineages are classified as follows: lineage 40 (*P. bauri* **sp. nov.**); lineages 26, 36 to 39, 41 to 43 (*P. brevirostris*), and lineage 35 (*P. ornatissimum*). The classification of lineage 28 (Otero County, New Mexico) and lineage 31 (Sandoval County, New Mexico) are uncertain; the voucher specimens and tissue collection records could not be found. However, they could represent *P. hernandesi*, *P. ornatissimum*, or interspecific hybrids. Lineage 34 (McKinley County, New Mexico) is *P. hernandesi*, or possibly a hybrid involving *P. ornatissimum*. The linkage of lineage 40 (Weld County, Colorado) with lineage 28 (Otero County, New Mexico) and as part of the GB/CP clade is incongruous with respect to both morphological and zoogeographic evidence. The remaining lineages (10 to 25, 27, 29, 30, 32, 33) are classified by my taxonomy as *Phrynosoma hernandesi* which is consistent with the classification of Zamudio *et al.* (1997), although lineages 10 and 11 are treated subspecifically as *P. h. ornatum*.

My morphological analysis and the molecular study of Zamudio *et al.* (1997) agree on the recognition of *Phrynosoma douglasii* as a distinct species. Also, the haplotype lineages (numbers 26, 36 to 39, 41 to 43) which represent *P. brevirostris* according to my taxonomy, comprise a discernible monophyletic clade, although nested as a shallow divergence within the larger group classified as *P. hernandesi* by Zamudio *et al.* (1997). The geographic range of this clade, as shown in fig. 8 of Zamudio *et al.* (1997) is largely coincident with my concept of the distribution of *P. brevirostris* (see my Fig. 6). The voucher specimen (RRM 2341) from which a tissue sample was taken for lineage 26 is illustrated in my Fig. 10A. It is noteworthy and quite evident on the basis of morphology that this is a specimen of *P. brevirostris*, not *P. hernandesi* (compare Fig. 10A with Fig. 22). In the preferred phylogeny, haplotype lineages 10 (Utah) and 11 (Nevada) of *P. h. ornatum* (my taxonomy) are linked together as the sister group to a nested clade comprising *P. hernandesi* from several localities in the Wasatch Range, Utah. This relationship is interpretable, suggesting the exchange of cytoplasmic genes between the two taxa which seems probable because the sampled localities of *P. hernandesi* in Utah are proximate to the eastern range limit of *P. h. ornatum.*

Several additional aspects of the topology of the preferred phylogeny are troubling. The phylogeny portrays the clade for *Phrynosoma douglasii* as basal to the remainder of the species complex, including *Phrynosoma ditmarsi* which is an enigmatic, morphologically divergent species and arguably not a member of the complex. There are no unambiguous morphological synapomorphies linking *P. ditmarsi* to the short-horned lizard species complex (Montanucci, 1987; Reeder & Montanucci, 2001), but see Hodges & Zamudio (2004) and Leaché & McGuire (2006) for mitochondrial and nuclear gene evidence. The topology of the preferred phylogeny renders the species complex paraphyletic with respect to *P. ditmarsi*. The basal position of *P. douglasii* seems quite improbable for several reasons: 1) *P. douglasii* occurs at the northern extreme of the geographic range of the complex and distant from the center of diversity for the species complex and the genus as a whole; 2) *P. douglasii* has a preponderance of apparently derived character states including small body size, greatly reduced cephalic horns, a truncated rostrofrontal profile, and a short, convex or rounded temporal shelf, and 3) *P. hernandesi* shares apparently plesiomorphic character states with *Phrynosoma orbiculare* (Linnaeus). The latter taxon is currently treated as a single, polytypic species (Horowitz, 1955; Montanucci, 1979); it is an out-group taxon with respect to the *Phrynosoma douglasii* species complex and is basal to both *P. hernandesi* and *P. douglasii* (Hodges & Zamudio, 2004; Leaché & McGuire, 2006). Character states shared between *P. hernandesi* and *P. orbiculare* include relatively long cephalic horns, an elevated frontal rim with enlarged frontal rim scales, a gradually sloping rostrofrontal profile, a relatively long tail, large melanistic spots on the abdomen with yellow, orange, or red pigment on the abdominal and gular surfaces, and complete and/or interrupted melanistic subcaudal bands. The character states shared with this out-group taxon suggest that *P. hernandesi* is probably the basal member of the *Phrynosoma douglasii* species complex.

FIGURE 6. Geographical distribution of the *Phrynosoma douglasii* (species complex) based on this study. The color-coded distributions of the taxa are: *Phrynosoma bauri* **sp. nov.** (brown); *P. brevirostris* (pink); *P. diminutum* **sp. nov.** (red); *P. douglasii* (blue); *P. hernandesi* (dark green); *P. h. ornatum* (light green); *P. ornatissimum* (orange), and *P. o. brachycercum* (purple). Hybrid zone on the Colorado Plateau indicated by hatched area; other hybrid zones not shown. Question marks indicate uncertain occurrences and range limits.

The discordance between my taxonomic arrangement and that of Zamudio *et al.* (1997) is difficult to explain, but could be due to differences in analytical methods, as well as the underlying characteristics of mitochondrial and nuclear genes. A tree-based approach to species delimitation using DNA sequence data requires determining the hierarchical level of divergence at which species should be recognized. As indicated in the foregoing discussion, this approach is clearly more subjective and less rigorous than species delimitation based on discrete character differences. In terms of the genes themselves, the morphological characters of organisms are determined by nuclear genes which differ from mitochondrial genes in several important ways including inheritance and rates of gene flow. Mitochondrial DNA is functionally haploid and uniparentally (female) inherited as a unit. Multilocus nuclear genes can segregate independently and are additive in nature. Also, in animal populations, the rates of cytoplasmic gene flow can differ from rates of nuclear gene flow (see Harrison 1993 and references therein), potentially resulting in discordant patterns of relationship. Nuclear genes in the genus *Phrynosoma* may number upwards of 20,000; this is a reasonable estimate based on the prediction of 22,962 protein-coding genes in *Anolis* obtained from a *de novo* assembly of deep transcriptomes (see Eckalbar *et al.* 2013). The study by Zamudio *et al.* (1997) was limited only to mtDNA sequence data, but the inclusion of nuclear gene data from multiple loci in a separate analysis may have produced a different topology and resolved additional taxa.

The exclusive use of mtDNA data to infer interspecific phylogeny has come into question. Leaché (2009) revealed discordance between mitochondrial and nuclear gene data in the phrynosomatid lizard genus *Sceloporus*. The incongruities pertained not only to weak or unresolved nodes, but also to strongly supported clades in his separate analyses. He argued for estimating species trees based on multilocus nuclear gene data, stating that the additive nature of independently segregating nuclear markers is superior, and that tapping into the nuclear genome to assemble data sets containing hundreds of independent markers offered greater potential to resolve difficult relationships than to simply continue to sequence "the remaining genes of the mtDNA locus". An increasing number of recent phylogenetic studies have found discordance between mitochondrial genes and nuclear genes, and have cautioned against the use of mtDNA sequence data for making inferences about phylogeny and speciation, recommending instead, the use of large numbers of unlinked nuclear genes for such analyses (Wiens *et al.* 2010, and references therein).

Taxonomic accounts

Each of the following taxonomic accounts includes a synonymy of the taxon name, the etymology of the taxon name, the taxonomic history including type specimen and type locality designations, a diagnosis, comparisons, description, distribution and habitat, and a remarks section summarizing problems, avenues for further research, and miscellaneous comments. Mensural and meristic characters used for diagnoses and descriptions include the mean ± two standard errors of the mean and observed limits in parentheses. A slash mark indicates counts taken from left/right respectively. Due to the early history of confusion associated with the originally proposed species and their geographic distributions, the list of synonyms is abbreviated, including only those synonymous names that can be referred with confidence to a given species. Synonyms are drawn primarily from publications of a taxonomic nature; sources such as state faunal works and ecological studies are not included.

Information on distribution is based primarily on locality records for examined specimens and literature records where the taxon can be identified with confidence. Latitude and longitude coordinates are provided for some localities that are difficult to find or that are historical settlements no longer in existence. Habitat data are drawn from several sources including information on specimen tags, literature records with habitat descriptions, and direct observations made at collection sites. Habitat associations for each short-horned lizard taxon were determined by superimposing known locality records over the potential natural vegetation map of the conterminous United States that accompanies the manual by Küchler (1964, 1975). The potential natural vegetation of an area is assumed to be that which prevails in the absence of disturbance or climatic change. Environmental factors such as topography, soil, and climate are determinants of the climax vegetation. However, at many localities the climax vegetation has been significantly altered by various anthropogenic factors including agricultural practices, over-grazing, fire, invasive exotic plant species (e.g. *Bromus tectorum*), and other disturbances. As the existing cover type may differ significantly from the potential natural vegetation (i.e. climax vegetation), the habitats described in the following accounts may be largely historical descriptions for many regions.

***Phrynosoma brevirostris* Girard 1858a**

(Figs. 7–8, 9C, 10)

Phrynosoma (Tapaya) brevirostris Girard 1858a:397.
Phrynosoma brevirostre Cope 1866:302.
Phrynosoma douglassi Gentry 1885:140 (part).
Phrynosoma douglassii hernandesi Cope 1900:413 (part).
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377(part).
Phrynosoma douglassii brevirostre Smith 1946:302.

Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii brevirostre Reeve 1952:913.
Phrynosoma douglassii hernandesi Reeve 1952:922 (part).
Phrynosoma douglassii ornatum Reeve 1952:930 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

FIGURE 7. Lectotype of *Phrynosoma* (*Tapaya*) *brevirostris* Girard (USNM 4592c) showing the typical dorsal pattern for this taxon.

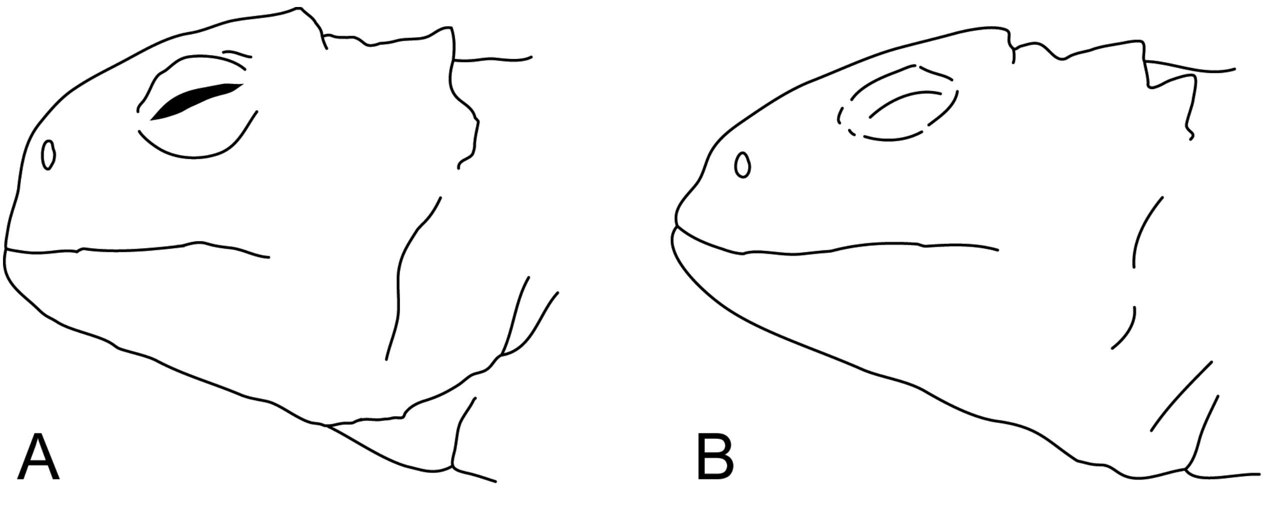

FIGURE 8. Rostrofrontal profile of *Phrynosoma brevirostris.* (A) Typical profile (UCM 13684, Montrose Co., Colorado); (B) Atypical profile (USNM 48122, Fremont Co., Wyoming).

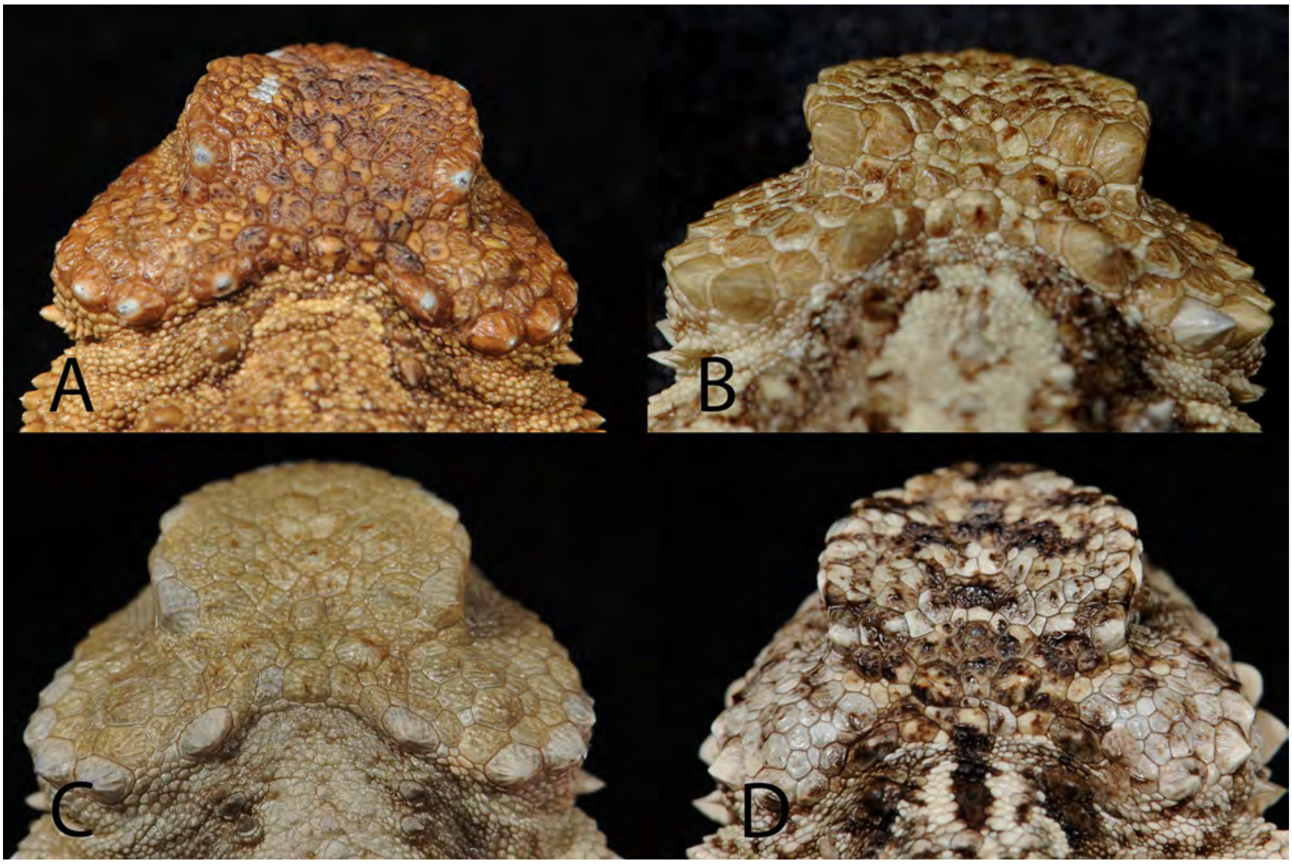

FIGURE 9. Posterodorsal aspect of head to show frontal rim morphology of (A) *Phrynosoma diminutum* sp. nov. (UMMZ 62252, Rio Grande Co., Colorado); (B) *Phrynosoma bauri* **sp. nov.** (RRM 2112, Weld Co., Colorado); (C) *Phrynosoma brevirostris* (MCZ 161058, Niobrara Co., Wyoming); (D) *Phrynosoma douglasii* (UMMZ 174250, Lake Co., Oregon).

Etymology. The specific epithet *brevirostris* comes from the Latin adjective *brevis,-e*, meaning "short", and a modified version of the second declension Latin neuter noun *rostrum*, meaning "snout", in reference to the short or abbreviated snout of this species. Apparently, Girard's (1858a) intent was to create a compound noun in apposition to the subgeneric name *Tapaya* (see Smith & Reeve, 1951 for origin of the name), crafting his new name in third declension feminine gender since *Tapaya* is apparently feminine. Although Girard's root word *rostris* does not exist in Latin, Cope (1866:302) modified Girard's name to *brevirostre* as though it were an adjective needing to agree with the neuter gender of *Phrynosoma*. However, since nouns used in apposition to other nouns retain their own gender (only adjectives must agree in gender with the name of the genus), Cope's alteration of the name was an unnecessary and incorrect subsequent spelling. Therefore, I retain Girard's original spelling for the available name. See ICZN articles 31.2.1. and 34.2.1.

Suggested common name: Great Plains Short-horned Lizard.

Type locality. Restricted to 9.6 km E of Agate, Sioux County, Nebraska. See below for explanation.

Taxonomic history. Girard (1858a) described this species from specimens in the U.S. National Museum (now called the National Museum of Natural History), but he did not designate the type material. In the museum's ledger, an underlined and capitalized annotation in red pencil indicates that USNM 208 is the "TYPE" of *Tapaya brevirostris*. Also, however, the word "cotypes" is written in pencil in the catalog entry for a series of nine specimens of this species under USNM 4592. Burt (1927) in a note on the type locality of this species published part of a letter from Doris Cochran which stated that USNM 208 is the type specimen. Cochran's letter made no reference to the series under USNM 4592. Reeve (1952:913) recognized USNM 208 as the type specimen on the basis of the ledger information, but he was evidently unaware of the specimens listed as cotypes in the ledger under USNM 4592. Cochran (1961), apparently having no recollection of her 1927 letter to Burt or his published note, and unaware of Reeve's (1952) observation, listed both USNM 208 and USNM 4592 (9 specimens) as "cotypes". Since usage of the words "type" and "cotype" can be considered equivalent to "syntype" (International Code of

Zoological Nomenclature 1999, Art. 73.2.1) and the word "type" is ambiguous with respect to "holotype," I believe a formal designation is necessary to remove any ambiguity.

Reeve's recognition of USNM 208 as the type is not unequivocal as he apparently did not examine it and was unaware of the series under USNM 4592. If Reeve had examined USNM 208 he would have almost certainly noted and commented on the presence of dorsolateral white spots. The white-spotted pattern is diagnostic for a morphologically distinctive group of populations that merits taxonomic recognition (see next account). I consider USNM 208 to be a specimen of the new taxon or a possible hybrid between it and *P. brevirostris*. The syntypes under USNM 4592 lack dorsolateral white spots and therefore conform to Girard's original description. In order to clarify the concept of *P. brevirostris* and set it apart from the new taxon, I designate USNM 4592c as the lectotype of *Tapaya brevirostris* as it closely agrees with Girard's original description (Fig. 7). I also designate the remaining eight specimens under USNM 4592 and USNM 208 as paralectotypes. According to ledger records, USNM 208 was collected at Pole Creek, Nebraska, by W. Wood (original field number 161) on July 26, 1856. The specimen was catalogued in December of 1857. The series under USNM 4592 was also collected by Wood (original field numbers 412–420) at the same locality in 1857. The series was catalogued on July 7, 1859, but apparently the specimens were studied by Girard prior to being cataloged.

Reeve (1952:913) emended the name of the type locality (Pole Creek) in accordance with its current geographic name, Lodgepole Creek, and restricted the type locality to near Dix, Kimball County, Nebraska. Subsequently, Cochran (1961) listed the type locality as it was originally entered in the ledger, and erroneously named S. W. Woodhouse as the collector of the type material. Reeve's restriction of the type locality is problematic because specimens from near Dix, as well as all other known localities along Lodgepole Creek, have conspicuous dorsolateral white spots. As indicated above, Girard's (1858a) original description of *P. brevirostris* makes no mention of dorsolateral white spots. The type locality should be restricted to a geographic site where specimens conform to Girard's original description of *P. brevirostris*. Populations occurring north of the North Platte River in western Nebraska are characterized by the absence of dorsolateral white spots. I therefore restrict the type locality to 9.6 km E of Agate, Sioux County, Nebraska, based on the occurrence of typical specimens (e.g. UMMZ 79610).

Diagnosis. *Phrynosoma brevirostris* can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout short, 42.9% ± 0.96 (34.9–50%) of orbit to rostral scale distance; (2) rostrofrontal profile more or less rounded or angular with a steep incline; (3) frontal rim not elevated, or only slightly elevated above the occipital shelf; (4) enlarged frontal rim scales 1.14 ± 0.12 (1–2) / 1.14 ± 0.12 (1–2); (5) temporal shelf short, 12.9% ± 0.67 (5.4–17.8%) in males, 16.4% ± 0.64 (9.5–25.4%) in females; (6) temporal shelf weakly to moderately convex; (7) cephalic horns short, third temporal horn length 10.3% ± 0.48 (6.6–16.7%); (8) cephalic horns slightly elevated to nearly vertical; (9) tympanum elliptic, narrow to moderately broad; (10) tympanum exposed; (11) tail moderately long, 220% ± 4.81 (176–276%) in males, 190% ± 3.48 (155–230%) in females; (12) dorsal spots small, wedge-shaped to slightly rounded; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots absent; (15) gular area with scattered melanistic spots, with or without vermiculations and with or without gray suffusion (melanin-dispersed phase); (16) abdomen with scattered melanistic flecks and patches, no melanistic spots (melanin-dispersed phase); (17) melanistic subcaudal bands absent (melanin-dispersed phase).

Comparisons. *Phrynosoma brevirostris* is distinguished from *P. h. hernandesi* by a rounded or angular and steeply inclined rostrofrontal profile, a frontal rim not elevated or only slightly elevated above the occipital shelf, fewer enlarged frontal rim scales, a shorter temporal shelf, and shorter occipital and temporal horns that are directed slightly upward to nearly vertical in the majority of specimens. It is further distinguished from *P. h. hernandesi* and some *P. h. ornatum* by the absence of large, melanistic spots on the abdomen and the absence of complete or interrupted melanistic subcaudal bands in the melanin-dispersed phase. *P. brevirostris* is distinguished from nominotypical *P. ornatissimum* by its frontal rim which is not elevated, or only slightly elevated above the occipital shelf, fewer enlarged frontal rim scales, a relatively longer tail, small wedge-shaped dorsal spots, absence of a discrete yellow and/or white line along the medial border of each dorsal spot (except *P. o. brachycercum*), and a gular pattern of scattered spots and short vermiculations with or without gray suffusion (melanin-dispersed phase). *P. brevirostris* can be distinguished from *P. douglasii* by its slightly longer occipital and temporal horns, a slightly longer temporal shelf that is nearly flat rather than convex and strongly rounded, a slightly broader elliptic and exposed tympanum. It is further distinguished from *P. douglasii* by a gular pattern of dark spots and/or vermiculations. Comparisons with *P. bauri* **sp. nov.** and *P. diminutum* **sp. nov.** are given in their respective accounts.

In the Colorado Plateau region of Utah, where *P. brevirostris* may occur in proximity to *P. h. hernandesi*, the two taxa may be distinguished by the usual presence of red pigment on the temporal shelf and horns as well as red pigment above the lateral fringe scales of the latter species.

Description. This account is based on the examination of specimens from the Upper Colorado River Basin of Utah, northwestern Colorado, northwestern Nebraska, Wyoming, South Dakota, North Dakota, Montana, and the Canadian provinces of Alberta and Saskatchewan (n = 262; see Appendix I).

Head depressed, broader than long; snout short, but somewhat protruding in some specimens; rostrofrontal profile more or less rounded or angular with a steep incline (Fig. 8); frontal area nearly flat; dorsal surface of the head covered with small, irregular, convex scales with rugosities formed by granulations and/or irregular ridges; frontal rim not elevated or only slightly elevated above occipital shelf (Fig. 9C); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf expanded posteriorly, weakly to moderately convex, but nearly flattened in ca.17% of sample; usually three small, subconical temporal horns, most posterior (third) largest, 10.3% (6.6–16.7%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one short occipital horn on each side, usually separated from temporal horn by one or two scales; supralabials small; three posterior infralabials slightly enlarged, continuous with usually three enlarged postlabials, 3.01 (2–4); postrictal spine 8.6% (5.6–14.1%) of head length; chinshields slightly enlarged, separated from infralabials usually by two or three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper row larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, ephemeral, with or without enlarged scales posteriorly; tympanum elliptic, narrow to slightly broad; tympanum exposed, but slight encroachment of granular scales in a few specimens; anterior margin of ear opening lacking enlarged scales, or with a variable number of slightly enlarged rounded or dentate-like scales; dorsal scales heterogeneous, but generally small, not overlapping; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 220% (176–276%) of head length in 62 males, 190% (155–230%) in 95 females; maximum snout-vent length = 83 mm.

Head uniform brown; a pair of dark brown nuchal blotches with indistinct borders; four (range three to five) pairs of dark brown dorsal spots between neck and sacral area; anterior edges of dorsal spots grade into dorsal field; posterior edges of spots smoothly even or denticulate, well defined by a white or yellow border, light-colored posterior border fragmented into spots or absent in some specimens; dorsal tail base with several pairs of spots, these merging as transverse bands distally; concealed surfaces of lips white, yellow, or yellow-orange; gular area and abdomen white, but in the melanin-dispersed phase the gular area has spots with or without vermiculations and with or without gray suffusion; chest and abdomen with sparsely scattered flecks or patches of melanistic suffusion; ventral tail unmarked (Fig. 10).

Variation. The occipital and temporal horns (third temporal horn) project at an angle above the horizontal to nearly vertical in the majority of specimens. In a sample of 21 specimens from the Canadian provinces, all have the occipital and temporal horns projecting upward, with nine specimens (42.8%) showing nearly vertical orientation. In 36 specimens from Montana, 31 specimens (86.1%) have upward directed occipital and temporal horns; three specimens (8.3%) have upright occipital horns, but the temporal horns are horizontally directed, and in two specimens (5.5%) both sets of horns are directed horizontally. In 83 specimens from Wyoming, 74 individuals (89.2%) have upward directed occipital and temporal horns; in six specimens (7.2%) the occipital horns are directed upward, but the temporal horns are directed horizontally; in three specimens (3.6%) both sets of horns are directed horizontally. In 28 specimens from northwestern Nebraska, 25 individuals (89.3%) have upward directed occipital and temporal horns; in three specimens (10.7%), the occipital horns are slanted upward, but the temporal horns are oriented horizontally. In 64 specimens from the Green and Upper Colorado River basins of Utah, 48 individuals (75.0%) have upward directed occipital and temporal horns; six specimens (9.3%) have upward directed occipital horns, but the temporal horns are horizontally directed, and in ten specimens (15.6%), both sets of horns are horizontally directed.

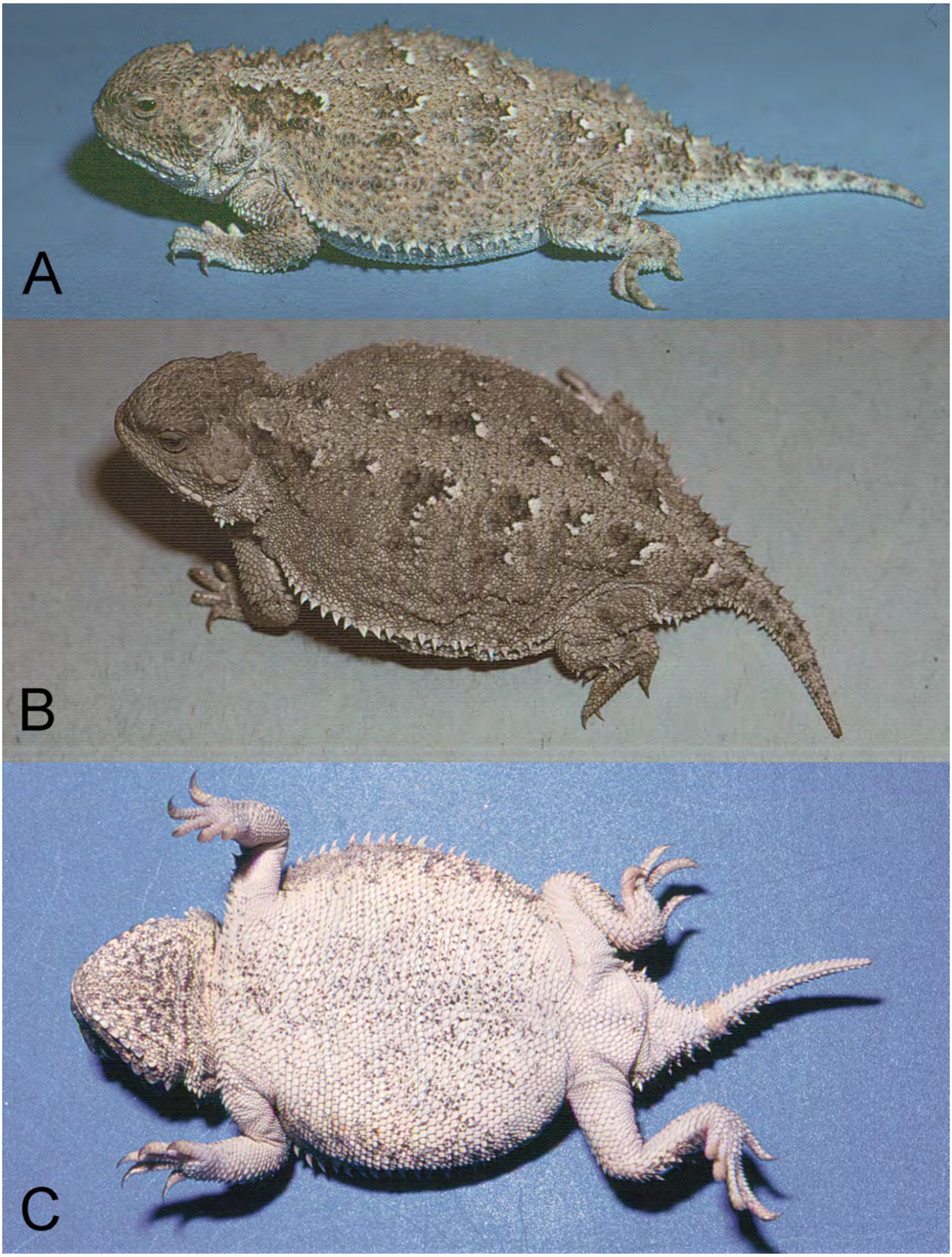

FIGURE 10. *Phrynosoma brevirostris*. (A) Adult male (RRM 2341) from Thompson, Grand Co., Utah. (B) Dorsal aspect of female from Nemiskam, Alberta, Canada. (C) Ventral aspect showing scattered gray flecks of female (RRM 3309) from Hailstone NWR, Stillwater Co., Montana.

The color of the dorsal field varies from pale gray to tan or yellowish brown to reddish brown depending on the prevailing color of the substrate. In dark brown or pale gray specimens, the nuchal blotches and dorsal spots tend to be dark charcoal in color. Posterior edges of nuchal blotches may be defined by a few white spots. Some specimens with a tan, yellowish brown, or reddish brown dorsum may have faint orange, peach or reddish pigmentation above the lateral fold, especially near the forelimb. In some areas of Utah east of the Wasatch Plateau, reddish specimens may be found on pink sandy soils. Reddish specimens also occur on similarly colored substrate near Warren, Carbon County, Montana. In northwestern Nebraska, specimens are typically yellowish tan, and the dorsal spots maybe faint. Reeve (1952) described the head as brownish gray with a few black flecks in the frontal area, but he did not indicate the geographic provenance of his specimens. I have noted yellowish flecks on the frontal area and other parts of the head in some specimens. In 71 specimens from Wyoming, six specimens (8.4%) from localities in Converse and Natrona counties have yellowish flecks. Also, among 28 specimens from Nebraska, six specimens (21.4%) from Dawes and Sioux counties have yellowish flecks.

In 225 specimens (90.7%), the dorsal spots are wedge-shaped; in 19 specimens (7.6 %) the spots are squarish or slightly rounded; four specimens (1.6%) have transverse bands. Variation in the shape of the dorsal spots does not show any geographically correlated pattern.

In 123 specimens preserved in the melanin-dispersed phase, 47 specimens (38.2%) have a gular pattern comprised of spots and short vermiculations, 41 specimens (33.6%) have scattered spots only, 17 examples (13.8%) have scattered spots within pale gray suffusion, 11 specimens (8.9%) have a pale gray suffusion without spots, and three specimens (2.4%) have only vermiculations. Twenty two specimens of the total also have melanin deposits in the abdominal area; in 19 specimens these appear as pale, scattered patches and in three specimens as flecks sparsely scattered about the center of the abdomen. On the chest area, twelve of the 22 specimens have patches of suffusion, and four specimens have sparse flecks. Immediately below the lateral fringe scale row, and often hidden by the folds of the epidermis, there are brown spots and short, irregular bars. These markings appear to be constant and little influenced by the phases of melanin aggregation and dispersion.

P. brevirostris was apparently derived from an ancestral stock similar to *P. hernandesi*, retaining the relatively long tail of its ancestor, but evolving a smaller body size, a shorter, more rounded rostrofrontal profile, a reduced temporal shelf, shorter cephalic horns, a reduced frontal rim with fewer enlarged frontal rim scales, and losing the large melanistic spots on the abdomen and melanistic subcaudal bands.

Distribution and habitat. *Phrynosoma brevirostris* ranges from northwestern Colorado southwestward into the Upper Colorado River Basin of Utah, and from northwestern Nebraska northward through extreme western portions of the Dakotas, and through Wyoming and Montana to the southern extreme of the Canadian provinces of Alberta and Saskatchewan (see Appendix II, maps 1, 2, 9, 11, 12, 15, 17, 19, 21).

In this geographic region, *P. brevirostris* is found in sagebrush and short-grass communities as well as open-canopied conifer savanna at higher elevations. Baxter & Stone (1985) reported it equally common in the short grass plains of eastern Wyoming and the sagebrush steppe of the central and southern parts of the state. In the western foothills of the Black Hills region of Wyoming, Peterson (1974) reported this species from 4.8 km SE Moskee, Crook County, in open conifer forest at 1,768 m (5,800 ft) elevation. In the Uintah Basin of Utah, Knowlton & Janes (1934) reported it in greasewood habitat (i.e. *Atriplex-Sarcobatus* association) near Ouray. I found it in the same habitat near Thompson, Utah. Werner *et al.* (2004) summarized its occurrence in Montana as east of the Continental Divide, principally on the plains, but with some records entering the mountain foothills along the upper headwaters of the Missouri River. Maxell *et al.* (2003) provided museum numbers by county and indicated that the range of the species is poorly documented in Montana. The authors reported the highest elevation record as 1,981 m (6,500 ft) from 5.2 km SE of Red Pryor Mountain, Carbon County, Montana. In western North Dakota, Wheeler & Wheeler (1966) stated that the species is found in rough terrain on the short-grass plains. In Nebraska, it is found in the uplands of the far-western Panhandle region, avoiding the Platte River Valley (*fide* Lynch, 1985; see also Ballinger *et al*., 2010). In Canada, Powell & Russell (1998) concluded that the species has a discontinuous, relictual distribution in southeastern Alberta and southwestern Saskatchewan where it occurs in mixed grass prairie. Populations appear to be confined to south-facing slopes, in grassland-badlands ecotone and Bearpaw shale outcrops.

In most regions, essential characteristics of the habitat include open, sparsely vegetated, sunlit areas at ground level, sandy or rocky soils, and rodent burrows providing easy access to underground retreats (Hammerson, 1999). I observed this species in association with prairie dog colonies near Price, Carbon County, Utah.

In Alberta, the climax vegetation in the eastern part of the Milk River Valley is mixed grass prairie association, the dominant fasciation being *Stipa-Bouteloua*, but the drier area south of Cypress Hills is dominated by *Bouteloua-Stipa* which also characterizes the localities in Saskatchewan (Powell & Russell, 1998).

In extreme northwestern Nebraska *P. brevirostris* is found on the plains and bluffs bordering the tributaries of the Niobrara and White rivers. The dominant, climax fasciations in this region include *Bouteloa-Buchloë* to the south of, and *Agropyron-Stipa* to the north of, the Pine Ridge, and *Bouteloua-Stipa-Agropyron* to the west. In South Dokota, *P. brevirostris* has been recorded from the western plains dominated by *Agropyron-Stipa*. In North Dakota, the species is restricted to the far western part of the state in the heavily dissected Badlands region through which the upper reaches of the Little Missouri River and its tributaries flow. The natural dominant climax vegetation here is exclusively *Agropyron-Stipa.* A more complex pattern of associations emerges in Wyoming. In eastern Wyoming, localities in the High Plains drained by the Belle Fourche and Cheyenne rivers are dominated by *Agropyron-Stipa*. Immediately to the west on the plains surrounding the north-flowing Powder River and the east-flowing North Platte River (east of Casper), the dominant, climax fasciation shifts to *Bouteloua-Stipa-Agropyron*. In north-central Wyoming, *P. brevirostris* occurs in *Agropyron-Stipa-Artemisia* shrubsteppe on the plains surrounding the Big Horn River, but this association is replaced by *Atriplex-Sarcobatus* along the lower segment of that river system; the Greybull River enters the Big Horn River near the center of this saltbush-greasewood community. In south-central and southwestern Wyoming, nearly all records for *P. brevirostris* are in sagebrush steppe (*Artemisia-Agropyron*). There are no records for *P. brevirostris* in the mountainous northwestern part of the state which is dominated by Douglas fir forest (*Pseudotsuga*) and by Western spruce-fir forest (*Picea-Abies*) at higher elevations. Similarly, records are absent from these needle-leaf forests in the Big Horn Mountains in north-central Wyoming and the Medicine Bow Mountains in the south, a range dominated by (*Pinus-Pseudotsuga*). In Montana, localities for *P. brevirostris* in the extreme eastern plains are dominated by Wheatgrass-needlegrass (*Agropyron-Stipa*) climax association, but in most of the central and northern plains region the climax vegetation is Grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*). In Gallatin County, *P. brevirostris* enters the foothills of the Rockies along the upper headwaters of the Missouri River; the climax vegetation at these localities is Foothills prairie (*Agropyron-Festuca-Stipa*).

Remarks. Koch & Peterson (1995) discuss the possible occurrence of *P. brevirostris* in Yellowstone National Park and refer to a record of a juvenile specimen taken near the park's West Entrance in 1954. I have examined this specimen (MVZ 72271); it appears to be *P. brevirostris*, but this determination is tentative. The authors also refer to an old record in the National Museum of Natural History (USNM 9458) from the Upper Firehole Basin. My examination of the USNM specimen reveals that it is *P. douglasii*, not *P. brevirostris* (see *P. douglasii* account for further comments). Baxter & Stone (1985) mention a record from 25 km south of Grand Teton National Park in the upper reaches of the Snake River drainage system. The specimen, which is from Hoback Canyon (ca. 17.9 km S of Jackson), is *P. brevirostris*. Johnson (2007) reported *P. douglasii* from Lincoln County in southwestern Wyoming. The specimen (YPM 10176) is a road-killed neonate. I cannot confirm that it is *P. douglasii* for it shares several characters with *P. brevirostris*. I provisionally regard it as the latter species, as all other records from the western and southwestern portions of the state (Lincoln, Sweetwater, Teton, Uinta counties) are *P. brevirostris*, including a specimen (USNM 48686) from north of Evanston along the Bear River. This drainage system provides a corridor of suitable habitat (sagebrush steppe) into adjacent southeastern Idaho and northern Utah. Van Denburgh (1922:380) lists the Bear River near Logan as a locality, but I was not able to find voucher specimens. However, a series of specimens (USNM 5321, 293322–24) collected by C. McCarthy from Box Elder Creek Canyon, Box Elder County, Utah, are *P. brevirostris*. Assuming these specimens are correctly catalogued, the record places *P. brevirostris* geographically proximate to both *P. douglasii* (Snowville, Utah), and *P. h. ornatum* (near Salt Lake City). Another record (CAS 228879) from Dry Canyon, along the lower western slope of the Bear River Range, Cache County, Utah, appears to be *P. h. ornatum*, or an intergrade with the nominotypical race. A mixed taxonomic series was collected by C. McCarthy in northern Utah, but precise locality data are lacking. In this series, USNM 4927 appears to be *P. brevirostris*, but it has large melanistic spots on the abdomen and a gular pattern of transverse lines, suggesting genetic influence from *P. h. ornatum*. USNM 293291–95, 293297 are *P. brevirostris*. USNM 293290 and 293296 are *P. douglasii*, and USNM 293289 is *P. h. ornatum* or an intergrade with the nominate race. Obviously, field surveys are needed in northern Utah and adjacent Idaho and Wyoming to determine the distribution limits and habitat relationships of *P. brevirostris*, *P. douglasii* and *P. h. ornatum*.

The distribution and habitat relationships of *P. brevirostris* and *P. hernandesi* in western Colorado merit further study. It appears, based on the limited voucher records, that *P. brevirostris* extends eastward through the Grand Valley into the Gunnison River Valley; it enters the Dolores River Valley and presumably also the adjacent Paradox Valley. Specimens morphologically similar to *P. hernandesi* have been collected from the intervening high elevation areas such as the Pinon Mesa and Uncompahgre Plateau. In the Big Gypsum Creek Valley and adjacent areas of San Miguel County, *P. hernandesi*, hybrids similar to *P. hernandesi* (and presumably involving *P. ornatissimum*), and *P. brevirostris* appear to occur in proximity to one another. The taxonomic assignment of populations in this area remains to be resolved.

Two extralimital records in Nebraska warrant mention. Both are of doubtful validity as they lie considerably east of the known range limits for the species. One specimen (MCZ 5951) is listed from the "Platte Valley" in Buffalo County; the other, a juvenile (40 mm SVL) is listed from Axtell, Kearney County (UNSM 6662).

Bryce Maxell (personal communication) reported *P. brevirostris* from just northwest of Butte, Montana, on reclaimed land near a former mining site. The population is prossibly introduced as the area lies well within the Rocky Mountains, beyond the westernmost known localities.

***Phrynosoma bauri* sp. nov.**

(Figs. 9B, 11–13)

Phrynosoma douglassi Gentry 1885:140 (part).
Phrynosoma douglassii hernandesi Cope 1900:413 (part).
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377(part).
Phrynosoma douglassii brevirostre Smith 1946:302 (part).
Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii brevirostre Reeve 1952:913 (part).
Phrynosoma douglassii ornatissimum Reeve 1952:927 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

Holotype. UCM 11356, adult male, collected from 12.8 km north of Orchard, Morgan County, Colorado, by V. Janzen on 10 May 1958 (Fig. 11).

Paratopotypes. UCM 11358–59, both males, collected by V. Janzen on 10 May 1958.

Etymology. The subspecific epithet *bauri* is a Latin patronym in the genitive singular, honoring the late Bertrand E. Baur, a longtime friend and avid student of *Phrynosoma*.

Suggested common name. Baur's Short-horned Lizard.

Type locality. The type locality is 12.8 km north of Orchard, Morgan County, Colorado.

Taxonomic history. As indicated under the account for *Phrynosoma brevirostris*, Reeve (1952:913) restricted the type locality of *P. douglassii brevirostre* [sic] to near Dix (in the vicinity of Lodgepole Creek), Kimball County, Nebraska. However, specimens from that locality do not conform to Girard's description of *P. brevirostris*, but represent *P. bauri* **sp. nov.**, as described herein. This also suggests that Girard's type material was probably not collected near Lodgepole Creek. Smith (1946) and Reeve (1952) recognized the populations of this taxon occurring in Nebraska and northeastern Colorado as *P. douglassii brevirostre* [sic], whereas those from southeastern Colorado and northeastern New Mexico the authors treated as *P. douglassii ornatissimum* [sic]. Maslin (1959), in his annotated check list of the amphibians and reptiles of Colorado, classified the short-horned lizards from the plains of eastern Colorado as *Phrynosoma douglassi brevirostre* [sic]. Hammerson's (1999) field guide to the herpetofauna of Colorado treated all populations in the state as *P. hernandesi*, following Zamudio *et al*. (1997).

Diagnosis. *Phrynosoma bauri* **sp. nov.** can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout short, 44.3% ± 0.99 (38.5–50%) of orbit to rostral scale distance; (2) rostrofrontal profile rounded or angular with a steep incline; (3) frontal rim usually elevated above the occipital shelf; (4) enlarged frontal rim scales 2.84 ± 0.23 (1–4)/ 2.65 ± 0.25 (1–4); (5) temporal shelf moderately short, 16.8% ± 0.90 (11.1–24.2%) in males, 18.1% ± 0.82 (12.9–23.0%) in females; (6) temporal shelf weakly to moderately convex; (7) cephalic horns moderately short, third temporal horn length 13.7% ± 0.38 (8.0–18.5%); (8) cephalic horns usually directed upward, ca. 45° to nearly vertical; (9) tympanum elliptic, moderately broad; (10) tympanum exposed; (11) tail moderately long, 226% ± 6.20 (169–279%) in males, 199% ± 4.47 (158–235%) in females; (12) dorsal spots small, wedge-shaped to slightly rounded; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots present; (15) gular area with scattered melanistic spots and vermiculations (melanin-dispersed phase); (16) abdomen with large melanistic spots (melanin-dispersed phase); (17) interrupted melanistic subcaudal bands absent or present distally, barely entering ventral surface (melanin-dispersed phase).

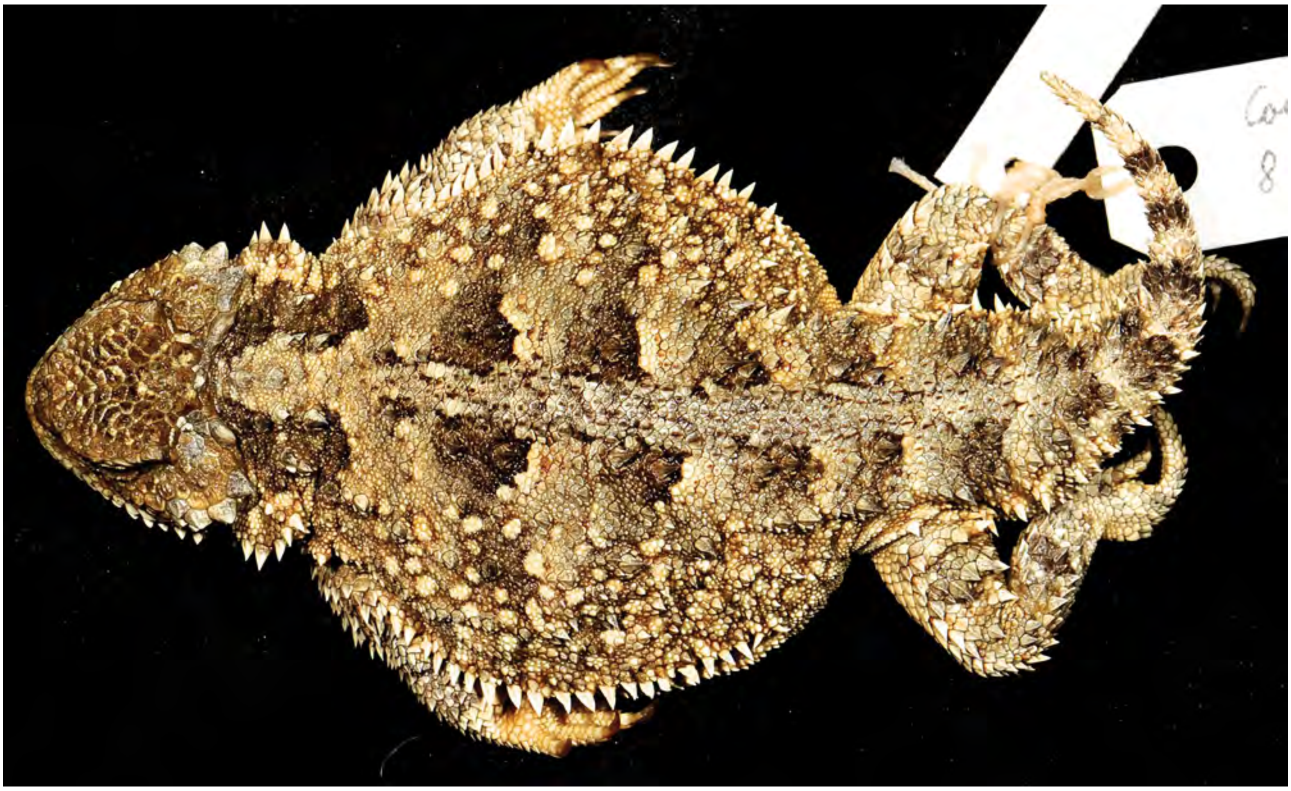

FIGURE 11. Holotype of *Phrynosoma bauri* **sp. nov.,** adult male from 12.8 km N of Orchard, Morgan Co., Colorado (UCM 11356).

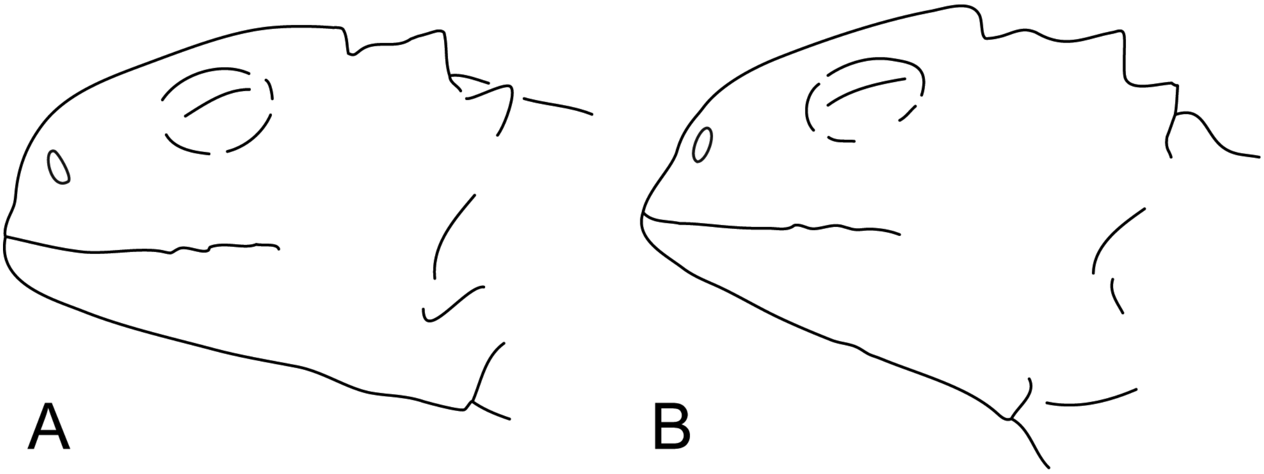

FIGURE 12. Rostrofrontal profile of *Phrynosoma bauri* **sp. nov.** (A) Typical profile (RRM 2470, Weld Co., Colorado); (B) Atypical profile (UNSM 1205, Kimball Co., Nebraska).

Comparisons. *P. bauri* **sp. nov.** differs discretely from *P. brevirostris* in having conspicuous white, rounded, dorsolateral spots. It also differs discretely from *P. brevirostris* in having rows of large, melanistic spots on the abdomen during the melanin-dispersed phase. By contrast, the abdominal pattern in *P. brevirostris* consists of scattered gray flecks and patches, or a coalesced, but pale gray suffusion. In *P. bauri* **sp. nov.** the nuchal blotches have a well defined yellowish-white, yellow or orange-yellow line bordering the medial and posterior edges. In *P.*

brevirostris, the nuchal blotches usually lack a light-colored border, but if present, it is white, poorly defined, and abbreviated. In *P. bauri* **sp. nov.** the frontal rim is typically well defined and elevated above the occipital shelf. In *P. brevirostris* the frontal rim is weakly defined and not elevated or only slightly elevated above the occipital shelf. *P. bauri* **sp. nov.** also has a significantly higher number of enlarged frontal rim scales, a longer temporal shelf, and a longer third temporal horn compared with *P. brevirostris*. The tail length (as a percentage of head length) does not differ significantly between male samples of the two taxa, but the tail is significantly longer in *P. bauri* **sp. nov.** females (Table 3). Comparisons with *P. diminutum* **sp. nov.** are discussed in the next account.

Phrynosoma bauri **sp. nov.** is distinguished from *P. h. hernandesi* by a shorter snout, a rounded or angular and steeply inclined rostrofrontal profile, a shorter temporal shelf (except *P. h. ornatum*), and shorter temporal horns (except *P. h. ornatum*), that are directed upward to nearly vertical. It is further distinguished from *P. h. hernandesi* and *P. h. ornatum* by the presence of dorsolateral white spots, and from *P. h. ornatum* by having a more elevated frontal rim and a higher number of enlarged frontal rim scales. *P. bauri* **sp. nov.** can be distinguished from *P. o. ornatissimum* and *P. o. brachycercum* by a relatively longer tail, small, wedge-shaped to slightly rounded dorsal spots (except *P. o. brachycercum*), absence of a discrete yellow and/or white line along the medial border of each dorsal spot (except *P. o. brachycercum*), a gular pattern of spots and short vermiculations with or without gray suffusion and black spots on the abdomen (melanin-dispersed phase). *P. bauri* **sp. nov.** can be distinguished from *P. douglasii* by its longer temporal shelf that is weakly to moderately convex (rather than strongly convex or rounded), an elevated frontal rim, longer occipital and temporal horns, a somewhat broader elliptic and exposed tympanum. It is further distinguished from *P. douglasii* by the presence of dorsolateral white spots, a gular pattern of dark spots and/or vermiculations rather than a gray suffusion only, and black spots on the abdomen (melanin-dispersed phase).

Description. This account is based on the examination of specimens from southeastern Wyoming, southwestern Nebraska, eastern Colorado, and northeastern New Mexico (n = 121; see Appendix I).

Head depressed, broader than long; snout short, but somewhat protruding in some specimens; rostrofrontal profile rounded or angular with a steep incline (Fig. 12); frontal area nearly flat; dorsal surfaces of the head covered with small, convex scales with rugosities formed by irregular ridges and granulations; frontal rim typically elevated above the occipital shelf (Fig. 9B); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf moderately short, expanded, weakly to moderately convex; usually three small, subconical temporal horns, most posterior (third) largest, 13.7% (8.0–18.5%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one short occipital horn on each side, usually separated from temporal horn by one or two scales; supralabials small; three posterior infralabials slightly enlarged, continuous with three to four enlarged postlabials, 3.47 (3–4); postrictal spine 10.5% (8.0–13.6%) of head length; chinshields slightly enlarged, separated from infralabials usually by two or three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper row larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, ephemeral, with or without enlarged scales posteriorly; tympanum elliptic, broad, and exposed; anterior margin of ear opening with a variable number of slightly to moderately enlarged dentate-like scales; dorsal scales heterogeneous, but generally small, not overlapping; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 226% (169–279%) of head length in 49 males, 199% (158–235%) in 47 females; maximum snout-vent length = 89 mm.

Head brown with scattered white flecks and/or lines outlining the dorsal head scales; a pair of dark brown nuchal blotches with medial and/or posterior borders defined by a discrete yellow and/or white line; four (range three to five) pairs of small wedge-shaped to slightly rounded dark brown dorsal spots between neck and sacral area; anterior edges of dorsal spots grade into dorsal field, posterior edges smoothly even or denticulate and defined by a discrete yellow or yellowish white border; border fragmented as dots in some specimens; dorsal tail base with one or more pairs of spots, these becoming transverse bars distally; large white spots scattered over dorsolateral areas of body, invading the vertebral area in some specimens; in the melanin-dispersed phase, gular area with melanistic spots, short lines and vermiculations; abdomen white with irregular rows of large melanistic spots (Fig. 13). Some specimens have patches and flecks of melanin on the central abdomen, but it is not known if the specimens are fully in the melanin-dispersed phase, or in a transitional state that would eventually lead to abdominal spots.

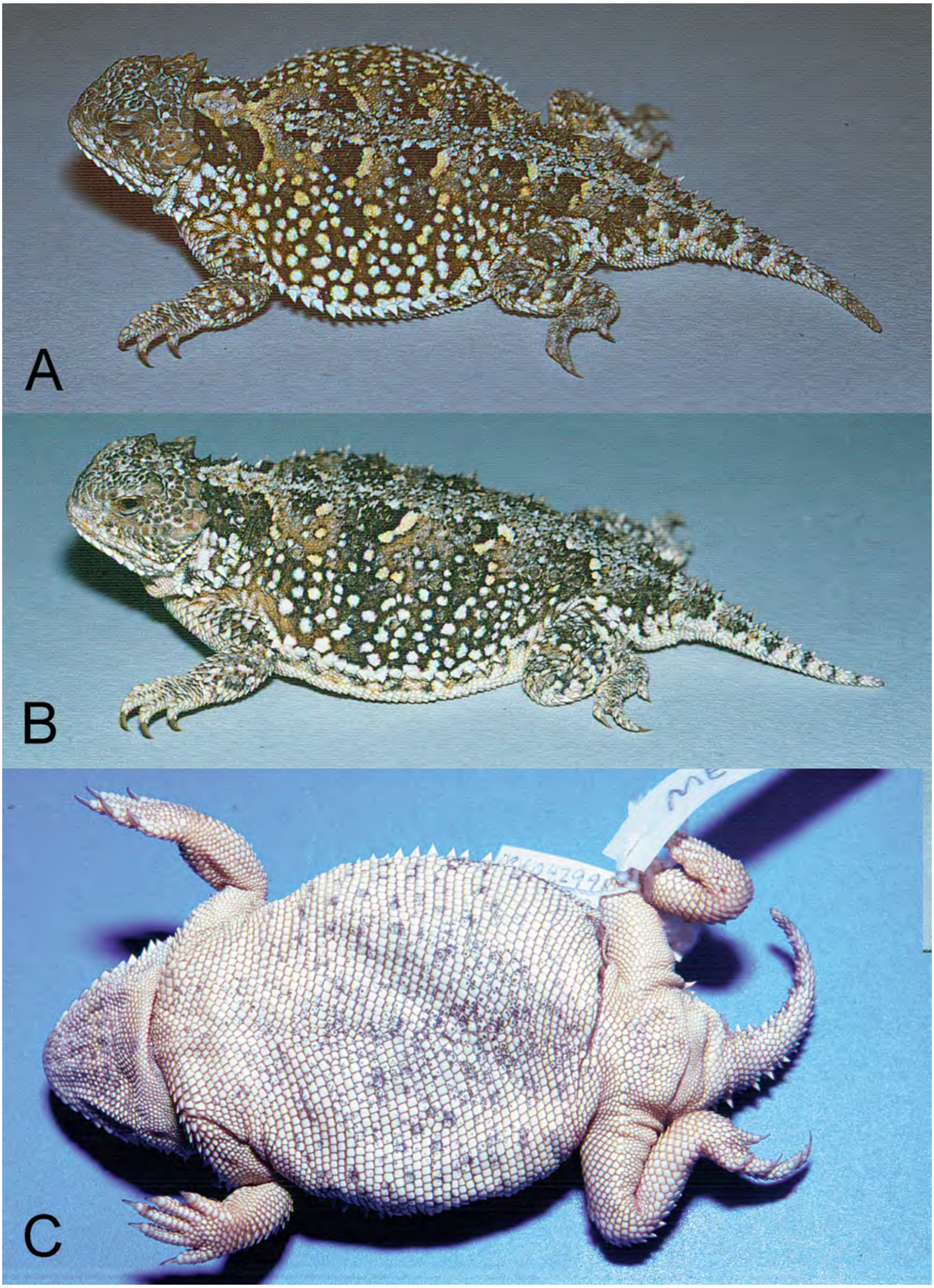

FIGURE 13. *Phrynosoma bauri* **sp. nov.** (A) Adult male (RRM 2204) and (B) adult female (RRM 2112) from 12.8 km N, 8 km E of Nunn, Weld Co., Colorado. (C) Female (MEL 1007) from 14.9 km NW Limon, Elbert Co., Colorado, ventral aspect showing rows of melanistic spots.

Description of holotype. Adult male, snout-vent length 70 mm, tail length 38 mm. Snout length 13.0 mm, head length 14.3 mm, rostral to temporal shelf distance 17.0 mm, frontal width 11.4 mm, head width 18.4 mm, interoccipital distance 5.7 mm, right occipital horn length 1.9 mm, right third temporal horn length 2.1 mm, left superciliary spine length 1.5 mm, right postrictal spine length 1.5 mm. Occipital horns directed upward at an angle slightly less than 45°; last (third) temporal horn directed slightly upward; rostrofrontal profile rounded; frontal rim elevated above occipital shelf; enlarged frontal rim scales 4/4; three occipital tubercles, the median flanked by two slightly larger tubercles; four postlabials, the most posterior largest, nearly touching postrictal spine; four dentate auricular scales on right side, uppermost smallest; lateral fringe scales 23 on left, 19 on right.

Color pattern of holotype in preservative. Dorsal surfaces of head, body, limbs, and tail pale brown. Frontal scales with a few whitish flecks. Nuchal blotches dark brown with traces of white borders along the posterior edges. Four pairs of more or less wedge-shaped, dark brown dorsal spots, one pair of band-like spots on sacrum; dorsal spots with white borders along the posterior edges; paired spots near and on sacral area with indistinct white borders. Tail with pairs of dark brown spots connected medially, forming crossbands distally on tail; about six pairs of spots and cross-bands on tail, each with faint white posterior borders. Dorsolateral areas of body with scattered large, white spots. Forelimbs pale gray-brown with a few whitish spots; hind limbs gray-brown with slightly darker brown bands on dorsal thigh and shank. Gular area and abdomen with traces of melanistic spots; subcaudal surfaces immaculate.

Variation. Variation was studied in 96 specimens from eastern Colorado. The dorsal spots are small and vary from wedge-shaped in 75 specimens (78%) to slightly round in 19 specimens (19.8%). White flecks or lines outlining the head scales are present in 45 specimens (46.8%) of the sample. The occipital and temporal horns are directed upward (ca. 45°) to nearly vertical in 85 specimens (88.5%), and of these, 13 specimens (13.5%) have occipital and temporal horns directed vertically or nearly so. An additional ten specimens (10.4%) have occipital horns directed upward, but the temporal horns are directed horizontally. One unusual specimen has horizontally directed occipital horns and vertically oriented temporal horns. No clinal patterns of variation have been detected within the range of this taxon.

Phrynosoma bauri **sp. nov.** may have arisen through ancient hybridization between *P. brevirostris* and *P. ornatissimum*. If so, the populations have stabilized through natural selection for there is considerable homogeneity throughout the range of this taxon. Like *P. ornatissimum*, *P. bauri* **sp. nov.** has conspicuous dorsolateral white spots. The tail length, however, is not intermediate between long-tailed *P. brevirostris* and short-tailed *P. ornatissimum*, but is similar to the former taxon. Two specimens from northeastern New Mexico, exhibit rather large, rounded dorsal spots, similar to the dorsal spots in *P. ornatissimum*. One specimen (TNHC 70982) is from 9.6 km SW of Farley in extreme southeastern Colfax County. The other specimen (MSB 7138) is from the Kiowa National Grasslands, 16 km N, and 6.4 km W of Roy in Harding County. The latter specimen is also interesting because its dorsal spots have indications of white medial borders characteristic of *P. ornatissimum.*

There is evidence from morphology and color pattern that *P. bauri* **sp. nov.** hybridizes with *P. hernandesi* where their ranges meet in southern Colorado and northeastern New Mexico. Two specimens (MEL 1001–02) from the west slope of Mosca Pass, Alamosa County, Colorado, are apparent hybrids between *P. bauri* **sp. nov.** and *P. hernandesi*. The specimens have wedge-shaped brown dorsal spots and dorsolateral white spots as in *P. bauri* **sp. nov.**, but red pigmentation on the temporal shelf and horns, and red pigment above the lateral fringe row as in typical *P. hernandesi*. The rostrofrontal profile is similar to that of *P. bauri* **sp. nov.,** or intermediate between the two species. There is also evidence of hybridization in a series collected 11.2 km SE of Russell on the western slopes of the Sangre de Cristo Mountains at 2,805 m (9,200 ft) elevation. Among eight specimens, three (CU 3723 B,C,G) are typical *P. bauri* **sp. nov.** Four specimens (CU 3723 A, D, E. F) appear to be hybrids with *P. hernandesi*; three of these lack dorsolateral white spots; the fourth has dorsolateral white spots, but has transverse dorsal bands and its rostrofrontal profile is nearly gradually sloping. The eighth specimen, a neonate, is difficult to classify although it appears to be typical *P. bauri* **sp. nov.** Several specimens from near Gardner, Huerfano County, Colorado, show a combination of traits from the two species. Three specimens (UCM 20120, 43323–24) are from southeast of Gardner; a fourth specimen (UCM 48463) lacks specific locality information. The specimens are large, ranging from 91 to 100 mm SVL. The snout is slightly protruding, and the rostrofrontal profile varies from gradually sloping to nearly angular with a steep incline; the temporal horns are oriented horizontally in two specimens, but directed slightly upward in the other two. The dorsal spots are wedge-shaped, but two specimens have nearly developed transverse bands. Three specimens have dorsolateral white spots. *P. hernandesi* is expected in the forested mountains near Gardner but voucher specimens are presently lacking. Traits of *P. hernandesi* are also evident in a specimen (KU 68087) reported by Kerfoot (1962) from near Raton Pass, Las Animas County, Colorado. The specimen is large, 104 mm SVL, and has a protruding snout with a gradually sloping rostrofrontal profile; the horns are directed upward, and a few white spots are present dorsolaterally on the body.

In New Mexico, a single specimen (OMNH 25207) from Mora, Mora County, at ca. 2,195 m (7,200 ft) has slightly elevated horns, a gradually sloping rostrofrontal profile, and dorsolateral white spots. A series of specimens (NMSU 1503–06, LACM 4348) from Raton, Colfax County, near 2,036 m (6,680 ft), are morphologically close to *P. bauri* **sp. nov.**, but show influence from *P. hernandesi*. The rostrofrontal profile is angular with a steep incline in one specimen, but rounded to nearly gradually sloping in the others. The third temporal horn is relatively short (13.0 to13.8% of head length) in three specimens, but longer (15.6 to 16.7% of head length) in two others. The occipital horns are directed upward to nearly vertical in all specimens, but the temporal horns are directed horizontally in two specimens. All specimens have dorsolateral white spots, although in some specimens the number of spots is reduced. Among six specimens from near Las Vegas, San Miguel County, at ca. 1,955 m (6,415 ft), one (OMNH 25214) has horizontally-directed occipital horns and a gradually sloping rostrofrontal profile, but also has dorsolateral white spots. Two other specimens (OMNH 25211 and 25209), have relatively long temporal horns (17.8 to 19.3% of head length), and the latter specimen also has a sloping rostrofrontal profile as well as dorsolateral white spots. One of four specimens from the Philmont Scout Ranch, Colfax County (UMMZ 230427), has a sloping rostrofrontal profile, the remaining three have rounded or angular and steeply inclined rostrofrontal profiles.

The few specimens collected from the Sangre de Cristo Mountains in western San Miguel, Mora, and Colfax counties, New Mexico, are referable to *P. hernandesi*. These specimens have a protruding snout and a gradually sloping rostrofrontal profile, and most have relatively long horns, oriented horizontally or inclined upward only slightly. All specimens lack dorsolateral white spots. Specimens referred to *P. hernandesi* include LACM 19705-06 from 5.8 km N of Pecos at 2,195 m (7,200 ft) elevation, ANSP 14866 and 15691 from Sapello Canyon, and MSB 1348 from Gallinas Canyon at 2,161 m (7,090 ft) elevation.

Distribution and habitat. *P. bauri* **sp. nov.** ranges from near Lodgepole Creek in southwestern Nebraska and southeastern Wyoming (south of the North Platte River), southward through the short-grass plains of eastern Colorado into northeastern New Mexico. In Wyoming, *P. bauri* **sp. nov.** has been recorded from near Wheatland in Platte County, and near Pine Bluffs and WNW of Carpenter in Laramie County. Westward, the Laramie Mountains (Pine-Douglas fir association) may impede contact with *P. brevirostris*. In New Mexico, it has been recorded from Colfax, Harding, Mora, San Miguel, and Union counties (see Appendix II, maps 9, 12, 14, 21). The southern limit of its distribution appears to coincide, more or less, with the upper Pecos River in San Miguel County, New Mexico. Contact with *P. ornatissimum* may occur on the plains of southern San Miguel and northern Guadalupe counties, New Mexico.

Much of the region occupied by *P. bauri* **sp. nov.** is dominated by Grama-buffalo grass (*Bouteloua-Buchloë*). Near Las Vegas, San Miguel County, New Mexico, there are some enclaves of Grama-galleta steppe (*Bouteloua-Hilaria*), remnants from the more southerly plains of New Mexico. Along the lower slopes of the Rockies in Colorado and New Mexico, the vegetative association shifts from Grama-buffalo grass to Juniper-pinyon woodland (*Juniperus-Pinus*), and then to Pine-Douglas fir (*Pinus-Pseudotsuga*); at the higher elevations contact and hybridization with *P. hernandesi* is expected, at least in some areas.

Remarks. Additional specimens are needed from the region north of Lodgepole Creek, Nebraska, as the northern limits of this taxon are not clearly established. Intermediate specimens between *P. bauri* **sp. nov.** and *P. brevirostris* are expected north of Lodgepole Creek, however, the taxonomic affinities of specimens from Gering, Scotts Bluff County, Nebraska, are uncertain. The specimens lack dorsolateral white spots, but they are all juveniles (ca. 34–35 mm SVL); the white spots in *P. bauri* **sp. nov.** typically begin to appear at a snout-vent length of about 42 to 46 mm or even greater. A juvenile specimen from near Cassa, Platte County, Wyoming, also lacks dorsolateral white spots, but it is probably *P. bauri* **sp. nov.,** based on its location south of the North Platte River. A specimen from Fort Laramie, Goshen County, Wyoming (USNM 4604) lacks dorsolateral white spots and has indistinct nuchal blotches. It is identified as *P. brevirostris*, but the precise collection locality, i.e. north or south of the North Platte River, is in question. The southern limit of the range of *P. bauri* **sp. nov.** also needs to be determined and any genetic interaction with *P. ornatissimum* should be investigated. As *P. bauri* **sp. nov.** has been collected from the western slopes of the Sangre de Cristo Mountains and from NE of Fort Garland, Costilla County, the possibility of contact and hybridization with *P. diminutum* **sp. nov.** along the southeastern margin of the San Luis Valley in Colorado, should be investigated.

Historical reports suggest that this short-horned lizard reached high densities on the plains of northeastern New Mexico. At the inception of the Mexican War of 1846, General Stephen W. Kearney marched into New Mexico to take Santa Fe. First Lieutenant W. H. Emory, Chief of the Engineer staff of General Kearney's command, kept an unofficial journal. Several entries, in particular those of August 9th, 11th, and 12th of 1846 mention observing pronghorn antelope and "horned frogs" in great abundance. On those dates, Kearney's column traversed the territory from near the Canadian River to Ocate Creek and then to the valley of the Mora River. During the summer of 1940, A. N. Bragg (in Bragg & Dundee 1949) reported that hundreds of these short-horned lizards were observed in the vicinity of Las Vegas, San Miguel County, New Mexico. Moderate densities of *P. bauri* **sp. nov.** have been noted in northeastern Colorado in recent decades, but current population trends within its range remain unknown.

***Phrynosoma diminutum* sp. nov.**

(Figs. 9A, 14–16)

Phrynosoma douglassi Gentry 1885:140 (part).
Phrynosoma douglassii hernandesi Cope 1900:413 (part).
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377(part).
Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii ornatissimum Reeve 1952:927 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

Holotype. UCM 61895, adult female, collected from Medano Road, just outside The Nature Conservancy's Medano Ranch, 2,308 m., Alamosa County, Colorado, by A. Schneider and A. Mitchell on 4 August 2006 (Fig. 14).

Paratypes. LSUMZ 13834–37, 13839–40, MEL 1013, 1015, 1016, MVZ 27042, UCM 3894, 3898, 48465–66, 51268, 61896, UMMZ 62242, 62244, 62247–52, 62255–58, 62261–64, USNM 8558, 44888, 44890. See Appendix I for locality data.

Etymology. The subspecific epithet *diminutum,* Latin perfect participle of *dēmĭnŭo*, *dēmĭnuĕre*, meaning "diminutive," is in reference to the small adult size of this species.

Suggested common name. San Luis Valley Short-horned Lizard.

Type locality. The type locality is Medano Road, just outside Medano Ranch, Alamosa County, Colorado.

Taxonomic history. Van Denburgh (1922), Smith (1946), and Reeve (1952) included Colorado, or at least the region of Colorado occupied by this taxon, as being part of the geographical range of *Phrynosoma douglassi ornatissimum* [sic]. Hahn (1968) was the first to comment on the small adult size of the short-horned lizards inhabiting the San Luis Valley of Colorado. Hahn (op. cit.) treated them as *Phrynosoma douglassi hernandesi* [sic] and regarded *ornatissimum* as a high elevation variant of *hernandesi,* a concept which he attributed to Gehlbach (1965:288). Although Gehlbach (op. cit) believed that environmental gradients produce both *hernandesi* and *ornatissimum* in a single geographic area, his viewpoint implied that *hernandesi*, not *ornatissimum*, was the high elevation form.

Diagnosis. *Phrynosoma diminutum* **sp. nov.** can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout short, 45% ± 1.87 (38.8–50%) of orbit to rostral scale distance; (2) rostrofrontal profile rounded or angular with a steep incline; (3) frontal rim not elevated, or only slightly elevated above the occipital shelf; (4) enlarged frontal rim scales 1.63 ± 0.23 (0–3) / 1.60 ± 0.22 (0–3); (5) temporal shelf short, 10.1% ± 0.95 (7.1–13.0%) in males, 11.7% ± 0.99 (6.2–15.8%) in females; (6) temporal shelf weakly to strongly convex; (7) cephalic horns short, third temporal horn length 10.4% ± 0.57 (6.7–13.5%); (8) cephalic horns slightly elevated to nearly vertical; (9) tympanum elliptic, moderately broad; (10) tympanum exposed; (11) tail moderately short, 215% ± 11.04 (180–239%) in males, 179% ± 4.94 (159–209%) in females; (12) dorsal spots small, wedge-shaped to slightly rounded; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots absent, but white dots, flecks, and vermiculations may be present; (15) gular area with scattered melanistic spots and/or vermiculations (melanin-dispersed phase); (16) abdomen with large melanistic spots or extensive dark suffusion (melanin-dispersed phase); (17) melanistic subcaudal bands absent or interrupted bands present distally (melanin-dispersed phase).

FIGURE 14. Holotype of *Phrynosoma diminutum* **sp. nov.,** adult female from near Medano Ranch, Alamosa Co., Colorado (UCM 61895).

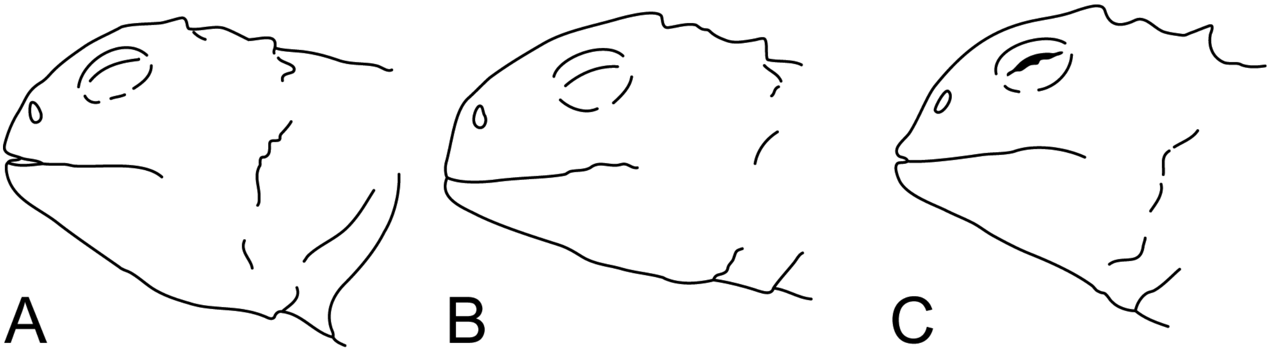

FIGURE 15. Rostrofrontal profile of *Phrynosoma diminutum* **sp. nov.** (A) Typical profile (UMMZ 62249, Rio Grande Co., Colorado); (B) Typical angular profile (MEL 1013, Alamosa Co., Colorado); (C) Atypical profile (UCM 3898, Costilla Co., Colorado).

Comparisons. *P. diminutum* **sp. nov.** differs discretely from *P. brevirostris* in having irregular rows of large, melanistic spots or extensive dark suffusion on the abdomen and widely interrupted subcaudal bands (as paired spots) during the melanin-dispersed phase. *P. diminutum* **sp. nov.** is further differentiated from *P. brevirostris* and from *P. bauri* **sp. nov.** in having a shorter, more convex temporal shelf and a relatively short tail. In *P. diminutum* **sp. nov.** and *P. brevirostris* the frontal rim is not elevated or only slightly elevated above the occipital shelf, but in *P. bauri* **sp. nov.** the frontal rim is usually well defined and elevated above the occipital shelf. *P. diminutum* **sp. nov.** also has a significantly lower number of enlarged frontal rim scales and a shorter third temporal horn than *P. bauri* **sp. nov.** (Table 3). *P. diminutum* **sp. nov.** differs further from *P. bauri* **sp. nov.** in lacking conspicuous white, rounded dorsolateral spots, although it may have small, white dots, vermiculations and flecks.

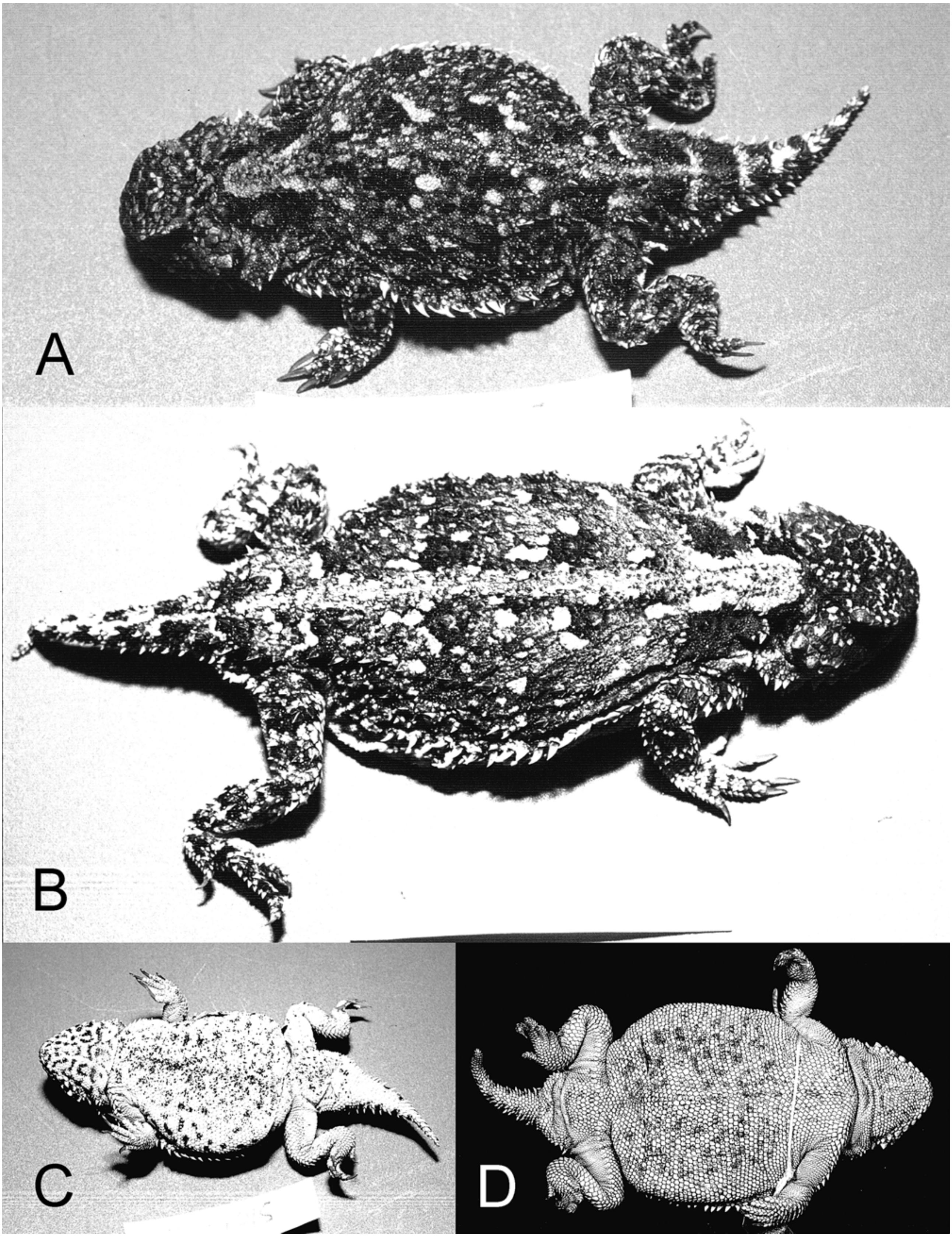

FIGURE 16. *Phrynosoma diminutum* **sp. nov.** (A) male (MEL 1015) from Zapata, Alamosa Co., Colorado; (B) female (MEL 1013) from same locality; (C) ventral aspect of male (MEL 1015); (D) ventral aspect of female (UMMZ 62250) from Monte Vista, Rio Grande Co., Colorado.

P. diminutum **sp. nov.** is characterized by small adult size (Hahn, 1968; Hammerson, 1999). Hammerson (1999:222) calculated a mean snout-vent length of 43 mm for males and 54 mm for females, with a maximum of 51 mm and 66 mm for males and females respectively. His comparisons with samples from northeastern, southeastern, and western Colorado revealed that all exceeded the size of the San Luis Valley specimens. The greatest size disparity was found between San Luis Valley samples and those from western and southwestern Colorado, and this is likely explained by the inclusion of *P. hernandesi*.

The males of *P. diminutum* **sp. nov.** and *P. brevirostris* are similar in mean snout-vent length although males of *P. brevirostris* exceed males of the former by 12 mm in maximum size. Males of both taxa are smaller than males of *P. bauri* **sp. nov.** Snout-vent length comparisons among females reveal that females of *P. diminutum* **sp. nov.** average smaller snout-vent length than females of *P. brevirostris*, and the latter are smaller than *P. bauri* **sp. nov.** (Table 5).

TABLE 5. A comparison of the mean snout-vent length (SVL), upper 25% of sample, and maximum size of *Phrynosoma bauri* **sp. nov.**, *P. brevirostris, and P. diminutum* **sp. nov.**

Taxon (n)	Mean SVL	Mean SVL (25%)	Max. SVL
P. bauri **sp. nov.**			
Males (48)	62.9 mm	69.5 mm	75 mm
Females (36)	72.8 mm	81.4 mm	86 mm
P. brevirostris			
Males (44)	49.5 mm	56.0 mm	65 mm
Females (77)	62.1 mm	76.8 mm	85 mm
P. diminutum **sp. nov.**			
Males (12)	48.5 mm	52.3 mm	53 mm
Females (23)	55.3 mm	63.0 mm	67 mm

P. diminutum **sp. nov.** is distinguished from *P. h. hernandesi* and *P. h. ornatum* by a smaller adult size, a rounded or angular and steeply inclined rostrofrontal profile, a frontal rim not elevated or only slightly elevated above the occipital shelf (except *P. h. ornatum*), a shorter temporal shelf, and shorter occipital and temporal horns. *P. diminutum* **sp. nov.** can be distinguished from *P. o. ornatissimum* and *P. o. brachycercum* by its smaller adult size, a frontal rim not elevated or only slightly elevated above the occipital shelf, a shorter temporal shelf, shorter occipital and temporal horns, a relatively longer tail, small wedge-shaped or rounded dorsal spots, absence of a discrete white and/or yellow line along the medial border of each dorsal spot (except *P. o. brachycercum*), and a gular pattern of scattered spots and vermiculations with or without gray suffusion and black spots on the abdomen (melanin-dispersed phase). *P. diminutum* **sp. nov.** is distinguished from *P. douglasii* by a gular pattern consisting of melanistic spots and/or vermiculations and melanistic spots on the abdomen (melanin-dispersed phase), a less convex temporal shelf, and a moderately broad, elliptic, and exposed tympanum.

Description. The following account is based on the examination of 42 specimens (12 adult males, 24 adult females, six juveniles) from the San Luis Valley of south-central Colorado (See Appendix I). Color photographs of live individuals further supplemented the description based on preserved material.

Head depressed, broader than long; snout short, but somewhat protruding in some specimens; rostrofrontal profile rounded or angular with a steep incline (Fig. 15); dorsal surfaces of the head covered with small, irregular, convex scales with surface rugosities formed by irregular ridges but relatively few granulations; frontal rim weakly defined, not elevated or only slightly elevated above occipital shelf (Fig. 9A); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf expanded posteriorly, weakly to strongly convex, but nearly flattened in 5.9% of sample; usually three small, subconical temporal horns, most posterior (third) largest, 10.4% (6.7–13.5%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one short occipital horn on each side, usually separated from temporal horn by one or two scales; supralabials small; three posterior infralabials slightly enlarged, continuous with usually two to three enlarged postlabials 2.7 (2–4); postrictal spine 9.4% (6.9–13.6%) of head length; chinshields slightly enlarged, separated from infralabials usually by two or three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper row larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, ephemeral, with or without enlarged scales posteriorly; tympanum elliptic, slightly broad; tympanum exposed (partly concealed with scales in one specimen); anterior margin of ear opening with a variable number of slightly enlarged, dentate-like scales; dorsal scales heterogeneous, but generally small, not overlapping; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 215% (180–239%) of head length in twelve males, 179% (159–209%) in 24 females; maximum snout-vent length = 67 mm.

Head brown or gray, and either uniform or with scattered white dots and flecks; in some specimens one or two narrow white lines cross the frontal area; anterior line may be interrupted medially or fragmented; faint pink or orange pigment may be present or absent on the occipital and temporal horns; dorsum gray or brown; a pair of dark brown nuchal blotches with indistinct borders or with medial borders well defined by a discrete white or yellow line, or by small white spots; four (range three to five) pairs of dark brown dorsal spots between neck and sacral area; anterior edges of dorsal spots grade into dorsal field; posterior edges of dorsal spots smoothly even or denticulate, bordered with bands of white, yellow, and/or orange pigment, or fragmented into irregular spots; posterior light-colored borders discrete or grading into dorsal field or absent in some specimens; dorsal tail base with pairs of spots that continue or fuse into transverse bands distally on tail; in some specimens, reddish pigment present above the lateral fringe row; gular area white with melanistic spots and/or vermiculations (melanin-dispersed phase); chest and abdomen with irregular rows of large melanistic spots (melanin-dispersed phase), overlain by dark gray suffusion in some specimens; subcaudal bands present as widely interrupted paired spots (melanin-dispersed phase) (Fig. 16).

Description of holotype. Adult female, snout-vent length ca. 60 mm, tail length 27 mm. Snout length 11.1 mm, head length 12.9 mm, rostral to temporal shelf distance 14.4 mm, frontal width 9.3 mm, head width 16.4 mm, interoccipital distance 4.2 mm, right occipital horn length 1.5 mm, right third temporal horn length 1.6 mm, left superciliary spine length 1.2 mm, right postrictal spine length 1.4 mm. Occipital horns directed horizontally; temporal horns (last, i.e. third) directed horizontally; rostrofrontal profile gradually rounded; frontal rim weakly defined, scarcely elevated above occipital shelf; enlarged frontal rim scales 1/1, nearly flattened; two low occipital tubercles; two postlabials on each side, last in contact with postrictal spine; ca. six dentate auricular scales on right side, lowermost in contact with postrictal; lateral fringe scales ca. 19 on left, 20 on right.

Color pattern of holotype in preservative. Dorsal surfaces of head, body, limbs, and tail medium brown. Frontal, occipital, and medial temporal areas with scattered white dots. Nuchal blotches dark brown with narrow white borders along medial edges. Four pairs of dark brown, rounded to slightly wedge-shaped dorsal spots, with an additional unpaired spot on right side; first pair of spots smaller, elongate and obscure; each dorsal spot has a discrete white line, intact or fragmented, along its posterior edge. Median white line on sacral area. Tail with pairs of dark brown spots border posteriorly with white and forming cross bands distally on tail. Dorsolateral areas of body with scattered white flecks and dots; white flecks and dots along vertebral area. Forelimbs and hind limbs brown with narrow, irregular white bands. Abdomen with irregular rows of large melanistic spots; area toward chest with scattered dark flecks; gular area with melanistic vermiculations and spots; tail lacking melanistic subcaudal bands.

Variation. In the series of 41 museum specimens, 17 individuals (41.4%) have occipital and temporal horns directed at an angle slightly above the horizontal; ten specimens (24.4%) have the occipital horns directed upward and the temporal horns directed horizontally; twelve specimens (29.2%) have both sets of horns directed horizontally, and two specimens (4.9%) have the occipital horns directed horizontally and the temporal horns directed slightly upward.

Variation in color pattern traits is based on museum specimens from the following localities: east of Antonito (3), northwest of Blanca (1), Fort Garland (1), Medano Ranch (2), Mesita (6), Mineral Hot Springs (3), Monte

Vista (19), and San Antonio (1). The dorsal spots are wedge-shaped in 13 specimens (68.4%) from Monte Vista; six specimens (31.6%) have somewhat rounded spots. The single specimen from San Antonio has slightly rounded spots. Specimens from all other sampled localities have wedge-shaped dorsal spots. The posterior light-colored borders of the dorsal spots are vivid and distinct in six specimens (31.6%) from Monte Vista as well as the specimens from northwest of Blanca, Fort Garland, Medano Ranch, Mesita, and San Antonio. The posterior light-colored borders are less vivid and grade into the dorsal field in 13 specimens (68.4%) from Monte Vista, as well as specimens from east of Antonito and Mineral Hot Springs. The head is uniform brown in the three specimens from east of Antonito; specimens from all other sampled localities have white dots, flecks, and/or transverse lines (intact or fragmented) on the dorsal surface of the head. White dots, flecks, and vermiculations are absent from the dorsolateral surfaces of the body in all specimens from Monte Vista, as well as in specimens from east of Antonito, Mineral Hot Springs, Saguache (one photo voucher), and San Antonio. Specimens from the remaining sampled localities have the dorsolateral whitish flecks and dots.

Additional color pattern information was recorded from photographs of 53 live adult individuals from Zapata Ranch. The dark dorsal spots are wedge-shaped in 49 adult individuals (92.4%); four lizards (7.6%) have slightly rounded dorsal spots. The posterior borders of the dorsal spots vary from yellow or yellow-orange to white and are distinct, not grading into the dorsal field in 52 lizards (98.1%). Dorsolateral white dots, flecks, and vermiculations are present in 23 adults (43.4%); in 15 lizards (28.3%) the white markings are few, and in 11 individuals (20.8%) they are absent. In four specimens (7.5%), the white dots and flecks are profusely scattered over the entire dorsal surface of the body. White dots and lines on the head are noted in 45 individuals (84.9%); only scattered dots and flecks are observed in six adults (11.3%), and the head is uniform, without white dots and flecks in two individuals (3.8%). The white lines and dots on the dorsal surfaces of the head and the dorsolateral white dots, flecks, and vermiculations on the body are considered forms of disruptive coloration, providing concealment in the habitat, especially on sandy substrates. The substrate at Zapata Ranch is predominantly sandy. Elsewhere in the San Luis Valley, the dorsal ground color of the lizards varies according to substrate. Dark specimens with obscure dorsal spots and indistinct posterior light-colored borders are usually found on stony, dark loam soils. Pale individuals are found on light-colored soils.

Pigmentation on the horns and above the lateral fringe row was also scored for 51 adult short-horned lizards at Zapata Ranch. The occipital horns have faint red or orange pigment in ten lizards (19.6%), but the pigment is lacking in 41 lizards (80.4%). The temporal horns, especially the largest, most posterior, have faint reddish pigment in 18 lizards (35.3%), but this color is absent in 33 lizards (64.7%). Red or pink pigmentation above the lateral fringe row is noted in ten lizards (19.6%), but 41 individuals (80.4%) lack the color.

Some adult *P. diminutum* **sp. nov.** from Zapata Ranch have bright red pigmentation on the rictus oris as in some specimens of *P. hernandesi*, but *P. diminutum* **sp. nov.** lack color on the interior surfaces of the infralabials. The red color is exposed when the mouth is opened during defensive display and may function to "startle" potential predators.

Distribution and habitat. *P. diminutum* **sp. nov.** is confined to the San Luis Valley of south-central Colorado (see Appendix II, Map 9). The southern extremity of the valley lies within northern New Mexico, and this taxon presumably occurs there as well. The San Juan Mountains are situated to the west of the valley; the Sangre de Cristo Mountains rim the valley on the east. The average elevation of the valley floor is about 2,300 m (7,500 ft). The dominant vegetation over an extensive central portion of the valley is Saltbush-greasewood (*Atriplex-Sarcobatus*) association. The western, southern and eastern margins of the valley, however, are dominated by grasslands, typically Wheatgrass-needlegrass (*Agropyron-Stipa*) association.

P. diminutum **sp. nov.** is allopatric with respect to *P. brevirostris*, and its ancestral stock may have originally entered the valley from the north through Poncha Pass, or from the southeast through La Veta Pass. The occupation of the valley by *P. diminutum* **sp. nov.** apparently predates the entry of *P. bauri* **sp. nov.** which only occurs along the southeastern margin of the valley. There it has been collected 8.8 km NE of Fort Garland and further southeast on the western slopes of the Sangre de Cristo Mountains 11.2 km SE of Russell, Costilla County. Assuming the collection data are accurate, *P. diminutum* **sp. nov.,** which also occurs near Fort Garland, may contact and potentially hybridize with *P. bauri* **sp. nov.** along the southeast edge of the valley.

Remarks. The distribution of *P. diminutum* **sp. nov.** along its eastern range margin and any ecological and/or genetic interactions with *P. bauri* **sp. nov.** merit study. The extent of its range into northern New Mexico needs to be determined.

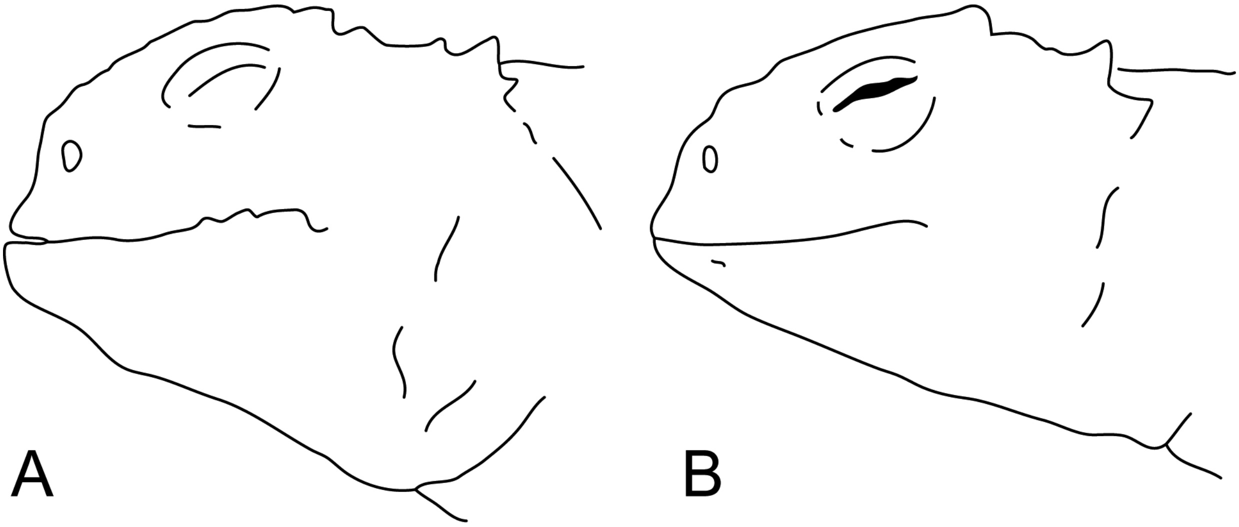

FIGURE 17. Rostrofrontal profile of *Phrynosoma douglasii.* (A) typical profile (CAS-SU 5791, Lake Co., Oregon); (B) atypical profile (RRM 2321, Deschutes Co., Oregon).

Phrynosoma douglasii (Bell 1828)

(Figs. 9D, 17–18)

Agama douglassii Bell 1828 (1833):105.
Phrynosoma douglassii Wagler 1830:146.
Phrynosoma (*Tapaya*) *douglassi* Girard 1858a:397.
Phrynosoma douglassii exilis Cope 1872:468.
Phrynosoma douglassii douglassii Cope 1875:49 (part).
Phrynosoma douglassii pygmaea Yarrow 1882a:443.
Phrynosoma douglassi Gentry 1885:140.
Phrynosoma douglassii douglassii Cope 1900:411.
Phrynosoma douglassii douglassii Van Denburgh 1922:368
Phrynosoma douglassii douglassii Smith 1946:299.
Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii douglassii Reeve 1952:918.
Phrynosoma douglasi Zamudio, Jones, and Ward 1997:302.

Etymology. Named in honor of David Douglas (1799–1834), British botanical collector and explorer. The correct spelling of the specific epithet is with a single "s" and a double "i". There is no broad consensus that the single "i" termination is "in prevailing usage" (ICZN, Art. 33.3.1.), and thus the original double "i" termination should stand. Although contrary to recommendation no.16, the original double "i" is the correct original spelling for the available name according to ICZN articles 33.4 and 33.5.

Suggested common name: Pygmy Short-horned Lizard.

Type locality. The type locality is along the Columbia River, Washington.

Taxonomic history. Thomas Bell described this species in 1828 (1833) on the basis of specimens in the British Museum collected by David Douglas from along the banks of the Columbia River. Originally considered a member of the genus *Agama*, it was transferred to the genus *Phrynosoma* by Wagler (1830), followed by Gray (1831).

In 1872, E. D. Cope published a report on the reptiles, amphibians and fishes collected by E. Campbell Carrington and C. M. Dawes during the F. V. Hayden geological survey of 1871 to southwestern Montana and Wyoming's Yellowstone region. Under the name *Phrynosoma douglassii* [sic] Cope recognized two forms, var. α which he referred to as "the usual form" listing it from Salt Lake City, and var. β, *exilis*, for a small form which he considered a geographical variety, from Carrington's Lake, Montana, and Fort Hall, Idaho. Hayden's survey route started at Ogden, Utah, entering the Centennial Valley of southwestern Montana through Monida Pass, and traversing the valleys of the Madison and Gallatin rivers before entering the Yellowstone drainage system. Carrington's Lake has never been located and it is not mentioned elsewhere in Hayden's 1872 report; its location will likely never be determined. Cope apparently named the lake to honor Campbell Carrington, the zoologist in the survey party, but presumably the lake was later given another name. Zoological specimens collected during Hayden's 1871 expedition were sent to the Smithsonian Institution, but there is no record of a specimen from Carrington's Lake, Montana. The name *exilis* was eventually placed in the synonymy of *P. douglasii* (Cope, 1900:411). Van Denburgh (1922) listed the name as a synonym of *P. douglassii ornatissimum* [sic]. Reeve (1952) treated it as a synonym of *P. d. douglassii* [sic] as did Schmidt (1953) who also restricted its type locality to Fort Hall, Idaho.

Yarrow (1882a) described the subspecies *pygmaea* on the basis of specimens collected from Fort Walla Walla and Fort Steilacoom, Washington, and the Deschutes River, Oregon. The Fort Steilacoom locality is very probably erroneous. Subsequently, Yarrow (1882b:70) designated two specimens under USNM 11473 as the type material, thereby restricting the type locality to the Deschutes River. Cope (1900:411) placed Yarrow's subspecies in the synonymy of *P. d. douglassii* [sic].

The type locality of *Phrynosoma douglasii* has not been further restricted, and perhaps there is little justification to do so. The Columbia River is a vast waterway and David Douglas traveled extensively from his base of operations at Fort Vancouver (Hammerson & Smith, 1991). It would be difficult, if not impossible, to determine more precisely where his specimens were collected. The British Museum lists the type material (BMNH 1946.8.10.52–53) as from "California", which conflicts with the published account of Bell (1828 [1833]), in which the type locality reads: *"In ora occidentali Americæ Borealis ad ripas fluminis Columbiæ".*

Diagnosis. *Phrynosoma douglasii* can be distinguished from other members of the species complex by the following combination of adult characters: (1) snout short, 44.6% ± 1.04 (36.6–49%) of orbit to rostral scale distance; (2) rostrofrontal profile strongly rounded or angular with a steep, nearly vertical, incline; (3) frontal rim not elevated, or only slightly elevated above the occipital shelf; (4) enlarged frontal rim scales 0.66 ± 0.21 (0–2) / 0.73 ± 0.20 (0–2); (5) temporal shelf short, 7.4% ± 0.86 (2.0–19.5%) in males, 10.3% ± 0.66 (1.9–17.5%) in females; (6) temporal shelf surface moderately to strongly convex (rounded); (7) cephalic horns very short, third temporal horn length 8.0% ± 0.13 (4.6–10.6%); (8) cephalic horns directed upward (ca. 45°) to vertical; (9) tympanum elliptic, typically narrow, or small and rounded; (10) tympanum exposed, or partly or entirely concealed by granular scales; (11) tail moderately short 214% ± 5.36 (158–255%) in males, 167% ± 4.14 (123–225%) in females; (12) dorsal spots small to moderately large, wedge-shaped, slightly rounded, or forming transverse bands; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots absent; (15) gular area with gray to charcoal suffusion or flecks (melanin-dispersed phase); (16) abdomen with scattered melanistic flecks or a gray suffusion, no melanistic spots (melanin-dispersed phase); (17) melanistic subcaudal bands absent (melanin-dispersed phase).

Comparisons. *Phrynosoma douglasii* can be distinguished from all other members of the species complex by its minute occipital and temporal horns (TH significantly shorter than in all other taxa, Table 3), the absence or weak development of the frontal rim (except *P. brevirostris* and *P. diminutum* **sp. nov.**), a low number of enlarged frontal rim scales, a short temporal shelf with a convex or strongly rounded surface, a narrow, elliptic tympanum, reduced to a small, rounded disc in some specimens, and usually concealed by scales. It is further distinguished from *P. h. hernandesi* and *P. h. ornatum* by its small adult size, vertical orientation of the occipital and temporal horns, a rounded or angular and steeply inclined rostrofrontal profile, and the absence of melanistic abdominal spots and melanistic subcaudal bands (melanin-dispersed phase). *P. douglasii* can be further distinguished from *P. ornatissimum* and its subspecies by its smaller adult size, pale gray to charcoal suffusion on the gular area (melanin-dispersed phase), absence of dorsolateral white spots and absence of a discrete yellow and/or white line along the medial border of each dorsal spot (except *P. o. brachycercum*).

In southern Oregon, southwestern Idaho, and northern Nevada, where *P. douglasii* may occur in proximity to *P. h. ornatum*, the two taxa may be distinguished by the usual presence of red pigment on the temporal shelf and horns as well as red pigment on the gular area and above the lateral fringe scales of the latter species. In addition, *P. douglasii* may have a dark, transverse band across the frontal area of the head, which is lacking in *P. h. ornatum*. In southwestern Montana, this trait will also help distinguish *P. douglasii* from *P. brevirostris.*

Description. This account is based on the examination of adult specimens primarily from California, Idaho, Oregon, Utah and Washington (n = 307; see Appendix I).

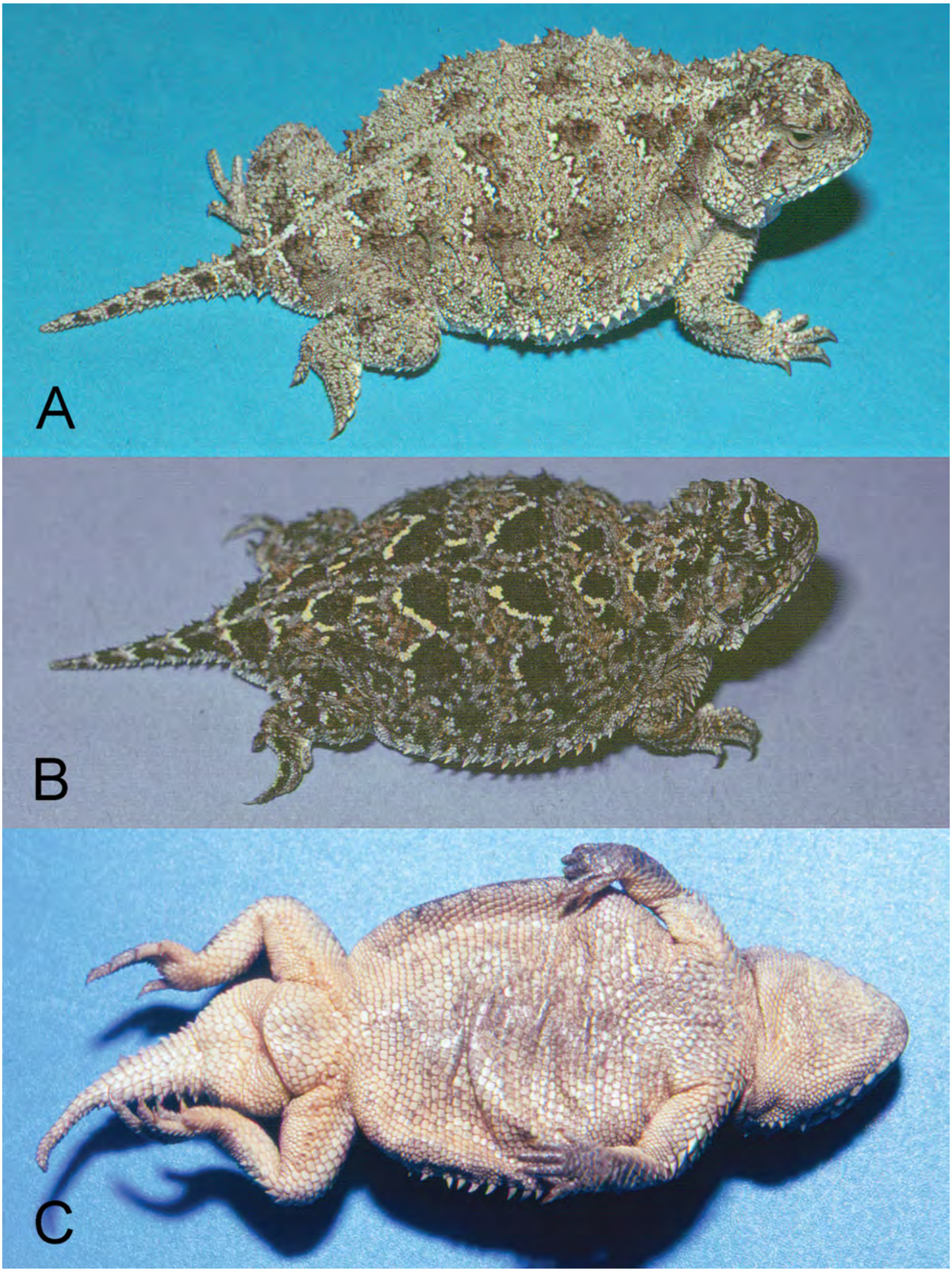

FIGURE 18. *Phrynosoma douglasii.* (A) adult female, large form (RRM 2393) from 16 km NW jct. U.S. 20 & 26, Butte Co., Idaho; (B) adult female, small form (RRM 2321) from lava field E of Mt. Washington, Deschutes Co., Oregon. (C) adult male (UMMZ 174199) from Santiam Junction, Linn Co., Oregon, showing ventral aspect with pale gray suffusion on abdomen and gular area.

Head depressed, broader than long; snout short, but slightly protruding in some specimens; rostrofrontal profile rounded or angular with a steep incline (Fig. 17); frontal area usually slightly depressed near the external nares; dorsal surfaces of the head covered with small, irregular, convex scales with rugosities formed by irregular and radiating narrow ridges and few, if any, granulations; frontal rim absent or only weakly developed, not elevated above occipital shelf (Fig. 9D); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf slightly expanded, little produced posteriorly, surface moderately to strongly convex; occipital emargination shallow; usually three minute, subconical temporal horns, most posterior (third) largest, 8.0% (4.6–10.6%) of head length; occipital shelf bears several small convex scales or tubercles which generally low and rounded, but in some specimens moderately elevated and pointed; interoccipital spine minute, blunt; one minute, occipital horn on either side, vertical, with slight lateral divergence, sometimes directed anteriorly; usually separated from temporal horn by two scales, rarely up to four scales; supralabials small; infralabials small, continuous with postlabials; usually three postlabials, 3.13 (2–4); postrictal spine 10.27% (7.6–14.8%) of head length; chinshields slightly enlarged, separated from infralabials usually by three (range: two to five) small sublabials; gular scales small, subequal; two prescapular dermal folds, upper fold larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a longitudinal gular fold on left and right sides, weakly developed, ephemeral, lacking enlarged scales; tympanum elliptic, narrow, or small and rounded, exposed, or partly or entirely concealed by granular scales; anterior margin of ear opening with small, granular scales and usually one to several elongate, pointed or tapered scales; dorsal scales heterogeneous, but generally small, not overlapping; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 214% (158–255%) of head length in 52 males, 167% (123–225%) in 91 females; maximum snout-vent length = 80 mm.

Frontal area of head usually with dark transverse band, with or without whitish borders; dark "satellite" bands may be present anteriorly and posteriorly; two to four dark dorsal spots in transverse rows; four to five (range three to six) rows between neck and sacral area; spots usually wedge-shaped, but rounded in some specimens; dorsal spots bordered posteriorly by white or yellow; posterior edges of dorsal spots denticulate or smoothly even; dorsal spots transversely connected, or nearly so in some specimens, forming undulating cross-bands; nuchal spots obscure, absent, or well defined with narrow white or yellow borders; one or two nuchal spots laterally on either side, and in many specimens separated by a narrow, elongated median spot; gular area, chest, and abdomen white, but in the melanin-dispersed phase with a uniform gray suffusion or sparsely scattered gray flecks (Fig. 18).

Variation. The occipital and temporal horns project nearly vertically in 206 of 304 specimens or 67.7% of the total. In 98 specimens (32.2%) the occipital horns project upward, but the temporal horns are directed horizontally. The orientation of the occipital horns shows a slight difference between the sexes. In males, the horns are slanted upward (ca. 45°) in 49.3%, and vertically directed in 50.6% of the sample, but in females 40% have upward-slanted horns and 60% have vertically-directed horns. Orientation of the cephalic horns shows no discernible differences across localities in Washington, Oregon, and Idaho.

In 217 lizards (71.3%), the dorsal spots are wedge-shaped; in 77 specimens (25.3%), some of the dorsal spots are more or less rounded, and in ten specimens (3.3%) the spots form undulating transverse bands.

The color of the dorsal field closely matches the substrate, and may vary from nearly black to gray, brown or red. I observed nearly black individuals on the basaltic soils of southern Idaho. Cope (1900) reported iron-rust brown individuals on the elevated basaltic region between Goose and Warner lakes near the California-Oregon border. Pale gray, nearly white, individuals were noted on the eroded, powdery soils at Fossil Lake, Oregon (Nussbaum *et al.* 1983). The transverse band on the frontal area is fragmented and nearly absent in some specimens from northern California, northern Nevada, and southern Idaho; the frontal transverse band also tends to be absent in pallid specimens from light-colored soils.

Populations of *P. douglasii* in the Cascade Ranges of Oregon are represented by somewhat smaller individuals than those from the sagebrush deserts of southeastern Oregon and Idaho. At Santiam Junction, Linn County, for example, the upper ten percentile for female snout-vent length (n = 77) varies from 56 to 58 mm, but at Cabin Lake (n = 60) it is 63 to 71 mm, and at Lake Abert (n = 17) it is 71 to 72 mm. Correlated with smaller body size is a reduction in the extent of the temporal shelf. The sample mean ± two standard errors and observed limits for males are 4.8% ± 0.48 (2.0–8.7%), n = 35 for Santiam Junction vs. 10.1% ± 1.08 (5.4–19.5%), n = 35, pooled from Lake County. The statistics for females are 8.1% ± 1.08 (1.9–13.8%), n = 30 for Santiam Junction vs. 11.5% ± 0.67 (6.3–17.5%), n = 63, pooled from Lake County.

Populations of intermediate body size may occur along the lower slopes of the Cascades bordering the eastern desert but this has yet to be demonstrated by adequate sampling.

The variation in proportional tail length suggests a cline correlated with latitude, the northern population (Santiam Junction) having, on average, a shorter tail than southern populations (Hart Mountain, Lake Abert). But additional samples are needed to confirm a clinal pattern. The sample mean ± two standard errors, observed limits, and sample size for females are as follows: Santiam Junction 161% ± 3.41 (123–194%), n = 74; Cabin Lake 178% ±3.69 (148–215%), n = 60; Lake Abert 195% ± 6.69 (176–225%), n = 17; Hart Mountain 191% ± 4.56 (176–207%), n = 16. Statistics for males are: Santiam Junction 205% ± 4.85 (158–233%), n = 32, and Lake Abert 230% ± 7.39 (198–255%), n = 20. Male samples are inadequate for Cabin Lake and Hart Mountain.

Smith (1946:300) pointed out that in this taxon, the tympanum may be naked or concealed by scales. The variation in this character was not studied thoroughly among populations, but data are available for Oregon samples from two localities. In a sample from Santiam Junction, Linn County (n = 30), the tympanum is exposed in 3 specimens (10%), partly concealed in 20 specimens (66.6%), and it is fully concealed by scales in 7 specimens (23.3%). At Cabin Lake, Lake County (n = 30), the tympanum is exposed in 3 specimens (10%), partly concealed in 12 specimens (40%), and completely concealed by scales in 15 specimens (50%). Among miscellaneous specimens (n = 13) from central Idaho and northern Utah, the tympanum is exposed in six lizards (46.1%); it is partly concealed in two specimens (15.4% of sample), and fully concealed in five specimens (38.5% of sample).

P. douglasii may have arisen from a progenitor similar to *P. brevirostris*; it has generally a smaller body size, with further reduction of the temporal shelf and loss of the frontal rim, a narrower tympanum, and greatly reduced cephalic horns. The rugose surfaces of the cephalic scales are formed by an intricate pattern of narrow ridges, hence differing from the slightly broader ridges and granulations found in *P. brevirostris. P. douglasii* may have evolved through allopatric speciation, with the Columbia River and Snake River systems possibly functioning as the primary geographic isolating mechanism.

Distribution and habitat. *P. douglasii* ranges from extreme southern British Columbia, south through the eastern half of Washington and northern Idaho, through the Cascades region and adjacent desert areas of Oregon, southward into northern California, northwestern Nevada, and eastward through central and southern Idaho. *P. douglasii* is also recorded from northern Utah near Snowville, Box Elder County (BYU 14755). Also, there are extralimital records from southwestern Montana and northwestern Wyoming (see **Remarks** below and Appendix II, maps 8, 10, 11, 13, 16, 19, 20, 21).

Populations of *P. douglasii* in Harney County, Oregon, appear to be allopatric with respect to those in southern Idaho. Records from the intervening region in southeastern Oregon (Malheur County) and southwestern Idaho (SW Cassia County, Owyhee County) are *P. hernandesi ornatum* (see Appendices I and II). However, there are two records for *P. douglasii* in Owyhee County: 18 km WSW of Three Creek near Murphy Hot Springs (IMNH 1254–55), and 50.3 km NNW of Three Creek (Jezkova, T., unpublished data). Nussbaum *et al*. (1983) report *P. hernandesi* from extreme southeastern Idaho, including Bear Lake, Franklin, and Oneida counties, and the southern parts of Bannock, Caribou and Cassia counties. Specimens I have examined from Bannock and Cassia counties are *P. douglasii* except in SW Cassia County where *P. hernandesi ornatum* occurs (also see **Remarks** under *P. brevirostris* account).

P. douglasii occurs in Sagebrush steppe (*Artemisia-Agropyron*) over much of the Columbia Plateau of eastern Washington based on museum records. Dice (1916) reported it only from the sagebrush regions of southeastern Washington. In Whitman County, Svihla & Svihla (1933) mentioned historical records for Almota and Rock Lake, and stated, without mentioning voucher specimens, that the species occurs in sagebrush areas along the Snake River Canyon. However, extensive grasslands also covered parts of eastern Washington that have now been converted to a monoculture of wheat. Fescue-wheatgrass association (*Festuca-Agropyron*) occurred along the upper reaches of the Columbia River and near its confluence with the Okanogan River. Southwest of Pullman southward to Walla Walla and into north-central Oregon, the climax association was Wheatgrass-blue grass (*Agropyron-Poa*), which also extended along the Clearwater River near Lewiston in northern Idaho. Relatively few historical records for *P. douglasii* are situated within these grassland climax communities. The physiognomy of dense, low to medium tall grass may have precluded the establishment of short-horned lizard populations over much of this habitat, except where exposed, friable soils were present.

In Oregon, populations east of the Cascades occur in Sagebrush steppe (*Artemisia-Agropyron*), but in the vicinities of Lake Abert and Fossil Lake, lizards have also been collected in Saltbush-greasewood (*Atriplex-*

Sarcobatus) association. In the Cascade Range, populations occur in open conifer forest associations, including Silver fir-Douglas fir forest (*Abies-Pseudotsuga*) and Fir-hemlock forest (Abies-Tsuga) mainly on the western slopes, and Grand fir-Douglas fir forest (*Abies-Pseudotsuga*), and Ponderosa shrub forest (*Pinus*) on the eastern slopes above the Sagebrush steppe. It should be emphasized that *P. douglasii* inhabits open-canopied forests with widely spaced trees and well-drained, friable soils. Dense forests, with closed canopies, impede the establishment of populations. In southern Idaho, known localities are dominated by Sagebrush steppe, and as yet, there are no confirmed records in Douglas fir forest (*Pseudotsuga*) and Western spruce-fir forest (*Picea-Abies*) in the mountain ranges north of the Snake River Plain.

Remarks. I have examined specimens of *P. douglasii* from the Centennial Valley of southwestern Montana (MCZ 42197) and Wyoming's Upper Firehole River Basin in the Yellowstone Region (USNM 9458). There is also a record of a juvenile *P. brevirostris* (taxonomic identity ambiguous) from near Yellowstone National Park's West Entrance in the Hebgen Valley of Montana (MVZ 72271). The latter record is positioned geographically between the two records for *P. douglasii*. No information is available for the collector or date of collection for the MCZ specimen. The *P. douglasii* from the Upper Firehole River Basin was collected by C. Hart Merriam during Hayden's expedition of 1872 to the Yellowstone region. No collection date is given in the original museum ledger, but presumably it was taken in August of 1872 while Merriam was making ornithological observations in the basin area (Skinner, 1928). Frederick B. Turner (in Koch & Peterson, 1995) suggested that the specimen from Yellowstone's West Entrance may have been a released pet. If the records are correct and represent naturally occurring populations, it would appear that *P. douglasii* entered the Centennial Valley and the Upper Firehole River Basin via the upper Snake River drainage system (although the latter is part of the Madison River drainage system), whereas *P. brevirostris* reached the Hebgen Valley by way of the upper Madison River basin. In any case, these records need to be verified by additional specimens which may eventually help to clarify the distributional relationships of the two taxa in this region.

The occurrence of *P. douglasii* in northern Utah and potential contact with *P. h. ornatum* and *P. brevirostris* should be investigated (also see account of the latter taxon). In addition to BYU 14755 from Snowville, Utah, Knowlton & Janes (1934:12) recorded specimens from 16 km W of Snowville and 12.8 km SW of Rosette in Box Elder County. Although I was not able to locate the specimens for study, these records likely represent *P. douglasii*, although the latter may represent *P. h. ornatum.*

The distribution of *P. douglasii* in northern California remains poorly known and in need of comprehensive field surveys. Reeve (1952:921) erroneously placed the "Clear Lake" record in Modoc County. But, Clear Lake Reservoir is an impoundment that was built in 1910 as part of the Klamath Water Project. The specimen in question (USNM 45138) was collected by Vernon Bailey on 7 June 1891 from Clear Lake (41° 23' 00" N, 123° 16' 29" W) in the Klamath Mountains of Siskiyou County. Bailey's record, long overlooked because of Reeve's error, should be investigated to determine if the species occurs in the Klamath Mountains, or if this record is simply a museum cataloguing error. However, another possible explanation is that Bailey misapplied the name "Clear Lake" to Medicine Lake, which had the older variant name of Crystal Lake. Unfortunately, Bailey's field notes from this time period seem to have been lost.

Townsend (1887) collected three specimens of *P. douglasii* (USNM 13792; two re-catalogued later as USNM 293438–39) from the western base of Mount Shasta in 1883. Reeve (1952:921) listed only two specimens, incorrectly as USNM 12792. Townsend's published report is at odds with the original ledger entry which states the locality as "Baird, Shasta County, California". Baird post office, located near the McCloud River ca. 64 km south (straight line) from Mount Shasta, was inundated following the impoundment of Shasta Lake in 1945. The discrepancy between ledger and published information appears to be a cataloguing error, the *P. douglasii* specimens being inadvertently mixed with other material collected near the McCloud River.

Cope (1883 [1884]) reported *P. douglasii* from the Willamette Valley of Oregon, based on two specimens (ANSP 12790–91) collected by Professor O. B. Johnson who was Cope's friend and a resident of Salem at the time. Cope (op. cit.) described the valley as very wet, this being reflected by the numerous salamanders in Johnson's collection. The *P. douglasii* may have been secured farther east in drier territory and inadvertently included with the Willamette Valley material. The record has never been substantiated by additional specimens, except until recently. In July of 2012, I received a report of a dead-on-the-road (DOR) horned lizard ca. 6.2 km (by air) NNE of Jefferson, Marion County, Oregon. The site is on Centerwood Road, adjacent to an open, grassy area near the top of a butte with mixed oak and Douglas Fir. The specimen was found by Alan D. Mudge, entomologist with the

Oregon Dept. of Agriculture. Unfortunately, the specimen was not salvaged, but Mudge stated that it closely resembled photographs of the Pacific Northwest taxon.

P. douglasii was reported from the vicinity of Osoyoos in the Okanagan Valley of British Columbia (Fannin, 1898 *in* Powell & Russell, 1998). There were subsequent reports from the region, but Orchard (1980) was of the opinion that few had any credibility. Powell & Russell (1998) reviewed the history of records from British Columbia, citing a possible valid report in1937 conveyed in a personal communication from Orchard. However, the authors were unable to rediscover the species following a brief search in remaining habitat to the east of Osoyoos Lake in 1991.

Van Denburgh & Slevin (1921) and Reeve (1952) recorded *P. douglasii* from Boise, Ada County, Idaho, but these records (CAS 45433–34; USNM 63266) are erroneous as they are based on misidentified specimens of *P. platyrhinos*. Records from Glenns Ferry, Elmore County, Idaho (PSM 8460–66) are also specimens of *P. platyrhinos*.

Phrynosoma hernandesi hernandesi **Girard 1858a**

(Figs. 19–20, 21A, 22–23)

Phrynosoma (Tapaya) hernandesi Girard 1858a:395.
Phrynosoma (Tapaya) ornatissima Girard 1858a:396 (part).
Phrynosoma douglassi Gentry 1885:140 (part).
Phrynosoma douglassii hernandesi Cope 1900:413.
Phrynosoma douglassii ornatissimum Cope 1900:415 (part).
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377 (part).
Phrynosoma douglassii hernandesi Van Denburgh 1922:382.
Phrynosoma douglassii hernandesi Smith 1946:304.
Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii hernandesi Reeve 1952:922
Phrynosoma douglassii ornatissimum Reeve 1952:927 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302.

Etymology. Although Girard did not explicitly so state, this taxon is named in honor of Francisco Hernández, presumably in recognition of his comprehensive work on the biota of Mexico. The correct spelling of the specific epithet is with an "s" (see Smith *et al*. 1999).

Suggested common name: Mountain Short-horned Lizard.

Type locality. The type locality is restricted to Fort Huachuca, Cochise County, Arizona. See discussion below for more information.

Taxonomic history. Girard (1858a) described this species from specimens in the U.S. National Museum (now called the National Museum of Natural History), but the type material used in the species description was not listed in Girard's work. Stejneger (1890:113), in discussing the relationships of *P. hernandesi* and *P. ornatissimum*, referred to USNM 107 and 198 as "Girard's types" of *P. hernandesi*. But the number 107 is a typographical error for as Reeve (1952:923) pointed out, museum records show that USNM 197 from Sonora, Mexico, is the type. Curiously, Cope (1900:414) did not list USNM 197, but listed USNM 198 from Santa Fe, New Mexico, indicating that it was the type. However, Reeve (op. cit.) designated USNM 197 as the type specimen based on his belief that only *P. ornatissimum* occurs at Santa Fe, New Mexico. Furthermore, he explained that the tag bearing the number USNM 198 was loose in a jar containing a specimen of *P. hernandesi* to which a metal tag bearing the number 3034 was tied. He surmised that this specimen belonged to another institutional collection because USNM 3034 is the type specimen of *Cnemidophorus gracilis*. However, Kenneth Tighe (personal communication) has little doubt that the specimen in question is USNM 198, explaining that there are many examples of old metal tags being replaced erroneously when they became corroded. Annotations in the museum's original ledger show that USNM 197 and 198 were designated cotypes. USNM 197 originally comprised two specimens one of which was sent to the Muséum National d'Histoire Naturelle in Paris. However, according to Ivan Ineich (personal communication) the specimen sent to Paris is not in the MNHN type collection. Therefore, USNM 197 is the lectotype of *P. hernandesi* (Fig. 19) based on Reeve's previous designation of it as the "type", and USNM 198 is regarded as a paralectotype.

FIGURE 19. Lectotype of *Phrynosoma* (*Tapaya*) *hernandesi* Girard (USNM 197), a juvenile showing expanded temporal shelf and horizontally directed temporal horns typical of this species.

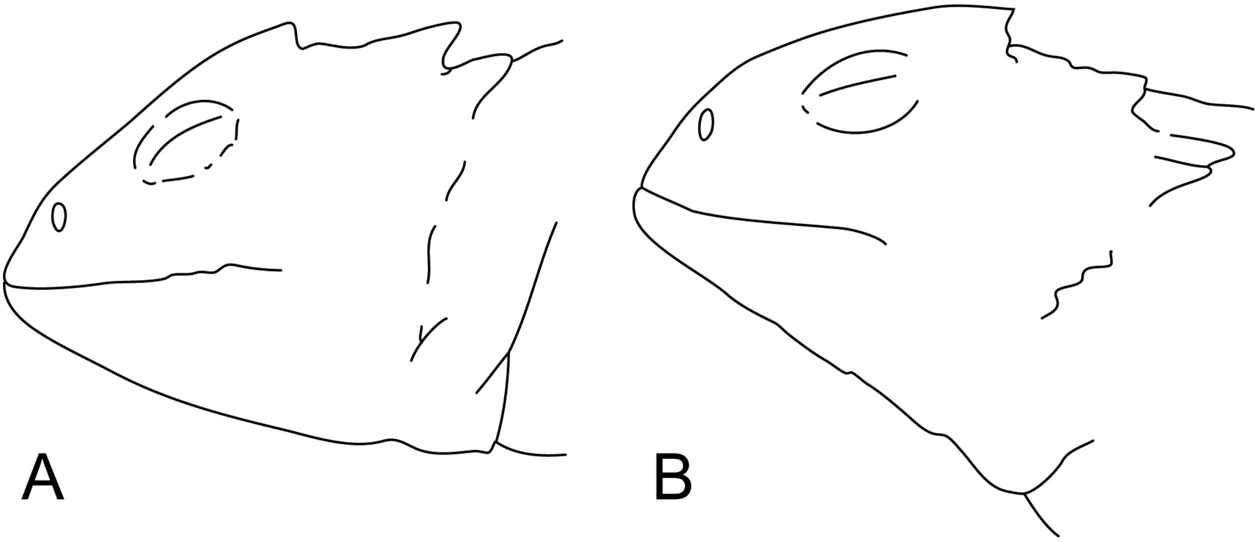

FIGURE 20. Rostrofrontal profile of *Phrynosoma hernandesi* (A) typical profile (ENMU 2673, Otero Co., New Mexico; (B) atypical profile (BYU 2821, Kane Co., Utah).

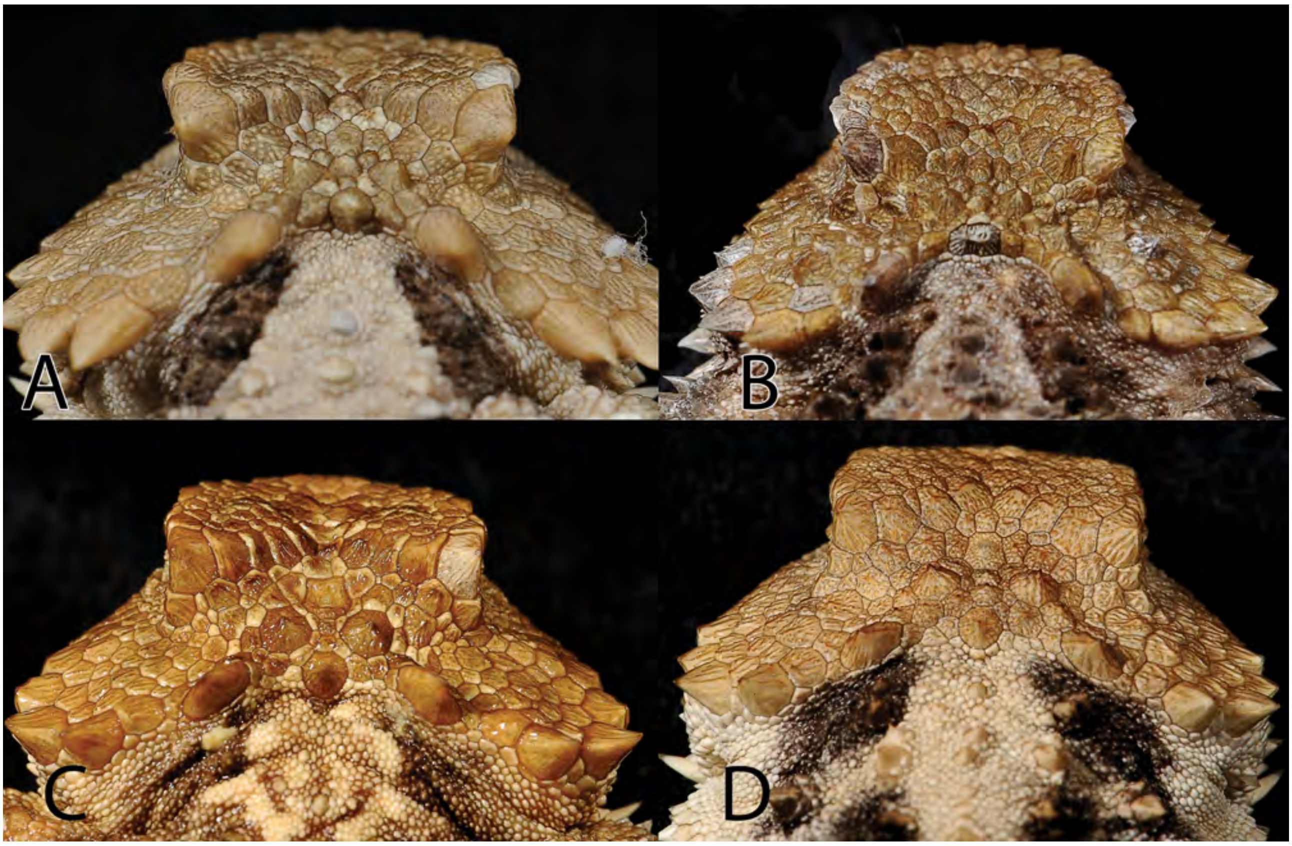

FIGURE 21. Posterodorsal aspect of head to show frontal rim morphology of (A) *Phrynosoma hernandesi* (MSB 36735, Socorro Co., New Mexico); (B) *Phrynosoma hernandesi ornatum* (USNM 60925, Salt Lake Co., Utah); (C) *Phrynosoma ornatissimum* (RRM 2206, Bernalillo Co., New Mexico); (D) *Phrynosoma ornatissimum brachycercum* (RRM 2103, Chihuahua state, Mexico).

Ledger records show that USNM 197 was collected by John H. Clark and received from Lt. Col. James D. Graham, but no date is given. According to Reeve (1952) the specimen was collected in 1857 when both men were part of a "geological survey party" in Sonora, Mexico. But this information is erroneous. In 1857, Col. Graham was in the Northwestern Lakes region as Superintending Engineer of Harbor Improvements (Cullum, 1891).

But in 1851, Col. Graham was involved with the U.S.–Mexico Boundary Survey and John H. Clark served as his assistant and was credited with collecting large numbers of reptiles, especially lizards (Axtell, 1981). Reeve (1952) designated Sonora, Mexico, as the type locality, but lacking more specific locality data, recommended a further restriction when more specimens became available. As the Gadsden Purchase was not consummated until 1853, the Gila River marked the southern boundary of Arizona. The survey party was traversing territory that was then part of the Mexican state of Sonora. Clark and Graham accompanied John R. Bartlett, United States Commissioner for the boundary survey; the party traveled west beyond Willcox Dry Lake to near the San Pedro River to meet with the Mexican Commission, and then turned south toward Noria de Santa Cruz in order to procure supplies (Bartlett, 1854). The specimen was probably collected north of Santa Cruz in what is now part of Arizona, most likely in the grasslands west of the southern San Pedro River Valley, the date of collection being September, 1851. Many days were spent in this area before the party found a passage though the mountains to Santa Cruz. Without further information, I arbitrarily restrict the type locality to Fort Huachuca, Cochise County, Arizona.

Diagnosis. *Phrynosoma h. hernandesi* can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout protruding, 49.4% ± 1.56 (42.5–57.3%) of orbit to rostral scale distance; (2) rostrofrontal profile rather flat, gradually sloping; (3) frontal rim usually elevated above the occipital shelf; (4) enlarged frontal rim scales 2.96 ± 0.15 (2–4) / 2.93 ± 0.13 (2–4); (5) temporal shelf long, 25.7% ± 0.96 (18.9–32.3%) in males, 26.1% ± 0.79 (17.2–36.2%) in females; (6) temporal shelf flat to weakly convex; (7) cephalic horns moderately long, third temporal horn length 18.2% ± 0.46 (10.3–24.1%); (8) cephalic horns directed horizontally or only slightly elevated; (9) tympanum elliptic, moderately broad to broad;

(10) tympanum exposed; (11) tail moderately long, 247% ± 8.87 (187–301%) in males, 219% ± 4.84 (175–272%) in females; (12) dorsal spots wedge-shaped or forming transverse bands; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots absent; (15) gular area with melanistic vermiculations and relatively few spots, with or without gray suffusion (melanin-dispersed phase); (16) abdomen with large melanistic spots or coalescing into dark suffusion (melanin-dispersed phase); (17) interrupted melanistic subcaudal bands present; bands may be complete distally (melanin-dispersed phase).

Comparisons. *Phrynosoma h. hernandesi* can be distinguished from *P.bauri* **sp. nov.,** *P. brevirostris*, *P. diminutum* **sp. nov.,** and *P. douglasii* by its protruding snout, gradually sloping rostrofrontal profile, frontal rim elevated above the occipital shelf (except *P. bauri* **sp. nov.**), high number of enlarged frontal rim scales, longer temporal shelf, and longer occipital and temporal horns that are usually directed horizontally. It is further distinguished from *P. brevirostris* and *P. douglasii* by the presence of large, melanistic abdominal spots, and interrupted or complete melanistic subcaudal bands (melanin-dispersed phase). *P. h. hernandesi* can be further distinguished from *P. douglasii* by an elliptic tympanum that is comparatively broad and naked, and by its large adult size. *P. h. hernandesi* can be distinguished from *P. ornatissimum* by its protruding snout and gradually sloping rostrofrontal profile, longer occipital and temporal horns that are horizontally directed or only slightly elevated, a relatively longer tail, absence of a discrete white and/or yellow line along the medial edge of each dorsal spot (except *P. o. brachycercum*), presence of wedge-shaped dorsal spots or dorsal cross-bands (except *P. o. brachycercum*), and in the melanin-dispersed phase, a gular pattern of vermiculations and relatively few spots with or without gray suffusion (as opposed to chevrons or wavy transverse bands), an abdominal pattern of large melanistic spots more or less in rows, and the presence of complete and/or interrupted melanistic subcaudal bands. Note that *P. h. hernandesi* has a significantly longer snout (ENR), more extensive temporal shelf (TRE), longer temporal horn (TH), and longer tail (TL) than all other taxa in the complex (Table 3).

In the Colorado Plateau region of Utah, where *P. h. hernandesi* may occur in proximity to *P. brevirostris*, the two taxa may be distinguished, in addition to the characters mentioned above, by the usual presence of red pigment on the temporal shelf and horns as well as red pigment above the lateral fringe scales of the former species.

Description. This account is based on the examination of specimens from northern Sonora, Mexico, the mountains of south, central and northern Arizona, the mountainous regions of New Mexico and southwestern Colorado, and the Wasatch Range of Utah (n = 510; see Appendix I).

Head broader than long; snout more or less protruding, rostrofrontal profile gradually inclined anteriorly; frontal area flat or slightly concave (Fig. 20); dorsal surfaces of the head covered with small, irregular, convex scales with rugosities formed by granulations and/or irregular ridges; frontal rim typically elevated above the occipital shelf (Fig. 21A); superciliary ridges distinct, terminating posteriorly in a spine that is shorter to slightly longer than the occipital horn; external nares laterally pierced in line of canthus rostralis; temporal shelf expanded, flat to weakly convex, well produced lateroposteriorly; occipital emargination deep; three temporal horns, most posterior (third) longest, 18.2% (10.3–24.1%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed, to elongate and pointed; interoccipital spine small, blunt; one occipital horn on each side, separated from third temporal horn by one or two scales; supralabials small; infralabials increasing in size posteriorly; usually three markedly enlarged postlabials, 3.1 (2–4); postrictal spine 13.7% (8.8–18.9%) of head length; chinshields slightly enlarged, separated from infralabials by usually three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper fold larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, usually bearing slightly enlarged, pointed scales; tympanum elliptic, broad, and exposed; anterior margin of ear opening with several dentate-like scales or more enlarged triangular, pointed scales forming a serrate border; dorsal scales heterogeneous, but generally small, not overlapping; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 247% (187–301%) of head length in 46 males, 219% (175–272%) in 76 females; maximum snout-vent length = 112 mm.

Dorsal ground color brown, yellowish brown, gray to nearly black, pink, or nearly red, depending on the predominant color of the substrate; one pair of large nuchal blotches; three to four pairs of dorsal spots between the neck and sacral area; nuchal blotches and dorsal spots brown, gray or black; spots wedge-shaped or forming transverse bands; posterior edges of the dorsal spots usually denticulate or smoothly even; anterior edge of dorsal spots grades into dorsal field; posterior edge of spots bordered by a light color that is well delineated, or grades into the dorsal field; posterior borders may be white, yellow, orange, pink, or red; narrow zone of red, pink, orange or yellow color usually present above lateral fringe row; occipital and temporal horns red, pink, orange, cream, usually contrasting with general color of head; concealed surfaces of lips white, yellow, pink or bright red; gular area white with yellow-orange to nearly red color centrally, or entirely washed with color; thoracic and abdominal areas white or with pink, orange or reddish-orange pigmentation; in melanin-dispersed phase, gular area with vermiculations and a few scattered spots, with or without a gray suffusion; abdomen with large rounded or irregular melanistic spots more or less in rows; in some specimens melanistic spots interconnected to produce reticulations; some specimens with extensive black suffusion; tail with interrupted melanistic subcaudal bands; bands may be complete distally (Figs. 22–23).

Variation. Several features of the dorsal color pattern in *P. h. hernandesi* display geographical trends. In southern localities, transverse dorsal bands occur at a higher frequency than dorsal spots. In the Wasatch Range of Utah, only four specimens (7.7%) have transverse bands, 41 specimens (78.8%) have wedge-shaped dorsal spots, and seven specimens (13.4%) have slightly rounded spots. In the San Francisco Peaks region of northern Arizona, 38 specimens (53.5%) have transverse bands, 31 specimens (43.6%) have wedge-shaped dorsal spots, and two specimens (2.8%) have slightly rounded spots. In the mountains of western New Mexico, 42 specimens (59%) have transverse bands and 29 lizards (41%) have wedge-shaped dorsal spots. In the Animas Valley and adjacent mountains, six specimens (50%) have transverse bands, four specimens (33.4%) have slightly rounded spots, and two specimens (16.6%) have wedge-shaped dorsal spots. In southern Arizona, 51 specimens (79.6%) have transverse bands, eight specimens (12.5%) have wedge-shaped dorsal spots, and five specimens (7.9%) have slightly rounded spots. In northern Sonora, 40 specimens (95.2%) have transverse bands, and two specimens (4.8%) have wedge-shaped dorsal spots.

In the majority of specimens from southern localities, the light-colored borders of the dorsal spots grade into the dorsal ground color. In 64 specimens from the mountains of southern Arizona, 56 specimens (87.5%) have light-colored borders that grade into the ground color; four specimens (6.25%) lack light-colored borders, and four specimens (6.25%) have discrete light-colored borders. Forty-two specimens (100%) from northern Sonora have light-colored borders that grade into the ground color. In 12 specimens from the Animas Valley of New Mexico, eight specimens (66.6%) have indistinct light-colored borders and four specimens (33.4%) completely lack light-colored borders. In 71 specimens from the mountains of western New Mexico, 61 specimens (86%) have light-colored borders grading into the dorsal field, six specimens (8.4%) lack light-colored borders, and four specimens (5.6%) have well-defined light-colored borders. In 71 specimens from the San Francisco Peaks region of northern Arizona, 36 specimens (50.7%) have light-colored borders grading into the dorsal ground color, and 35 lizards (49.3%) have discrete light-colored borders. In Utah's Wasatch Range, 33 specimens (63.4%) have light-colored borders fading into the dorsal field, and 19 individuals (36.5%) have distinct light-colored borders.

Some specimens from the southern part of the Wasatch Range, Utah, (e.g. Duck Creek-Navajo Lake, Bryce Canyon, Escalante Mountains and Pausaugunt Plateau) have elongate nuchal blotches that extend to, and often connect with, the first pair of dorsal spots. This pattern trait has not been observed in specimens from Arizona, New Mexico, or Sonora.

Typically, *P. h. hernandesi* has a narrow zone of red pigment that runs above the lateral fringe row. The color extends from near the foreleg insertion to about one-third the length of the fringe row, or it may run the entire length. The red pigment has been noted in Arizona specimens from the San Francisco Peaks and Hualapai Mountains, but it is subdued or absent from the majority of specimens from the Santa Catalina Mountains. Some specimens from the Cerbat Mountains and San Francisco Peaks have pale yellow rather than red pigment above the fringe row. In New Mexico, the red color has been noted in specimens from the Jemez, Manzano, Sangre de Cristo, San Francisco and San Pedro mountains, but absent from the few specimens examined from the San Mateo Mountains. In all specimens examined from northern Sonora and from the Animas Valley of New Mexico, the red color is absent or faded to pink. In Utah, it has been noted in the few specimens examined from Navajo Lake (Kane County) and the Pausaugunt Plateau (Garfield County). At least some specimens from the Davis Mountains of west Texas also have the red color.

Some specimens from southeastern Utah and adjacent Colorado have a white vertebral stripe. The length of the stripe varies; in some specimens it begins near the nuchal blotches, in others about midway on the back, extending to the base of the tail. In a few specimens it is limited to sacral area and base of the tail. The dorsal stripe was noted in specimens from north and west of Blanding (Elk Ridge) and near Monticello, San Juan County, Utah, and from Mesa Verde, Montezuma County, and Gypsum Creek, San Miguel County, Colorado.

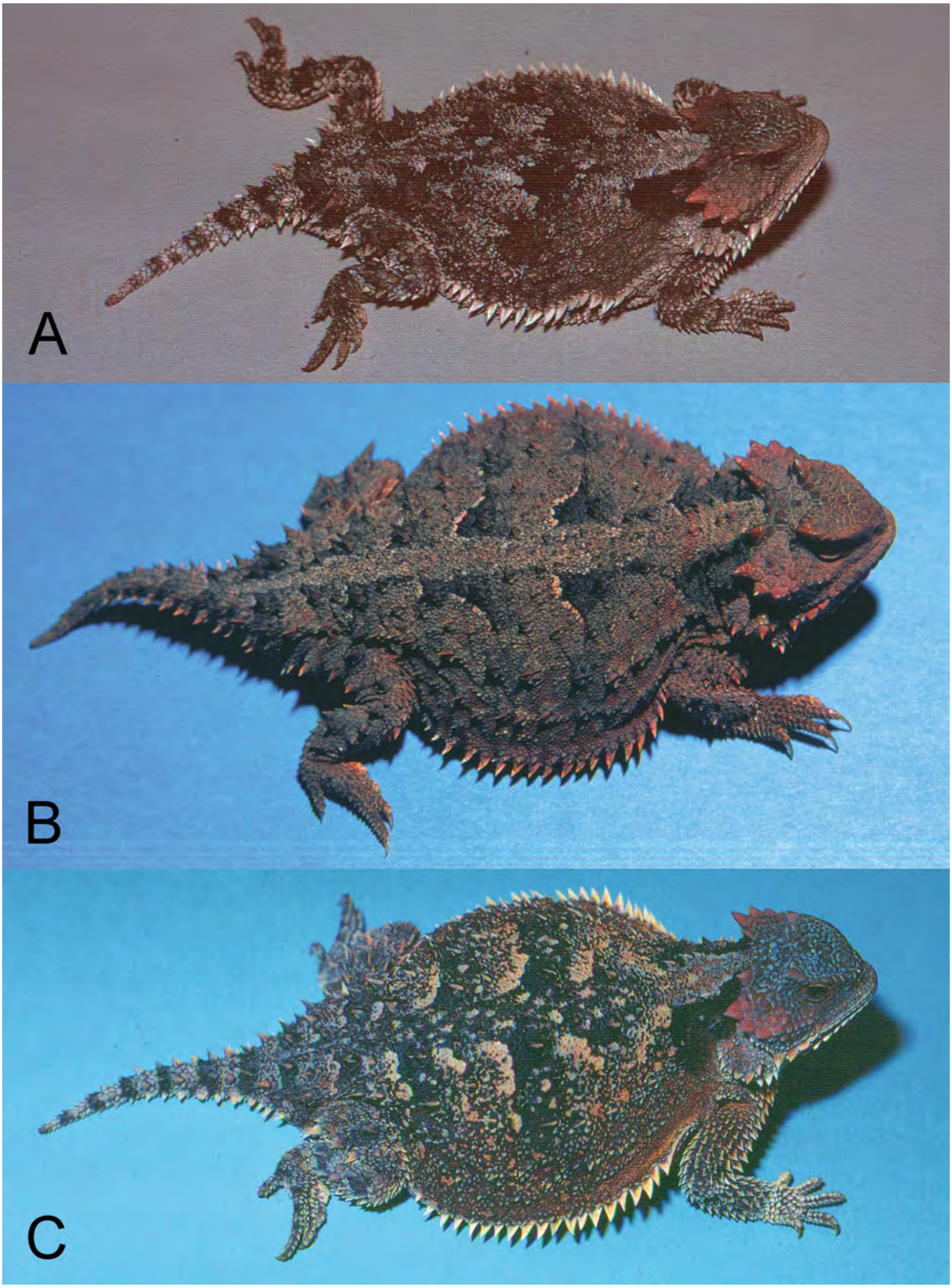

FIGURE 22. *Phrynosoma hernandesi.* (A) adult female (RRM 2115) from Santa Catalina Mts., Pima Co., Arizona. (B) adult female (RRM 03-1) from 4 km NW Gallina, Rio Arriba Co., New Mexico; (C) adult female (RRM 2310) from Elden Mountain, Coconino Co., Arizona.

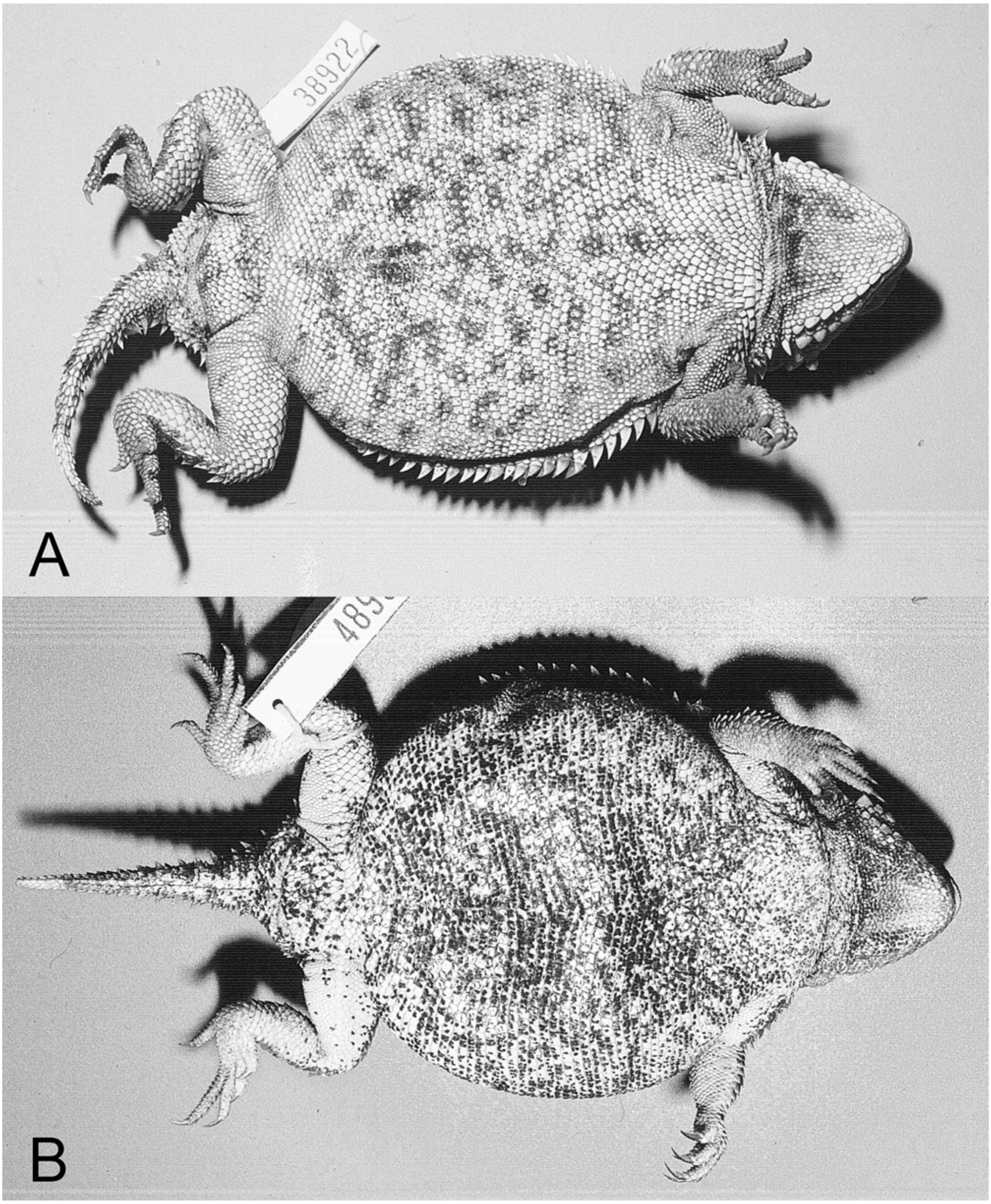

FIGURE 23. Ventral aspect of *Phrynosoma hernandesi.* (A) adult female with large melanistic spots (MSB 38922) from near Mule Creek, Grant Co., New Mexico; (B) adult female with dark suffusion (MSB 48987) from 12 km S Cloudcroft, Otero Co., New Mexico.

The head is generally uniform in color, but occasional specimens have white, bluish white or pale yellow flecks, especially in the frontal area. In 27 specimens from the San Francisco Peaks of northern Arizona, six specimens have light-colored flecks. In 28 specimens from the Santa Catalina Mountains of southern Arizona, two specimens have light-colored flecks. Three of 27 specimens from scattered locations in Cochise County, Arizona, have whitish flecks on the head, but the flecks are absent in all of 42 specimens examined from northern Sonora as well as ten specimens from the Animas Valley of southwestern New Mexico. The light-colored flecks are absent in 71 specimens from the mountains of Grant and Catron counties, New Mexico, but a few specimens with the flecks have been noted from the Sandia and Manzano mountains. In the Sacramento and Guadalupe mountains of southern New Mexico, some specimens have narrow white borders outlining the frontal scales.

The reddish color of the occipital and temporal horns varies ontogenetically, with juveniles and sub-adults having more subdued hues than adults. The color may be confined to the tips of the horns, or extend over much of the temporal shelf. The color of the occipital and temporal horns also shows inter-locality variation. The horns of lizards from the Cerbat and Hualapai mountains, Mogollon Rim, and San Francisco Peaks region are usually bright red although in a few individuals the color is pale pink or orange-pink. Short-horned izards from the Santa Catalina Mountains also have pink to orange-pink horns. In northern Sonora and the Animas Valley of southeastern New Mexico, most specimens have pink to cream colored horns, less commonly red. The horns of lizards from the San Francisco, San Pedro and Jemez mountains of New Mexico are usually dark red. The horn color of lizards from several localities in the Wasatch Range of Utah (e.g. Hurricane Cliffs, Navajo Lake, Pausaugunt Plateau) is typically red or pink.

A comparison of samples of *P. h. hernandesi* from the San Francisco Peaks, southeastern Arizona, and northern Sonora reveals significant differences in proportional tail length. The variation suggests a cline correlated with latitude, with the northern samples having a longer average tail length (as a percentage of head length) than southern samples. But additional samples are needed to clearly demonstrate a cline. The sample mean ± two standard errors, observed limits, and sample size for males are as follows: San Francisco Peaks 287% ± 6.94 (266–301%), n = 10; southeastern Arizona 247% ± 8.33 (215–272%), n = 16; northern Sonora 224% ± 7.21 (187–260%), n = 19. The statistics for females are as follows: San Francisco Peaks 233% ± 6.62 (207–272%), n = 30; southeastern Arizona 213% ± 4.90 (177– 251%), n = 52; northern Sonora 202% ± 7.04 (175–246%), n = 23.

P. h. hernandesi from the Wasatch Range in Utah exceeds the limits of variation for several characters compared with typical representatives of the species from Arizona and New Mexico. The characters include the orientation of the occipital and temporal horns, the relative length of the temporal horns, and the profile of the rostrofrontal area of the head.

The sample from the Wasatch Range has a higher proportion of upward directed horns compared with other populations of *P. h. hernandesi*. In a series of 24 specimens from the Wasatch Range (vicinity of Kolob Plateau, Navajo Lake, Cedar Mountain, Cedar Breaks, Bryce Canyon, Table Cliff Plateau), eight specimens (33.3%) have horizontally directed horns, eleven specimens (45.8%) have occipital horns directed slightly upward and temporal horns directed horizontally; five individuals (20.8%) have both occipital and temporal horns directed slightly upward.

In a series of nine specimens from the Henry Mountains (an isolated range east of the Wasatch Uplift), three specimens (33.3%) have horizontally directed occipital and temporal horns; one individual (11.1%) has occipital horns directed slightly upward, and five specimens (55.5%) have both sets of horns directed upward.

Short-horned lizards from the Kaibab Plateau south of the Wasatch Range in northern Arizona show similar variation. Seven specimens (38.9%) have horizontally directed occipital and temporal horns; three specimens (16.6%) have only upward directed occipital horns, and eight specimens (44.4%) have upward directed occipital and temporal horns.

By contrast, a relatively high percentage of specimens from more southerly localities have horizontally directed occipital and temporal horns. Just to the south of the Colorado River, in northern Arizona (San Francisco Peaks, Flagstaff), the occipital and temporal horns are horizontally directed in 53 specimens (74.6%); in 16 specimens (22.5%) the occipital horns project upward but the temporal horns are directed horizontally; in two specimens (2.8%), both sets of horns are directed upward. In short-horned lizards from the mountains of southern Arizona (Chiricahua, Huachuca, Santa Catalina, and Santa Rita mountains), the occipital and temporal horns project horizontally in 51 specimens (79.6%); in nine specimens (14.0%) the occipital horns project at an angle above the horizontal and the temporal horns are horizontally directed; in four examples (6.3%) both sets of horns project upward. In a series from the mountains of western New Mexico (Grant and Catron counties), the occipital and temporal horns project horizontally in 63 specimens (88.7%), and in two specimens (2.8%) the occipital horns project upward and the temporal horns project horizontally; in six specimens (8.5%) both sets of horns are elevated above the horizontal. In 12 specimens from the Animas Valley of southwestern New Mexico (Hidalgo County), the occipital and temporal horns project horizontally in ten specimens (83.3%) and in two specimens (16.7%) they project at an upward angle. In lizards from northern Sonora, the occipital and temporal horns project horizontally in 41 of 42 specimens (97.6%), and in one individual (2.4%) the horns project at a slight angle above the horizontal.

Specimens from the Wasatch Range have relatively short temporal horns. In 24 specimens, the third temporal horn is 13.3% (9.1–17.9%) of head length. Two specimens with the shortest horns (9.1% and 9.7% of head length) are from Bryce Canyon. Two specimens with the longest horns (17.4% and 17.9% of head length) are from the vicinity of Orderville, Kane Co, Utah. The third temporal horn is also relatively short in lizards from the Henry Mountains, the average is 12.5% (10.1–14.9%) of head length in eight specimens, and only 15.6% of head length in a ninth specimen. Lizards from the Kaibab Plateau also have short horns. The length of the third temporal horn averages 14.2% (10.0–18.3%) in a sample of 18 specimens.

South of the Grand Canyon, there is a marked increase in the length of the third temporal horn. In nine specimens from the South Rim of the Grand Canyon, the length averages 19.1% (15.1–23.7%) of head length. Farther south, in the San Francisco Peaks region, temporal horn length is 17.5% (13.0–23.2%) of head length in 27 lizards. Samples from more southerly areas show little change in the temporal horn length. In 65 lizards from the mountains of western New Mexico (Catron and Grant counties), horn length is 17.8% (11.7–24.1%) of head length. In 64 specimens from the mountains of southern Arizona, temporal horn length averages 18.5% (13.5–23.7%) of head length, and in 42 specimens from northern Sonora, the temporal horn length averages 18.4% (14.0–22.3%) of head length.

The rostrofrontal profile shows variability in the short-horned lizards from the Wasatch Range. Fifteen specimens (62.5%) have a gradually inclined rostrofrontal profile and protruding snout as in typical *P. h. hernandesi*, but seven specimens (29.2%) have a slightly rounded profile, and two specimens (8.3%) show an angular profile. Nine specimens from the Henry Mountains show a gradually inclined profile, but the snout appears to be less protruding than in typical *P. h. hernandesi*. The rostrofrontal profile of Kaibab Plateau short-horned lizards is gradually sloping in six specimens (33.3%), rounded in nine specimens (50%), and rather angular and steeply inclined in three specimens (16.6%).

The temporal shelf is also shorter in *P. h. hernandesi* from the Wasatch Range and Henry Mountains compared with samples from Arizona and Sonora. A subset of samples of females in the same body size class was compared; data for males were inadequate. The mean and observed limits are as follows: Wasatch Range (n = 15 females), 21.6% (18.1–27.1%); Henry Mts. (n = 3 females), 20.6% (20.2–21.1%); SE Arizona-Sonora (n = 11 females), 26.0% (22.8–29.8%). Although a history of genetic interaction with *P. brevirostris* may account for the morphology of Utah *P. h. hernandesi*, clinal variation along a latitudinal gradient may be an alternative explanation. Populations in the San Francisco Peaks region, which lies south of the Grand Canyon and presumably beyond the genetic influence of *P. brevirostris*, show a temporal shelf with an intermediate expansion compared with populations to the north and south. The mean ± two standard errors, observed limits, and sample size for females are: Wasatch Range, 19.1% ± 1.4 (9.3–27.1%), n = 35; San Francisco Peaks, 23.0% ± 1.2 (17.2–30.3%), n = 35; SE Arizona-Sonora, 27.6% ± 0.79 (20.3–36.2%), n = 72.

In summary, a notable proportion of the *P. h. hernandesi* from the Wasatch Range, the Henry Mountains, and the Kaibab Plateau have upward directed cephalic horns, relatively short temporal horns, a relatively short temporal shelf, and a tendency toward a rounded rostrofrontal profile. The range of variation in these characters suggests that *P. h. hernandesi* in eastern Utah experienced a history of genetic interaction with *P. brevirostris*, although for the temporal shelf length, a latitudinal cline cannot be ruled out.

Distribution and habitat. *P. h. hernandesi* ranges from northern Sonora (recorded as far south as Sierra de la Madera, ENE of Moctezuma) through the isolated mountain ranges and grasslands of southeastern Arizona northward along the Mogollon Rim. It ranges across the Coconino and Kaibab plateaus and follows the Wasatch Range in Utah. It occurs in the Pavant Range west of the Sevier River, and in the Henry Mountains northeast of the Escalante River, but presently there are no records from the Uinta Mountains in Utah. In northwestern Arizona there are records for the Hualapai and Cerbat mountains, Shivwits Plateau (near Snap Point) and the Mount Trumbull area. In northeastern Arizona, it skirts most of the Little Colorado River Basin, but it or putative hybrids (with *P. ornatissimum*) occur in the Chuska Mountains in the border region with New Mexico. In New Mexico it ranges from the Animas Valley in the southwestern corner northward through the mountains of the western and north-central parts of the state. It enters southwestern Colorado, and presumably also south-central Colorado along the Sangre de Cristo Range, although records are presently lacking. *P. h. hernandesi* also occurs in the Sacramento and Guadalupe mountains of southern New Mexico and the Sandia and Manzano mountains in the north-central region; these montane populations are partly or completely surrounded by *P. ornatissimum* in the desert grasslands below. The ecological relationships and genetic interactions of these taxa are discussed elsewhere (see below). In west Texas it is known from the Guadalupe and Davis mountains, and is expected in the Delaware and Apache mountains (see Appendix II, maps 3, 5, 7, 9, 14, 18, 19).

In northern Sonora, southeastern Arizona, and the adjacent Animas Valley of New Mexico, the dominant vegetation is Grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*); it is replaced by Oak-juniper woodland (*Quercus-Juniperus*) along the lower slopes of mountain ranges, and at higher elevations Arizona pine forest (*Pinus*) dominates. At the highest elevations of the Mogollon Rim, Arizona pine forest is the dominant vegetation, and it is replaced by Juniper-pinyon woodland (*Juniperus-Pinus*) on the lower slopes. On the southwest facing slopes below the Juniper-pinyon woodland is a mixed association of Oak-juniper woodland and Mountain mahogany-oak scrub (*Cercocarpus- Quercus*) extending from near Globe to north of Prescott, Arizona. In the San Francisco Peaks region, *P. h. hernandesi* occurs in Juniper-pinyon woodland on the lower slopes, Arizona pine forest at middle elevations, and Spruce-fir-Douglas fir forest (*Picea-Abies-Pseudotsuga*) and Southwestern spruce-fir forest (*Picea-Abies*) at the highest elevations. The same sequence of habitats is found on the Kaibab Plateau, but without the Southwestern spruce-fir forest. In all these vegetative associations, populations occur in open areas usually with friable soils where the trees and shrubs are widely spaced.

In the Wasatch Range of Utah, *P. h. hernandesi* occurs in several climax fasciations including Arizona pine forest (*Pinus*), Spruce-fir-Douglas fir forest (*Picea-Abies-Pseudotsuga*) and Western Spruce-fir forest (*Picea-Abies*). In some areas, *P. h. hernandesi* may also occur in Juniper-pinyon woodland, except along the western slopes where the nominate race appears to be replaced by *P. h. ornatum* (see next account). Near 39° N latitude northward along the mountain axis east of Provo and Salt Lake City, *P. h. hernandesi* (or *P. h. ornatum*) occurs in Mountain mahogany-oak scrub (*Cercocarpus-Quercus*) on the lower slopes, and Douglas fir forest (*Pseudotsuga*) at higher elevations.

In the mountains of New Mexico, *P. h. hernandesi* has been recorded at lower elevations in Juniper-pinyon woodland, and at higher elevations in Pine-Douglas fir forest. This pattern has been noted in the Black Range, Mimbres, Mogollon and San Mateo mountains for the western part of the state, and in the Sierra Nacimiento, Jemez, Sangre de Cristo, San Pedro, Sandia and Manzano mountains in the central and northern regions. However, the highest peaks of the Mogollon, Sierra Nacimiento, Jemez, and Sangre de Cristo mountains are dominated by Southwestern spruce-fir forest (*Picea-Abies*). The same vegetation sequence is observed in the Sacramento Mountains of southern New Mexico, but in the Guadalupe Mountains, the lower slopes are dominated by Oak-juniper woodland and only a small, high elevation area supports Pine-Douglas fir forest. Remarkably, Gehlbach (1965) obtained specimens in Alpine tundra at 3,424 m on Mount Taylor in northwestern New Mexico. In the Davis Mountains of west Texas, all records of *P. hernandesi* are in Oak-juniper woodland habitat.

Remarks. *P. h. hernandesi* from the Wasatch Range of Utah is poorly represented in institutional collections. Further collecting is needed to obtain a better understanding of the distribution limits and geographic variation of the species in that region. In west Texas, it should be sought in the Delaware and Apache mountains as well as other adjacent ranges. There is a record for Deming, Luna County, New Mexico (ANSP 21119) that is probably inaccurate or erroneous. The specimen may have been collected in the nearby Florida Mountains or the southern end of the Cookes Range.

As yet, there are no records of *P. hernandesi* from the highest elevations of the Sangre de Cristo Mountains east of the San Luis Valley in Colorado, although specimens are known from these mountains in New Mexico. Specimens and photographic vouchers from Mosca Pass and southeast of Russell show combinations of traits from *P. bauri* **sp. nov.** and *P. hernandesi*, leading to speculation that *P. bauri* **sp. nov.**, which occurs along the eastern slopes and at lower elevations, has genetically swamped smaller, relictual populations of *P. hernandesi* previously occurring in the high elevation areas. This question should be investigated further.

Phrynosoma hernandesi ornatum **Girard 1858b, comb. nov.**

(Figs. 21B, 24–26)

Phrynosoma ornatum Girard 1858b: pl. 21, figs. 1-5.
Phrynosoma douglassi Gentry 1885:140 (part).
Phrynosoma douglassii hernandesi Cope 1900:413 (part).
Phrynosoma douglassii hernandesi Richardson 1915:423 (part).
Phrynosoma douglassii ornatum Stejneger 1919:3.
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377 (part).
Phrynosoma douglassii ornatum Smith 1946:307.
Phrynosoma douglassii ornatissimum Smith 1946:305 (part).
Phrynosoma douglassii douglassii Reeve 1952:918 (part).
Phrynosoma douglassii hernandesi Reeve 1952:922 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

Etymology. The Latin word *ornatus –a - um,* (participle of the verb *orno*), meaning "adorned" or "decorated" or "embellished". As no type description exists, one can only speculate as to Girard's intended reference, but possibly to contrasting dark and light-colored markings on the dorsum.

Suggested common name: Salt Lake Valley Short-horned Lizard.

Type locality. The type locality is the valley of the Great Salt Lake, Utah.

Taxonomic history. *Phrynosoma ornatum* is illustrated in Girard's atlas (Girard 1858b; plate 21, figs. 1–5) from material collected near Salt Lake, Utah, the type locality. According to Stejneger (1919), Girard was ambivalent about the validity of *Phrynosoma ornatum* and while his text (Girard 1858a) was in press, he decided to place the name in the synonymy of *Tapaya douglasii* (the name *Tapaya* having the taxonomic rank of subgenus). However, Girard's decision came too late to alter the caption for the illustrations in plate 21. Thus, the name *Phrynosoma ornatum* remained available by virtue of its use in the caption for the figures. Stejneger (1919) considered the name and associated illustrations as a sufficient and valid description. He believed that this taxon was not related to *P. hernandesi*, and was distinct enough from *P. douglasii* to be treated as a subspecies. He therefore revived the name and applied it to the populations occurring in the Salt Lake Valley of Utah; Stejneger's action was followed by Smith (1946) and Reeve (1952).

Reeve (1952:847) indicated that the type specimen of *Phrynosoma ornatum* was unknown. Nearly a decade later, Benjamin H. Banta initiated a search to determine if it was still extant, eventually reaching the conclusion that UMMZ 3849 was the missing holotype (Banta, 1970). However, Montanucci (2010) investigated the matter further and discovered that Girard's illustrations (figs. 1–5) were based on two specimens, a female and a male, which together constituted syntypes. Furthermore, Montanucci determined that UMMZ 3849 was not the male syntype used in Girard's fig. 5, and he assumed the male syntype to be lost. With regard to the female syntype, Montanucci found that USNM 234 (an adult female, and one of three specimens procured by J. Bowman in the Salt Lake Valley), bears considerable similarity to the specimen in figs. 1–4 in plate 21 of Girard's atlas, and suggested that it could be the missing female syntype.

Diagnosis. *Phrynosoma hernandesi ornatum* can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout truncate to more or less protruding, 45.3% ± 1.62 (39.2–54.2%) of orbital to rostral distance; (2) rostrofrontal profile gradually rounded or obtusely angular to flat and gradually sloping; (3) frontal rim not elevated, or only slightly elevated above the occipital shelf; (4) enlarged frontal rim scales 1.64 ± 0.28 (0–3) / 1.77 ± 0.29 (0–3); (5) temporal shelf moderately short, 17.3% ± 0.83 (13.2–22.6%) in males, 19.8% ± 0.73 (11.8–27.0%) in females; (6) temporal shelf flat or weakly to moderately convex; (7) cephalic horns moderately short, third temporal horn length 13.9% ± 0.38 (8.8–21.0%); (8) cephalic horns directed horizontally or elevated (ca. 45°); (9) tympanum elliptic, moderately broad to broad; (10) tympanum exposed; (11) tail moderately long, 222% ± 6.41 (188–271%) in males, 199% ± 3.66 (161–235%) in females; (12) dorsal spots wedge-shaped or forming transverse bands; (13) light-colored borders of dorsal spots confined to posterior edges; (14) dorsolateral white spots absent; (15) gular area with vermiculations and scattered melanistic spots, with or without gray suffusion (melanin-dispersed phase); (16) abdomen with large melanistic spots or scattered flecks (melanin-dispersed phase); (17) interrupted and/or complete melanistic subcaudal bands present (melanin-dispersed phase).

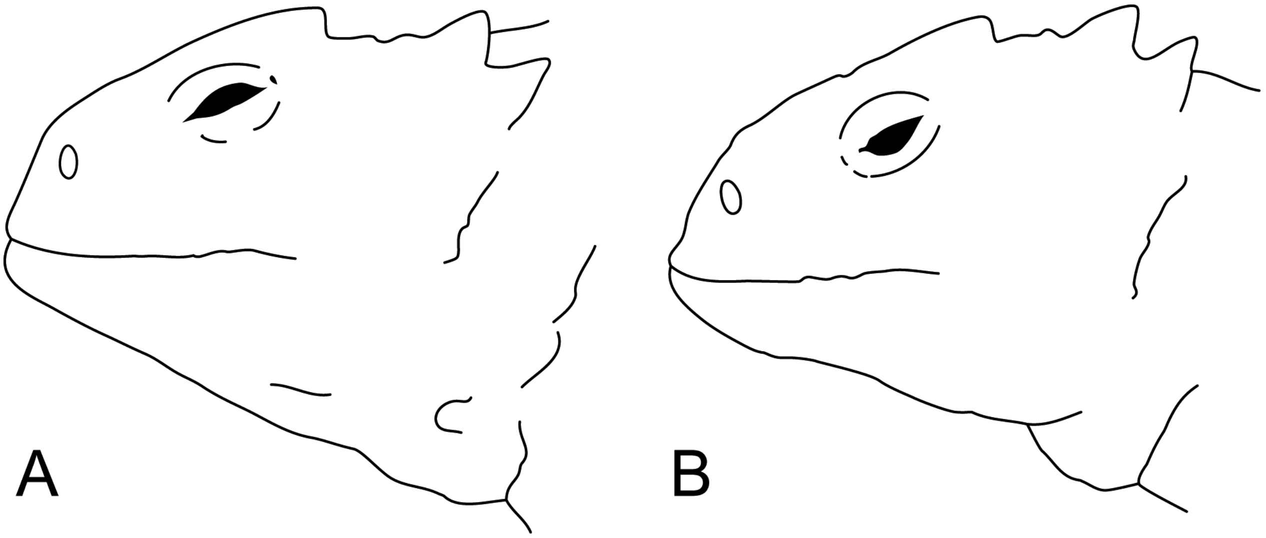

FIGURE 24. Rostrofrontal profile of *Phrynosoma hernandesi ornatum.* (A) typical profile (UMMZ 59572, Salt Lake Co., Utah); (B) atypical profile (USNM 60959, Salt Lake Co., Utah).

Comparisons. *Phrynosoma hernandesi ornatum* can be distinguished from the nominate race by a less protruding snout and usually more rounded or angular rostrofrontal profile, a frontal rim not elevated or only slightly elevated above the occipital shelf, a significantly lower mean number of enlarged frontal rim scales, a temporal shelf more or less convex and less produced lateroposteriorly, and shorter occipital and temporal horns on average (except when compared with Wasatch Range *P. hernandesi*). About 18.5% of *P. h. ornatum* have a more or less flattened temporal shelf compared with 54% of the nominotypical *hernandesi* having a flattened temporal shelf. This race also has a higher percentage of upward-directed occipital horns compared with New Mexico and Arizona samples of *P. hernandesi*, but not Utah samples (see **Variation**).

P. h. ornatum can be distinguished from *P. bauri* **sp. nov.**, *P. brevirostris, P. diminutum* **sp. nov.** and *P. douglasii* by its slightly protruding snout and gradually rounded rostrofrontal profile, longer temporal shelf (except *P. bauri* **sp. nov.**) and longer occipital and temporal horns (except *P. bauri* **sp. nov.**). It is further distinguished from these taxa by the usual presence of red pigment on the cephalic horns, presence of pink or red pigment on gular and chest areas, and in the melanin-dispersed phase, the presence of large, melanistic abdominal spots (except *P. bauri* **sp. nov.** and *P. diminutum* **sp. nov.**) or scattered flecks (except *P. brevirostris*), and interrupted or complete melanistic subcaudal bands. *P. h. ornatum* can be further distinguished from *P. douglasii* by its comparatively broad, elliptic, and exposed tympanum, and by its large adult size. *P. h. ornatum* can be distinguished from *P. ornatissimum* by a more protruding snout and gradually sloping rostrofrontal profile, a slightly shorter temporal shelf, a relatively longer tail, absence of a discrete white and/or yellow line along the medial edge of each dorsal spot (except *P. o. brachycercum*), absence of dorsolateral white spots (except most *P. o. brachycercum*), wedge-shaped dorsal spots or dorsal cross-bands (except *P. o. brachycercum*), presence of reddish color on the cephalic horns contrasting with the general hue of the head, and in the melanin-dispersed phase, a gular pattern of gray suffusion with spots and vermiculations (as opposed to chevrons or wavy and irregular transverse bands), presence of large melanistic spots on the abdomen, and the presence of melanistic subcaudal bands.

Description. This account is based on the study of specimens from the Basin and Range physiographic region of Utah situated west of the Wasatch Range, including the Great Salt Lake Valley, and the Sevier, Black Rock, and Escalante deserts to the south. Also included are specimens from southwestern Idaho, and most of central, eastern, and northern Nevada except the elevated region north and west of the Smoke Creek and Black Rock deserts (n = 171; see Appendix I).

Head broader than long; snout moderately protruding, rostrofrontal profile gradually rounded or obtusely angular, gradually inclined in some specimens (Fig. 24); frontal area nearly flat; dorsal surfaces of the head covered with small, irregular, convex scales with rugosities formed by granulations and/or irregular ridges; frontal rim not elevated or only slightly elevated above the occipital shelf (Fig. 21B); superciliary ridges distinct, terminating posteriorly in a spine usually equal to or slightly shorter than the occipital horn; external nares laterally pierced just below line of canthus rostralis; temporal shelf weakly to moderately convex, but nearly flat in 18.5% of sample; moderately expanded and produced lateroposteriorly; occipital emargination deep; three short temporal horns, most posterior (third) largest, 13.9% (8.8–21%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one occipital horn on each side, separated from third temporal horn by one or two scales; supralabials small; infralabials increasing in size posteriorly; usually three enlarged postlabials, 2.86 (2–4); postrictal spine 12.4% (7.2–18.9%) of head length; chinshields slightly enlarged, separated from infralabials usually by three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper fold larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, usually bearing slightly enlarged, pointed scales; tympanum elliptic, broad, and exposed; anterior margin of ear opening with several slightly enlarged dentate-like scales or further enlarged triangular, tapered scales forming a serrate border; dorsal scales heterogeneous, but generally small, not imbricate; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail 222% (188–271%) of head length in 41 males, 199% (161–235%) in 81 females; maximum snout-vent length = 98 mm.

Dorsal ground color pale brown, yellowish brown, reddish brown, or whitish gray to dark gray-brown depending on the predominant hue of the substrate; one pair of large nuchal blotches; three to four pairs of dorsal spots between the neck and sacral area; nuchal blotches and dorsal spots usually gray to black; dorsal spots seldom rounded, usually wedge-shaped or forming transverse bands; posterior edges of dorsal spots usually denticulate or smoothly even, with light-colored borders that are discrete or grade into dorsal field; light-colored borders are white and/or yellow; a narrow zone of red, orange-red to pale orange pigment above lateral fringe row; spines of lateral fringe white, or sometimes yellow (in males); occipital horns with or without reddish color; largest and next to largest temporal horns with red or pink, contrasting with gray or gray-brown color of head; reddish color may extend onto temporal shelf; concealed surfaces of lips white, pink or red; gular area white with or without pinkish suffusion near gular fold; in melanin-dispersed phase, gular area with vermiculations and melanistic spots with or without dark gray suffusion; venter white; in melanin-dispersed phase, chest with dark flecks or patches of gray suffusion; abdomen with scattered flecks or with patches of gray suffusion centrally, and/or with large rounded or irregular melanistic spots, in rows or scattered; in a few specimens melanistic spots interconnected to produce reticulations; underside of tail with melanistic bands, interrupted or complete, especially distally (Figs. 25–26).

Variation. Nevada and Utah samples differ for average tail length, although the observed limits of variation are similar. The sample means are significantly different ($P < 0.05$) for females and nearly significant for males. The sample mean ± two standard errors, observed limits, and sample size for males are: Nevada (pooled samples) 235% ± 11.99 (193–271%), n = 13; Utah (pooled samples) 217% ± 6.55 (188–258%), n = 28. The statistics for females are: Nevada 208% ± 5.04 (175–235%), n = 35; Utah 192% ± 4.28 (161–224%), n = 46.

In samples from Nevada, the occipital and temporal horns are directed horizontally in 13 specimens (26%); in 18 specimens (36%) the occipital horns project slightly upward, but the temporal horns are directed horizontally; in 19 individuals (38%) both sets of horns project slightly upward, but with the occipital horns nearly vertical in four specimens.

In samples from Utah, the occipital and temporal horns are directed horizontally in seven specimens (7.8%); in 23 specimens (25.8%) the occipital horns project slightly upward, but the temporal horns are directed horizontally; in 59 specimens (66.3%) both sets of horns project slightly upward, but with the occipital horns nearly vertical in 12 specimens.

In four specimens from southwestern Idaho, three have upward directed occipital and temporal horns (the occipital horns are nearly vertical in two specimens), and one specimen has upward slanted occipital horns but the temporal horns are directed horizontally.

The shape of the dorsal spots does not show any geographic pattern, but varies within local populations. In Nevada samples, 32 specimens (64%) have wedge-shaped dorsal spots, 11 specimens (22%) have transverse bands, and seven examples (14%) have slightly rounded spots. In samples from Utah, 74 specimens (83.1%) have wedge-shaped dorsal spots, nine specimens (10.1%) have transverse bands, and six examples (6.7%) have slightly rounded spots.

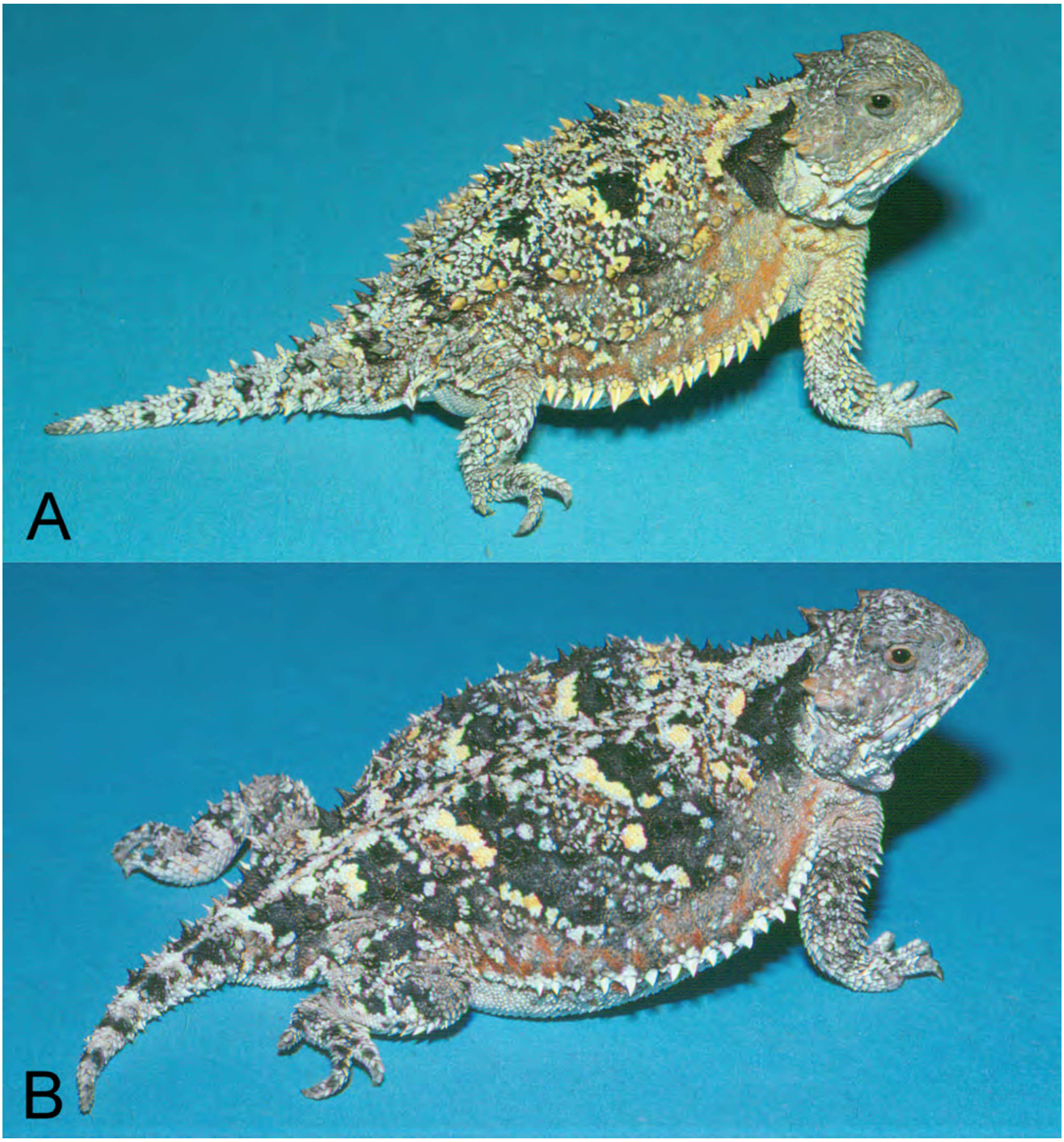

FIGURE 25. *Phrynosoma hernandesi ornatum.* (A) adult male (RRM 2438) and (B) adult female (RRM 2471) from 11.2 km S Currie, Elko Co., Nevada.

Smith (1946) characterized this race as "frequently nearly uniform gray", and Reeve (1952:932) referred to its generally paler color compared with nominotypical *hernandesi*. Reeve's impression may have been influenced, in part, by studying specimens preserved in the melanin–aggregated phase. However, especially pale specimens with faint dorsal spots and indistinct light-colored borders are also associated with alkali flats, and tend to be gray, whereas specimens from darker substrates may be various shades of brown. In Nevada, there is also a close correspondence with soil color; specimens from dark soils are generally dark gray brown or reddish brown, those from whitish soils are pale gray. Some specimens are speckled with white, yellow, orange and red especially in the mid-dorsal area. The speckling may be so intense as to obscure or obliterate the light-colored posterior borders of the dorsal spots. The head may be uniform or have a few, scattered light-colored flecks.

In samples from Nevada, 30 specimens (60%) have dorsal spots with light-colored borders grading into the dorsal field, and 20 specimens (40%) have discrete light-colored borders. In Utah's Bonneville Basin, 68 specimens (76.4%) have light-colored borders fading into the dorsal field, and 21 examples (23.6%) have discrete light-colored borders. Faint dorsal spots with faded borders as part of a generally subdued dorsal pattern, may provide enhanced concealment on alkali substrate.

Distribution and habitat. *P. h. ornatum* ranges from west of the Wasatch Uplift in Utah westward into northern Nevada, southwestern Idaho and adjacent southeastern Oregon (see Appendix II, maps 10, 13, 16, 19).

In Utah, the distribution of *P. h. ornatum* coincides with the limits of the basin of Pleistocene Lake Bonneville. It has been recorded from the Great Salt Lake Valley including the Rush Valley, Sevier and Black Rock deserts north and south of the lower Sevier River, respectively, and the Escalante Desert to the south. Southernmost records in Iron County include west of Cedar City in the vicinity of Dry Lake, and just south of Kanarraville at 1,661 m (5,450 ft) elevation in Juniper and sagebrush association. Remarkably, it has also been collected in the Beaver Dam Mountains west of St. George in Washington County (BYU 37195). This record needs to be confirmed by additional specimens.

Presumably, *P. h. ornatum* enters the Sevier River Valley, but the limits of its distribution there are unknown; specimens from the Pavant Range (ca. 2,744 m; 9,000 ft) west of the Sevier River and in the San Pitch Mountains west of the San Pitch River appear to be the nominate subspecies. Stuart (1932) did not record any short-horned lizards from the floor of the Pavant Valley at ca. 1,555 m (5,100 ft), but found specimens (referable to *P. h. ornatum*) in abundance in the nearby foothills of the Pavant Range in sagebrush and juniper habitat at an elevation of ca.1,982 m (6,500 ft). Specimens from Indianola at 1,804 m (5,917 ft) elevation in the upper Thistle Creek Valley and from Hobble Creek Canyon east of Springville, Utah County, are also referable to *P. h. ornatum*. Reeve (1952) classified specimens from Mount Timpanogos north of Provo as *ornatum*. The elevation at which these specimens were collected was not recorded, but the specimens agree with *P. h. ornatum* in the morphology of the frontal rim, temporal shelf, and length of the third temporal horn.

In Nevada, *P. h. ornatum* occurs in the central, eastern, and northern parts of the state, except the elevated region north and west of the Smoke Creek and Black Rock deserts where it is apparently replaced by *P. douglasii.* Although Ruthven (1915) reported it only from the floor of Maggie Basin in areas of fine soil, it is now known to inhabit high mountain ranges as well as desert basins; it has been recorded from the Santa Rosa Mountains (near Granite Peak at 2,134 m [7,000 ft] elevation), the Ruby Mountains, the White Pine Mountains (near the ghost town of Hamilton), the White Rock Mountains near the Utah border, and in the Monitor Range at 2,500 m (8,200 ft) elevation; it is expected in the adjacent Toquima and Toiyabe ranges. It is also known from the Humboldt River basin, including the tributaries of Maggie Creek, Suzie Creek, and Marys River. It also occurs along the north-flowing Salmon Falls Creek and Owyhee and Little Owyhee River valleys extending into southwestern Idaho.

The first Idaho collections were from ca. 11 to 17.6 km north of the Nevada state line, and between Juniper Lake Basin and the South Fork of the Owyhee River in Owyhee County. These collections were made by Henry S. Fitch in 1937, but Reeve (1952:921) apparently neglected to study the specimens and erroneously listed them under his *P. douglassii douglassii* [sic]. Jezkova (unpubl. data) recorded *P. h. ornatum* from 6.9 km NNW of Three Creek in Owyhee County and from the vicinity of Trout Creek Mountain, in SW corner of Cassia County. It occurs as far north as the lower reaches of Squaw Creek south of Marsing, Owyhee County (UAZ 1992).

In Oregon, *P. h. ornatum* is known from the Oregon Canyon Mountains, Malheur County, and expected to occur in the Trout Creek Mountains of adjacent Harney county. The first collection of this taxon was made by C. Maser in 1976 from Mud Spring, Malheur County (PSM 10420-21). Subsequently, St. John *et al*. (2012) reported it (as the nominotypical subspecies) from apparently the same locality. As an aside, the Oregon Canyon Mountains are not known by that name by the residents of the region; the entire uplift is known as the Trout Creek Mountains (Alan St. John, personal communication).

Much of the Lake Bonneville Basin is a mosaic of two vegetative associations, Saltbush-greasewood (*Atriplex-Sarcobatus*) and Great Basin sagebrush (*Artemisia*) and both are occupied by *P. h. ornatum*, although there is no information concerning relative densities or habitat preferences. There are only a few records for *P. h. ornatum* from Juniper-pinyon (*Juniperus-Pinus*) habitat in isolated mountain ranges within the Lake Bonneville Basin area. Pack (1918) reported it from Saltbush-greasewood association just west of Salt Lake City, and over subsequent decades it was collected in this habitat at various localities in the basin farther south and west (e.g. Orr's Ranch in Skull Valley). Knowlton & Thomas (1936) referred to the habitat as "salt desert shrub formation", consisting of sagebrush, shadscale, greasewood, rabbitbrush, and juniper. South of the Great Salt Lake Desert the Saltbush-greasewood community covers a large area extending from near Fish Springs well beyond the dry bed of Sevier Lake. On the east side of Salt Lake City near Fort Douglas, and in parts of the Rush Valley, *P. h. ornatum* has been collected in Great Basin sagebrush. Intergradation between *P. h. ornatum* and the nominate subspecies is expected in the upper limits of the Juniper-pinyon woodland along western slopes of the Wasatch Range. However, few specimens have been collected from this presumptive contact zone.

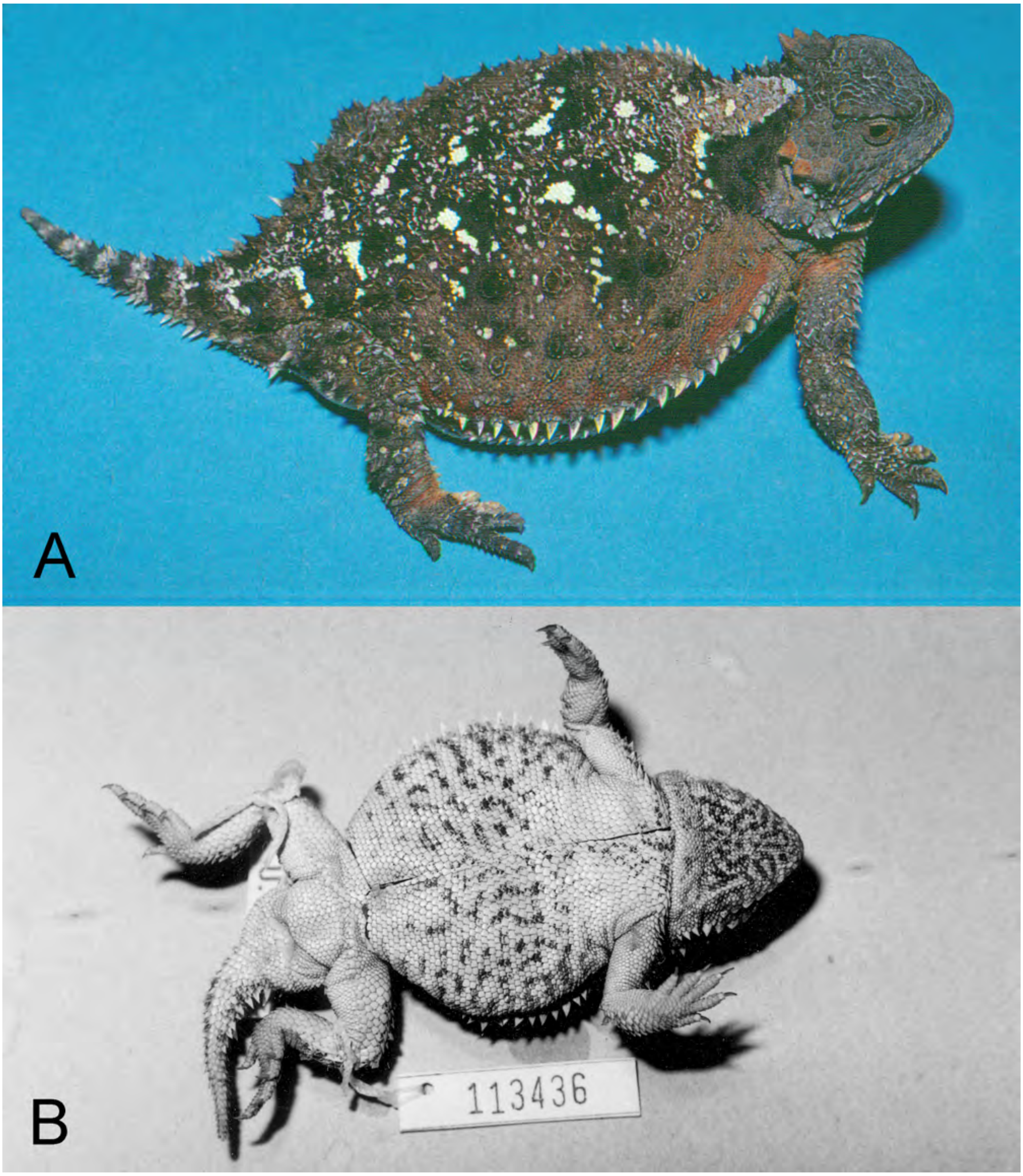

FIGURE 26. *Phrynosoma hernandesi ornatum* (A) adult female (RRM 2416) from SW of Jackpot, Elko Co., Nevada. (B) ventral aspect of male (LACM 113436) from near Grantsville, Tooele Co., Utah, showing rows of irregular melanistic spots.

In Nevada, *P. h. ornatum* occurs in Great Basin sagebrush at various localities in the Humboldt River basin and at Duck Creek north of Ely. In the Owyhee Desert north northwest of Carlin, and along the Owyhee and Little Owyhee rivers flowing into Idaho, the habitat is Sagebrush steppe (*Artemisia-Agropyron*). In the various mountain ranges, vegetation communities sequentially shift along an elevation gradient. At the highest elevations of the Santa Rosa and Ruby Mountains, for example, the dominant association is Great Basin pine (*Pinus*), changing to Juniper-pinyon woodland at lower elevations, and finally to Great Basin sagebrush on the desert floor. Elevation records for *P. h. ornatum* range from under 1,524 m (5,000 ft) to 2,500 m (8,200 ft) in the Monitor Range, indicating that this subspecies occurs across these various habitats.

Remarks. Several records for Nevada are problematic. Two specimens (UNLV 846-47) are listed from "Del Mar Mesa" at 3,048 m (10,000 ft) in Nye County, Nevada. This physiographic feature name cannot be found in any geographic information database, but there is speculation that the locality refers to the Delamar Mountains. However, that mountain range, with its highest peak at 2,408 m (7,900 ft), is located in Lincoln County, not Nye County. I have studied the specimens, and they appear to be closer to nominotypical *hernandesi* than to *ornatum*. The rostrofrontal profile of the larger specimen is like that of *hernandesi.* Furthermore, the dorsal pattern, especially with the elongate nuchal blotches, is reminiscent of the pattern of some specimens from the southern Wasatch Range in Utah.

Records for Pyramid Lake, Washoe County, and for Humboldt Sink, Churchill-Pershing County, Nevada, are erroneous and based on misidentified specimens of *Phrynosoma platyrhinos*. However, the report by Stebbins (1985) of an isolated population at Wadsworth, Nevada, is apparently valid. The specimen in question (UU 175) is *P. h. ornatum* and was collected in May of 1902. No additional specimens have since been collected from that locality.

Yarrow (1882b) listed two specimens from "Saint Thomas, Arizona", but Richardson (1915) disputed the accuracy of Yarrow's record, stating that Saint Thomas is actually located in Nevada (also suggested by Van Denburgh, 1922:381). According to Carlson (1974) Saint Thomas was a former settlement in Clark County, Nevada, near the confluence of the Virgin and Muddy rivers; the townsite was inundated by the impoundment of Lake Mead in 1938. Although Richardson believed the museum specimens were lost, both are still housed in the National Museum of Natural History (USNM 11849 and 293410). The National Museum database lists as a possible alternative locality "Fort Thomas", Graham County, Arizona. I have examined the specimens and they differ from other specimens of *P. hernandesi* from Graham County, but closely resemble material from the Colorado Plateau of Arizona. In any case, Saint Thomas, Nevada, was located in Creosote bush (*Larrea*) desert, a thermally extreme habitat unsuitable for short-horned lizards. Dr. Edward Palmer is listed as having collected the two specimens in 1870. Cope (1883 [1884]) provided a descriptive account of Dr. Palmer's herpetological collection from Saint Thomas, Nevada. It is noteworthy that Cope did not mention any specimens of short-horned lizards.

T. Jezkova (unpublished data) reported *P. hernandesi* (= *P. h. ornatum*) from ca. 6.9 km NNW of Three Creek, Owyhee County, and from the northwest slope of Trout Creek Mountain in the southwest corner of Cassia County, Idaho. But two specimens from 18 km WSW of Three Creek near Murphy Hot Springs (IMNH 1254–55) are *P. douglasii*. Jezkova (unpublished data) also reported *P. douglasii* from ca. 50.3 km NNW of Three Creek, Owyhee County, Idaho. These records presently provide a somewhat ambiguous picture of the distributional relationships of the two taxa. Further field work is needed to obtain a better concept of the distributional limits of *P. h. ornatum* and *P. douglasii* in northern Nevada, southeastern Oregon, and across southern Idaho.

Phrynosoma ornatissimum ornatissimum **Girard 1858a**

(Figs. 21C, 27–31)

Phrynosoma (Tapaya) hernandesi Girard 1858a:395 (part).
Phrynosoma (Tapaya) ornatissima Girard 1858a:396.
Phrynosoma douglassi Gentry 1885:140 (part)
Phrynosoma douglassii hernandesi Cope 1900:413 (part).
Phrynosoma douglassii ornatissimum Cope 1900:415.
Phrynosoma douglassii ornatissimum Van Denburgh 1922:377.
Phrynosoma douglassii hernandesi Van Denburgh 1922:382 (part).

Phrynosoma douglassii hernandesi Smith 1946:304 (part).
Phrynosoma douglassii ornatissimum Smith 1946:305.
Phrynosoma douglassii ornatissimum Reeve 1952:927.
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

Etymology. The Latin word *ornatus –a – um,* (participle of the verb *orno*), with the neuter superlative suffix, -*issimum*, meaning "the most highly adorned" or "…decorated" or "… embellished."

Suggested common name: Desert Short-horned Lizard.

Type locality. The type locality is restricted to the Rio Grande Valley at Albuquerque, Bernalillo County, New Mexico. See discussion below for further information.

Taxonomic history. Girard (1858a) described this species on the basis of specimens in the U.S. National Museum (= National Museum of Natural History), but he did not designate a type specimen. Reeve (1952:928) stated that Stejneger (1890:113) designated USNM 204 (2 specimens) as the type material used by Girard. Gehlbach (1965) stated erroneously that Stejneger (op. cit.) had designated neotypes. But Stejneger made no formal type designation, he merely indicated that the "type" was extant and could serve as a basis for comparison with the type material of *P. hernandesi.* Stejneger's use of the singular noun and verb suggests that he thought there was only a single type specimen. However, museum records show that USNM 204 consists of two syntypes.

According to the ledger records, the syntypes were collected in the Zuni Mountains of New Mexico by S. W. Woodhouse. Cope (1900:417) lists the specimens as having been received from Captain Lorenzo Sitgreaves who led the government-sponsored expedition to explore the Zuni and Colorado rivers. Samuel Woodhouse officially served as medical surgeon but also collected zoological specimens during the expedition, which departed Albuquerque, New Mexico, in 1851 (Adler, 1978).

My examination of the two syntypes, both females, reveals that they represent two different species. One specimen belongs to *Phrynosoma hernandesi*, and the other is referable to *P. ornatissimum* based on the application of the name following Reeve's (1952) concept. It is also evident from the details of Girard's description that he had a mixed series of specimens and that characteristics from both species were incorporated into his description. However, Reeve (1952:928), noting the association between the medial light-colored borders of the dorsal spots and the short tail, provided a relatively more definitive diagnosis of *P. ornatissimum*, which facilitates the current application of the name (see **Diagnosis** below). The specimen representing *P. hernandesi*, is now a paralectotype, and has been recatalogued as USNM 576284; the remaining specimen retains the original number USNM 204 and is here designated as the lectotype of *P. ornatissimum* (Fig. 27).

A revision of the type locality is also necessary. The lectotype has a short tail (171% of head length); this is far below the lower limit of New Mexico *P. hernandesi* but well within the observed limits for *P. ornatissimum*. The lectotype also has discrete, narrow, white lines forming the medial and posterior borders of the dorsal spots, and traces of dorsolateral white spots (the dorsal epidermis is badly abraded). This combination of traits does not pertain to any known population occurring in the Zuni Mountains, but it characterizes short-horned lizards from the Rio Grande Valley. As the lectotype conforms to the Rio Grande Valley material, it is likely that Woodhouse collected this specimen while the Sitgreaves Expedition was still in the vicinity of Albuquerque. Therefore I restrict the type locality of *Phrynosoma ornatissimum* to the Rio Grande Valley at Albuquerque, Bernalillo County, New Mexico.

Diagnosis. *Phrynosoma ornatissimum* can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout truncate, 43.8% ± 1.39 (35.2–50%) of orbit to rostral scale distance; (2) rostrofrontal profile rounded or angular with a steep incline; (3) frontal rim well elevated above the occipital shelf; (4) enlarged frontal rim scales 3.20 ± 0.16 (2–4) / 3.21 ± 0.21 (2–4); (5) temporal shelf moderately long, 22.9% ± 0.98 (16.7–28.4%) in males, 23.1% ± 0.68 (17.9–30.0%) in females; (6) temporal shelf weakly to moderately convex; (7) cephalic horns moderately short, third temporal horn length 13.9% ± 0.41 (10.5–16.7%); (8) cephalic horns elevated (ca. 45°) to nearly vertical; (9) tympanum elliptic, moderately broad; (10) tympanum exposed; (11) tail short, 193% ± 4.51 (139–224%) in males, 160% ± 3.16 (118–196%) in females; (12) dorsal spots large, rounded; (13) discrete white and/or yellow line along medial and posterior edges of each dorsal spot; (14) dorsolateral white spots present; (15) gular area with melanistic spots and short lines forming a series of chevrons or wavy transverse bands (melanin-dispersed phase); (16) abdomen with scattered gray flecks and patches, no large melanistic spots (melanin-dispersed phase); (17) melanistic subcaudal bands absent (melanin-dispersed phase).

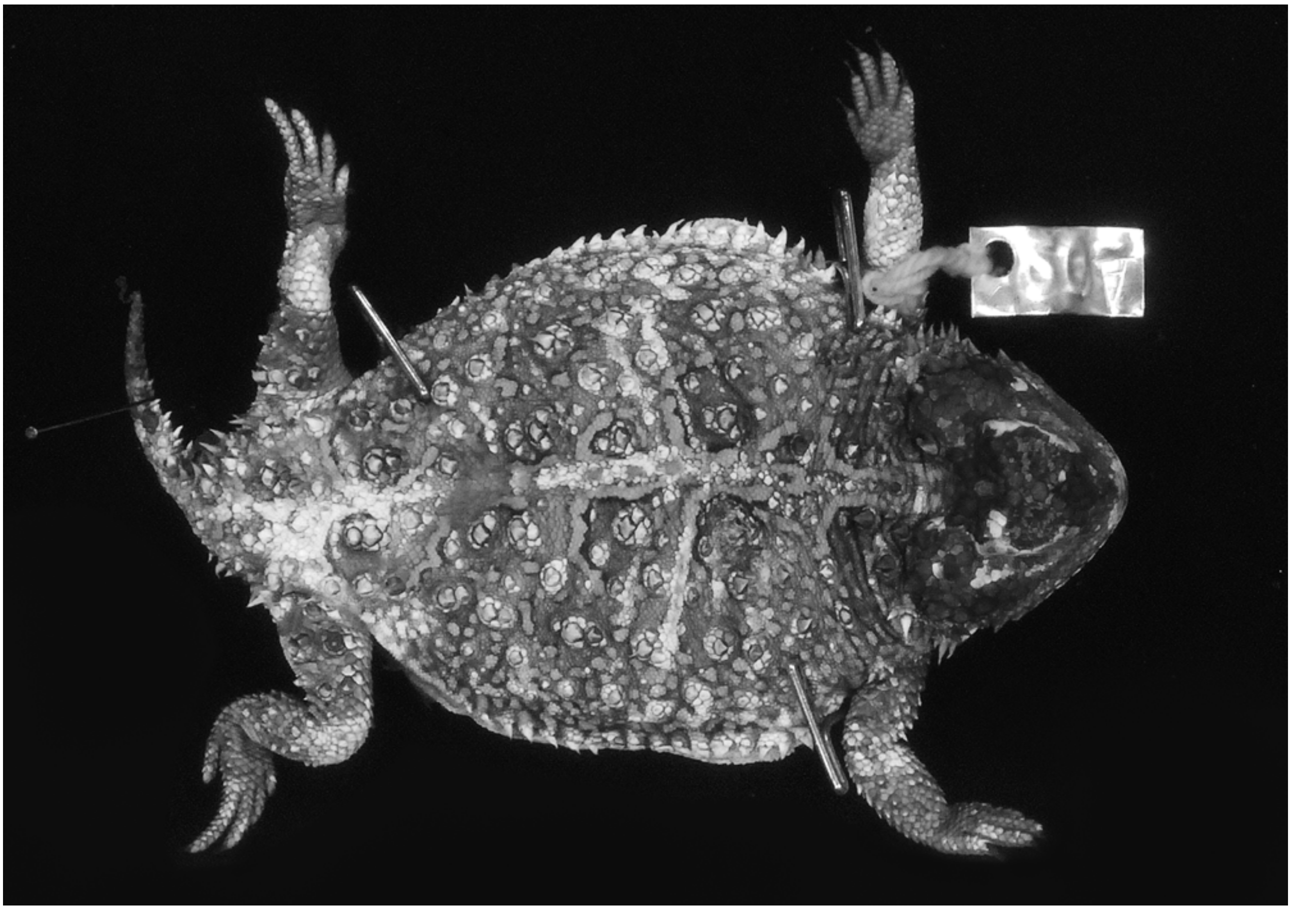

FIGURE 27. Lectotype of *Phrynosoma ornatissimum* (USNM 204). Dorsal pattern is obscured from abrasion and fading due to age. Note the short tail.

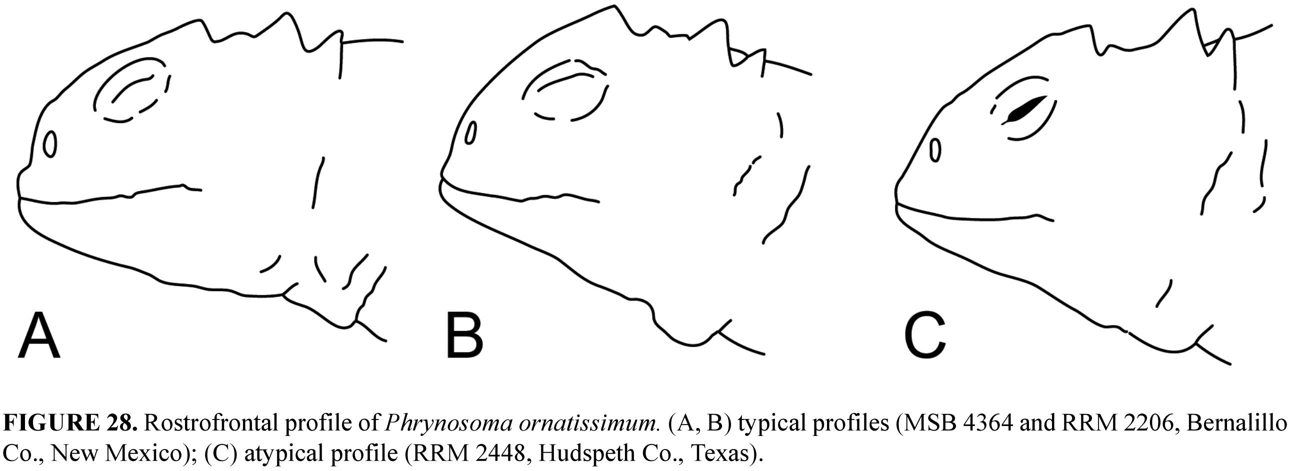

FIGURE 28. Rostrofrontal profile of *Phrynosoma ornatissimum.* (A, B) typical profiles (MSB 4364 and RRM 2206, Bernalillo Co., New Mexico); (C) atypical profile (RRM 2448, Hudspeth Co., Texas).

Comparisons. *Phrynosoma o. ornatissimum* can be distinguished from *P. h. hernandesi* and *P. h. ornatum* by its more truncate snout and rounded or angular and steeply inclined rostrofrontal profile, its slightly shorter temporal shelf, and its shorter occipital and temporal horns (except *P. h. ornatum*) that are usually directed upward to nearly vertical, and its short tail. It is further distinguished from *P. hernandesi* and its subspecies by the presence of large rounded dorsal spots with discrete, narrow, white and/or yellow lines forming the medial and posterior borders of the dorsal spots, a series of chevrons or wavy, irregular transverse bands on the gular area (melanin-dispersed phase), absence of large, melanistic spots on the abdomen (except some *P. h. ornatum*), and absence of interrupted or complete melanistic subcaudal bands. Cope (1900:415–16) erroneously ascribed to this taxon a more obtuse head and a deeper occipital emargination owing to the temporal shelf being produced farther posteriorly than in *P. hernandesi*; just the reverse is true (Table 3). *P. ornatissimum* can be distinguished from *P. brevirostris, P. diminutum* **sp. nov.** and *P. douglasii* by the frontal rim well elevated above the occipital shelf (except *P. bauri* **sp. nov.**), the high number of enlarged frontal rim scales, the longer temporal shelf, and melanistic chevrons or wavy transverse bands on the gular area (melanin-dispersed phase). *P. ornatissimum* can be distinguished further from *P. douglasii* by its large body size, moderately broad, elliptic and exposed tympanum. Note that *P. ornatissimum* and its subspecies *brachycercum* (next account) have the shortest mean tail length of all other taxa within the complex (except for the female sample of *P. douglasii*, Table 3).

Description. This account is based on the examination of adult specimens from the short-grass plains of central New Mexico and west Texas (n = 142; see Appendix I).

Head depressed, broader than long; snout short, but somewhat protruding in some specimens; rostrofrontal profile rounded or angular and steeply inclined (Fig. 28); dorsal surfaces of the head covered with small, irregular, convex scales with rugosities formed by granulations and irregular ridges; frontal rim well elevated above occipital shelf (Fig. 21C); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf expanded, weakly to moderately convex, produced posteriorly, occipital emargination deep; usually three short temporal horns, most posterior (third) largest, 13.9% (10.5–16.7%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one short occipital horn on each side, usually separated from temporal horn by one or two scales; supralabials small; infralabials small, slightly enlarged posteriorly and continuous with typically three enlarged postlabials, 3.3 (2–4); postrictal spine 14.7% (9.8–19.3%) of head length; chinshields slightly enlarged posteriorly, separated from infralabials by usually two or three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper row larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, ephemeral, usually with enlarged scales posteriorly; tympanum elliptic, relatively broad, exposed; anterior margin of ear opening with granular scales or with one to several slightly enlarged, dentate-like scales; dorsal scales heterogeneous, but generally small, not imbricate; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail short, 193% (139–224%) of head length in 57 males, 160% (118–196%) in 79 females; maximum snout-vent length = 110 mm.

Head brown, uniform or with scattered light-colored spots; a pair of darker brown to charcoal nuchal blotches bordered by a discrete white or yellow line; dorsum pale brown, with usually three or four pairs of darker brown to charcoal dorsal spots between neck and sacral areas; dorsal spots bordered medially and posteriorly by narrow, well-defined white and/or yellow lines; anterior edges of dorsal spots usually grade into dorsal field; dorsal tail base with several pairs of dark spots, becoming dark transverse bands separated by white distally on tail, or distal tail uniform brown; dorsolateral areas of body with scattered white spots; vertebral area uniform or with short white lines and spots; concealed surfaces of lips white, pink or red; gular area white, with a pattern of dark chevrons or transverse wavy lines in the melanin-dispersed phase; chest and belly white with scattered dark flecks or small melanistic patches (in the melanin-dispersed phase); ventral tail unmarked (Fig. 29–30). In general appearance, *P. ornatissimum* and *P. bauri* **sp. nov.** are superficially similar (Fig. 31) and have been confused in the literature (Smith, 1946:306, plate 81B).

Variation. The occipital and temporal horns project vertically, or nearly so in 110 out of 142 specimens (77.5%); in 30 specimens (21.1%) both sets of horns project upward, but at a lower angle (ca. 45°). In two specimens (1.4%) the occipital horns are directed upward, but the temporal horns are directed horizontally.

In 81 specimens (57.0%) the head is uniform brown, but in 48 specimens (33.7%) the head is speckled with small, white or yellowish spots; in 13 specimens (9.2%), the white spots form two or three transverse bands. The vertebral area is unmarked in 46 specimens (32.4%), but has white spots and short lines in 96 specimens (67.5%).

The dorsal ground color varies across localities in New Mexico. The majority of specimens are yellowish brown to tan or gray brown, but several specimens from near Albuquerque, Bernalillo County are chocolate brown such that the limits of the dorsal spots are imperceptible save for the narrow white borders. Pink specimens have been collected near Bernardo, Socorro County. One specimen from southwest of Albuquerque is virtually patternless. Another nearly uniform specimen comes from the alkali flats west of Lordsburg, Hidalgo County.

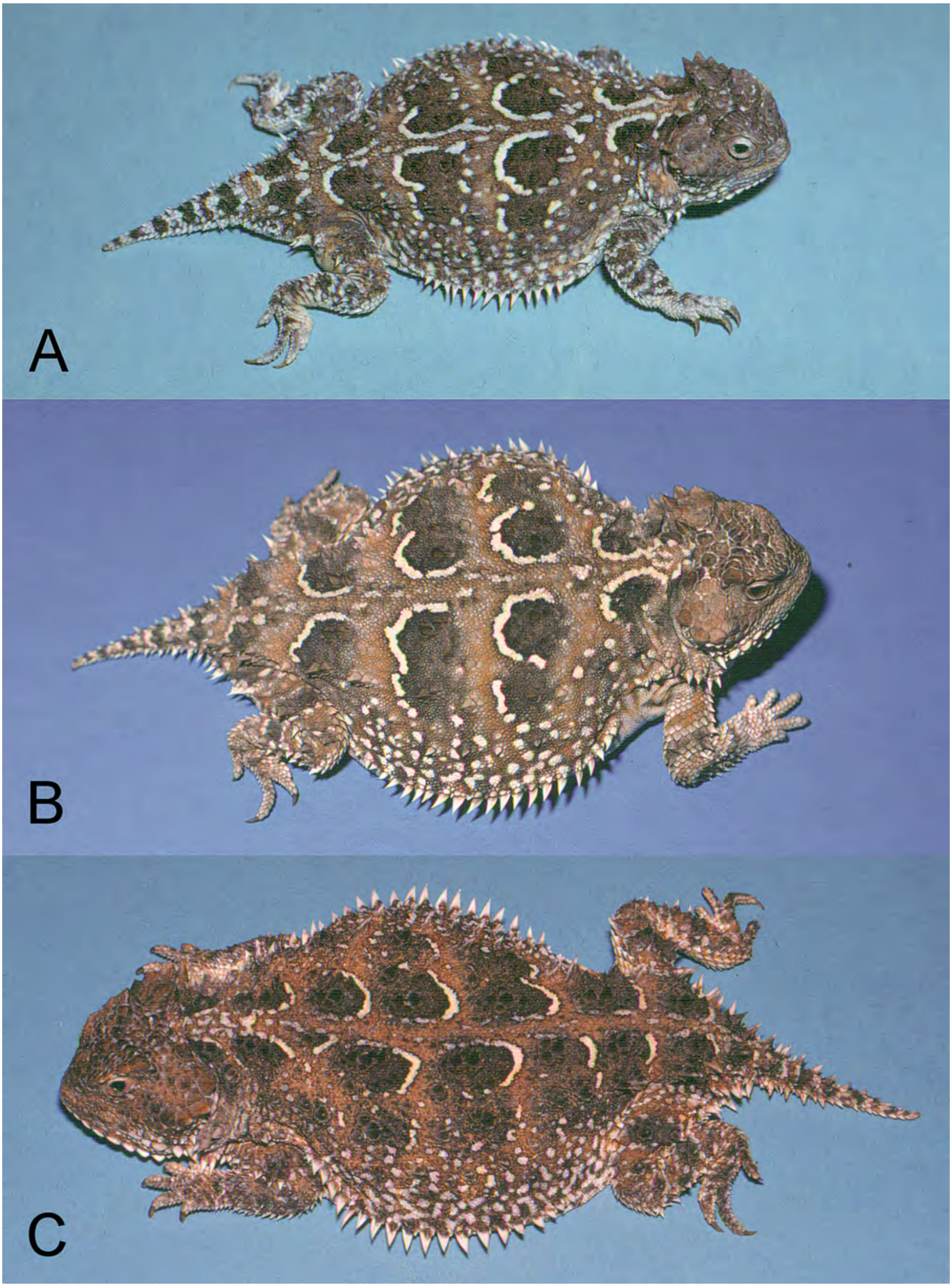

FIGURE 29. *Phrynosoma ornatissimum.* (A) adult male (RRM 2339) and (B) adult female (RRM 2206) from Albuquerque, Bernalillo Co., New Mexico. (C) adult female (RRM 2474) from near Diamond A Ranch, Hudspeth Co., Texas.

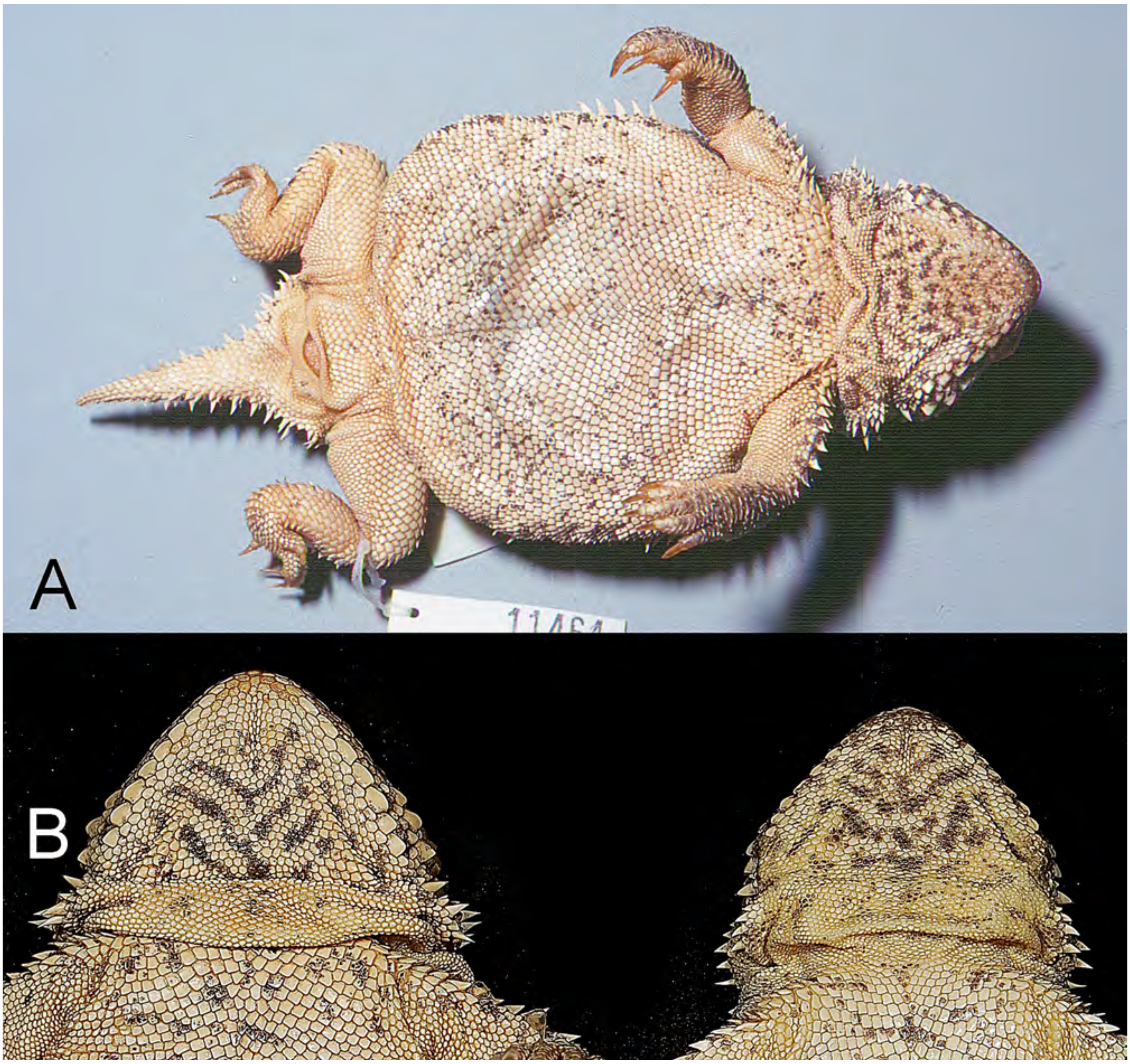

FIGURE 30. *Phrynosoma ornatissimum.* (A) female with scattered flecks on abdomen (MSB 11464); (B) gular pattern of female (RRM 2206, left) and male (RRM 2339, right); all specimens from Albuquerque, Bernalillo Co., New Mexico.

P. o. ornatissimum appears to have evolved from an ancestor similar to *P. hernandesi*, retaining the elevated frontal rim and enlarged frontal rim scales of *P. h. hernandesi*, but developing a more rounded rostrofrontal profile, shorter cephalic horns, and a much shorter tail. It has also lost the large melanistic spots on the abdomen and melanistic subcaudal bands.

Distribution and habitat. *P. o. ornatissimum* occupies much of central and southern New Mexico, ranging south into west Texas (see Appendix II, maps 7, 9, 14, 18). In New Mexico, it has been recorded from near Abiquiu and Santa Fe in the north, and as far east as the Lincoln-De Baca County line east of Lon on NM 247. In the southeast, it has been recorded from about 64 km E of Roswell, Chaves County, in the vicinity of the Mescalero Sands. The record from 8 km W of Hope, Eddy County, plotted by Degenhardt *et al* (1996) is erroneous and based on a misidentified specimen of *P. cornutum* (AMNH 161257). The northeastern limits of the range appear to be south and west of the upper Pecos River in southwestern San Miguel County. In the region farther north *P. ornatissimum* is replaced by *P. bauri* **sp. nov.** West of the Rio Grande, *P. ornatissimum* has been collected 16 km west of Abeytas. It has also been collected at the Ake Ranch (33° 51' 33" N, 107° 44' 26" W) at the southeastern edge of the Plains of San Augustin, Catron County, but the more northern and western parts of the plains are occupied by *P. h. hernandesi* or putative hybrids (e.g. MSB 4348). In southwestern New Mexico, it has been recorded from 3.2 km south of Lordsburg on NM 338, and on alkali flats 22.4 km west of Lordsburg. A specimen (UMMZ 55740) morphologically close to *P. ornatissimum,* or perhaps a hybrid lacking the medial white borders of the dorsal spots, was collected near Santa Rita del Cobre, ca. 24 km E Silver City, Grant County, New Mexico. Southward from New Mexico, it extends across the Otero Mesa to at least as far as the Hueco and Cornudas mountains in Hudspeth County, Texas.

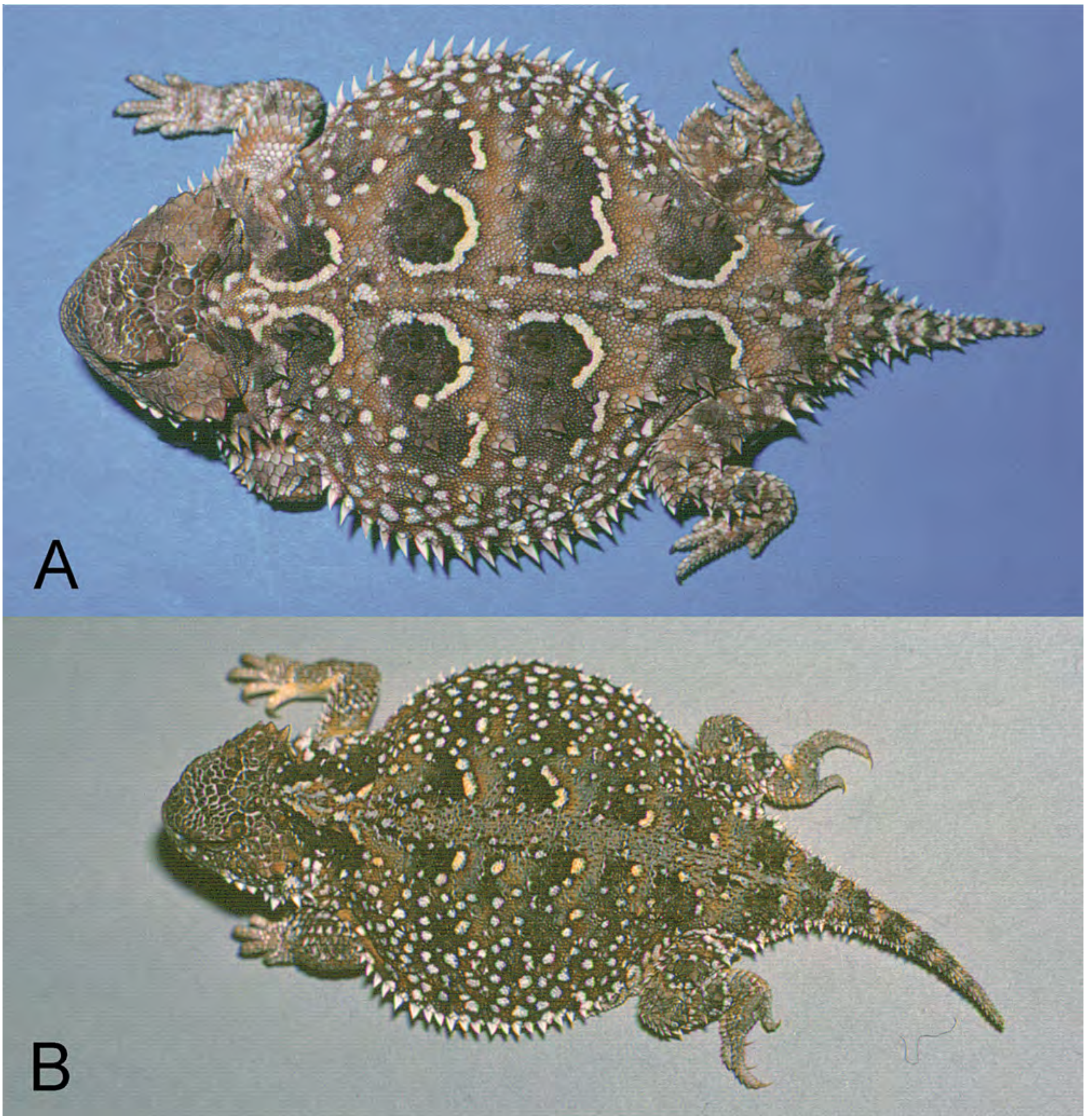

FIGURE 31. Comparison between (A) *Phrynosoma ornatissimum* (RRM 2206, female) and (B) *Phrynosoma bauri* **sp. nov.** (RRM 2210, female). Note differences in the dorsal pattern and proportional tail length.

This species is primarily a denizen of the arid short-grass plains. In the Estancia Valley, east of the Sandia and Manzano mountains, *P. ornatissimum* has been collected in Grama-galleta steppe (*Bouteloua-Hilaria*), but presumably it also occurs in the Saltbush-greasewood (*Atriplex-Sarcobatus*) association in lower areas of the valley. Grama-galleta steppe is also the dominant habitat farther east and south on the plains, where this short-horned lizard has been taken at Vaughn (Guadalupe County), Encino, Pedernal, Torrance, and Lucy (Torrance County), and Corona and east of Lon (Lincoln County). In the Rio Grande Valley near Albuquerque, large numbers of *P. ornatissimum* have been collected in Grama-galleta steppe, and also in the Saltbush-greasewood habitat closer to the river. The species ranges south along the Rio Grande Valley in these habitats to near the confluence of the Rio Salado and Rio Grande rivers, beyond which these associations are replaced by Creosote bush-tarbush (*Larrea-Flourensia*) in which *P. ornatissimum* appears to be absent. However, the species presumably continues southward on higher terrain away from the river in Grama-galleta steppe and Juniper-pinyon woodland (*Juniperus-Pinus*). On the slopes of the Sandia Mountains, this species has been recorded in Juniper-pinyon woodland up to an elevation of 1,860 m (6,100 ft). It has also been collected in this habitat farther south on the Chupadera Mesa (Socorro County). The records from south and west of Lordsburg, Hidalgo County, are in Grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*), and the few localities in west Texas are dominated by Grama-tobosa prairie (*Bouteloua-Hilaria*). The grasslands farther south in Mexico are occupied by the subspecies *P. o. brachycercum* (see the following account).

Remarks. Gehlbach (1965) surmised, with very little evidence, that *P. hernandesi* and *P. ornatissimum* are ecophenotypic products of an altitudinal cline in a single, morphologically variable species. However, his conclusion is untenable and refuted by distributional and ecological data. Although the distributions of *P. hernandesi* and *P. ornatissimum* are partitioned by elevation (and corresponding habitat) over much of central New Mexico, this is a general pattern for which there are notable exceptions supporting the argument for two distinct species. There are localities in New Mexico where these morphologically disparate short-horned lizards occur in close proximity to one another without an associated altitudinal or ecological gradient. For example, as previously mentioned, *P. o. ornatissimum* has been recorded southwest of Lordsburg, Hidalgo County, New Mexico, in Grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*). *P. hernandesi* has also been collected in the same habitat farther south in the Animas Valley. Also, both taxa occur in adjacent parts of the Plains of San Augustin (Catron County) in Grama-galleta steppe (*Bouteloua-Hilaria*) habitat. On the West Mesa near Albuquerque, the two species are sympatric or nearly sympatric. *P. ornatissimum* has been recorded from The Volcanoes (35° 08' 42" N, 106° 46' 10" W) on the West Mesa near Albuquerque (CWU 252, MSB19337); another specimen from the area appears to be *P. hernandesi* (NMSU 2050). North and east of the Sandia Mountains both taxa and their hybrids have been collected in the same habitat only a few kilometers apart. In the Gallinas Mountains, lizards morphologically similar to *P. ornatissimum* occur in coniferous forest at 2,622 m. This is an exception to the general pattern of habitat preferences. It suggests that if *P. hernandesi* once occupied this montane area, it was genetically absorbed or displaced by *P. ornatissimum*. In the Colorado Plateau region of Arizona, hybrids morphologically similar to *P. ornatissimum* occur south of Sanders, Apache County, within a few kilometers of lizards morphologically close to *P. hernandesi*, without accompanying gradients in elevation or habitat. Similar associations among hybrids and parental *P. hernandesi* are found at other locations on the plateau (see Map 7). In conclusion, the concept that *P. hernandesi* and *P. ornatissimum* are clinal forms of one variable species can be dismissed.

The general pattern of distribution over much of New Mexico of montane islands of *P. hernandesi* surrounded by *P. ornatissimum* occupying the adjacent short-grass plains can be explained by a history of climatic fluctuations, presumably during Pleistocene and Recent Epochs, resulting in vertical shifts in woodland and grassland habitats. The occurrence of *P. hernandesi* in New Mexico likely predated that of *P. ornatissimum* and was temporally correlated with the expansion of woodlands. Subsequently, environmental changes conducive to the development of arid grasslands resulted in the spread of *P. ornatissimum* and the vertical retreat of woodland savannas occupied by *P. hernandesi.* Where mountain and plains habitats meet, *P. hernandesi* and *P. ornatissimum* contact and hybridize to a greater or lesser extent, but the dynamics of hybridization are poorly understood and in need of detailed genetic and ecological studies (see discussion on hybridization below).

Further collecting is needed in eastern and northeastern New Mexico to obtain a clearer concept of the distribution limits of this species and where it meets *P. bauri* **sp. nov.** Texas records are few and Reeve (1952) plotted two localities along the Rio Grande south of El Paso that apparently lack voucher specimens and appear to be erroneous. Cope (1900:417) lists USNM 205 as *P. ornatissimum*, a specimen received from Lt. William H. Emory and collected between the Pecos River and Rio Grande. Unfortunately, the specimen is now lost, but more recent records place the species in the region of the Otero Mesa.

I have examined several specimens of *P. hernandesi* collected in residential areas or on school grounds in both Albuquerque and El Paso. There are several possible explanations for these lowland records: a cataloguing error, a natural occurrence, or human transport. The most likely explanation for these cases is that the lizards were collected from montane sites (which are frequented by many visitors each season) and the lizards subsequently escaped or were released in urban areas in the lowlands.

Limited observations on foraging activity of *P. ornatissimum* were noted in Hudspeth County, Texas. In August, during hot weather, desert short-horned lizards became active before dawn and were observed feeding at *Pogonomyrmex* ant colonies during the early morning hours. Later in the morning, desert short-horned lizards apparently took shelter in burrows and only Texas horned lizards (*P. cornutum*) were observed foraging. A study of temporal resource partitioning between the two horned lizard species could prove interesting.

Phrynosoma ornatissimum brachycercum **Smith 1942, comb. nov.**

(Figs. 21D, 32–35)

Phrynosoma douglassii brachycercum Smith 1942:362
Phrynosoma douglassii brachycercum Reeve 1952:916.
Phrynosoma douglassii hernandesi Reeve 1952:922 (part).
Phrynosoma hernandezi Zamudio, Jones, and Ward 1997:302 (part).

Etymology. The Greek word roots βραχύς = *brachys* an adjective meaning "short" and κέρκος = *kerkos* or *cercus*, a feminine noun meaning "tail", in reference to the very short tail in this race. Smith (1942) modified *brachycercus* (used as a trinomial) to *brachycercum* as though it were an adjective needing to agree with the neuter gender of *Phrynosoma*. Although nouns used in apposition to other nouns retain their own gender (only adjectives must agree in gender with the name of the genus) such that Smith's modification of the name was unnecessary, his use of the word as an adjective must be followed. See ICZN articles 31.2.1 and 34.2.1.

Suggested common name: Short-tail Short-horned Lizard.

Type locality. The type locality is Durango City, Durango, Mexico.

Taxonomic history. Smith (1942) originally described this form as *Phrynosoma douglassii brachycercum* [sic] on the basis of four specimens from "Durango," Mexico, collected by Dr. Edward Palmer in September of 1896. Smith designated USNM 23993, the largest of four females, as the holotype (Fig. 32), and the remaining two adults and one juvenile (USNM 23994–23996), as paratopotypes. Reeve (1952) did not alter the classification of this form, and repeated Smith's (1942) original diagnosis and description. There was some uncertainty about the precise location of Palmer's specimens, but Reeve (op. cit.) restricted the type locality to Durango (city) on the basis of a specimen (KU 28068) taken just north of the city.

Diagnosis. *Phrynosoma ornatissimum brachycercum* can be distinguished from other members of the *P. douglasii* species complex by the following combination of adult characters: (1) snout short, 45.4% ± 2.15 (40.8–50%) of orbit to rostral scale distance; (2) rostrofrontal profile abruptly rounded or angular with a steep incline; (3) frontal rim well elevated above the occipital shelf; (4) enlarged frontal rim scales 2.75 ± 0.22 (2–3) / 2.82 ± 0.26 (2–4); (5) temporal shelf moderately long, 20.9% ± 2.31 (15.1–26.8%) in males, 22.6% ± 1.39 (14.7–32.0%) in females; (6) temporal shelf weakly to moderately convex; (7) cephalic horns moderately short, third temporal horn length 12.7% ± 0.72 (7.3–18.2%) of head length; (8) cephalic horns elevated (ca. 45°) to nearly vertical; (9) tympanum elliptic, moderately broad; (10) tympanum exposed; (11) tail short, 189% ± 14.47 (149–238%) in males, 153% ± 5.50 (117–193%) in females; (12) dorsal spots wedge-shaped or slightly rounded, or transverse bands present; (13) light-colored borders, discrete or grading, confined to posterior edges of each dorsal spot; (14) dorsolateral white spots absent or present; (15) gular area with melanistic spots and short lines forming a chevron pattern or an undulating series of bands (melanin-dispersed phase); (16) abdomen with scattered gray flecks and patches, no large melanistic spots (melanin-dispersed phase); (17) melanistic subcaudal bands absent (melanin-dispersed phase).

Comparisons. *P. o. brachycercum* has essentially the same morphology, including tail proportions, as nominotypical *P. ornatissimum*, but differs from most specimens of the nominate subspecies by the absence of the discrete yellow or white line along the medial border of the dorsal spots (100% of 45 specimens), and by the absence of dorsolateral white spots (86% of 45 specimens). Also, in the nominate subspecies the brown dorsal spots are typically large and rounded, but in this race, the spots vary from small, rounded or wedge-shaped to transverse bands (see below). Smith (1942) also considered the keeled chest scales as diagnostic, but many specimens which I examined lack this trait.

FIGURE 32. Holotype of *Phrynosoma ornatissimum brachycercum* (USNM 23993). Note the short tail.

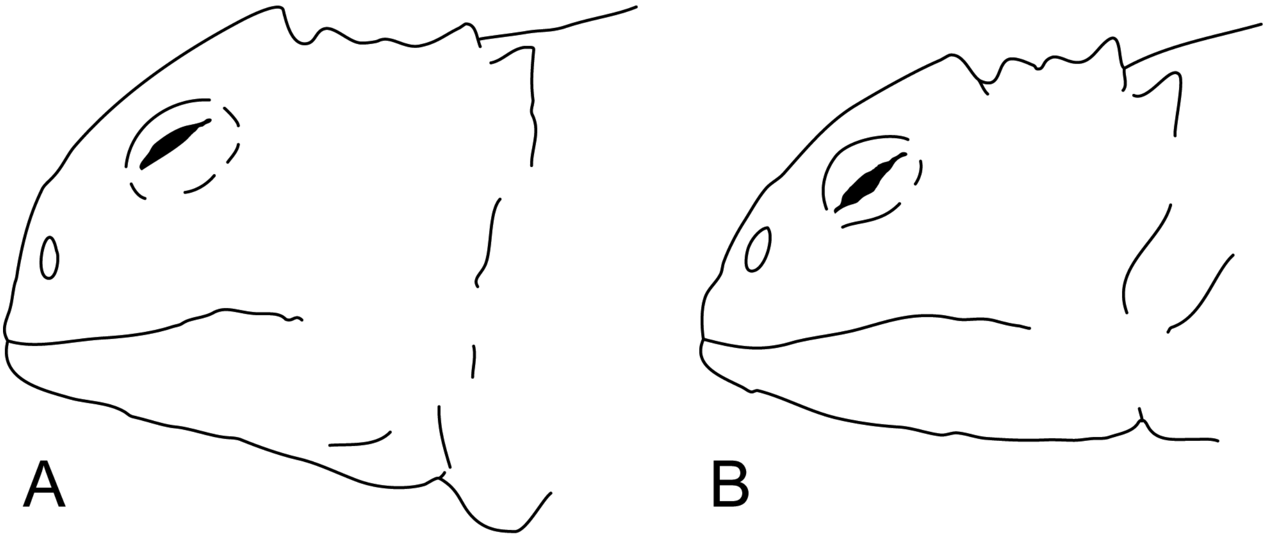

FIGURE 33. Rostrofrontal profile of *Phrynosoma ornatissimum brachycercum.* (A) typical profile (KU 45314); (B) atypical profile (UTEP 2520); specimens from Santo Tomas and Sierra del Nido, Chihuahua, Mexico, respectively.

P. o. brachycercum can be distinguished from *P. h. hernandesi* and *P. h. ornatum* by its more truncate snout and abruptly rounded or angular and steeply inclined rostrofrontal profile, its slightly shorter temporal shelf, and its shorter occipital and temporal horns (except *P. h. ornatum*) that are usually directed upward to nearly vertical, and its short tail. It is further distinguished from *P. hernandesi* and its subspecies by a series of chevrons or wavy transverse bands on the gular area (melanin-dispersed phase), absence of large, rounded or irregular melanistic spots on the abdomen (except some *P. h. ornatum*), and absence of interrupted or complete melanistic subcaudal bands. *P. o. brachycercum* can be distinguished from *P. bauri* **sp. nov.** by its short tail, absence of dorsolateral white spots (in most specimens), absence of large melanistic spots on the abdomen, and a gular pattern consisting of chevrons or wavy transverse bands. *P. o. brachycercum* can be distinguished from *P. brevirostris, P. diminutum* **sp. nov.** and *P. douglasii* by its frontal rim well elevated above the occipital shelf, its high number of enlarged frontal rim scales, its longer temporal shelf, and its melanistic chevrons or irregular, wavy transverse bands on the gular area. *P. o. brachycercum* can be further distinguished from *P. douglasii* by its large body size, moderately broad, elliptic, and exposed tympanum.

Description. This account is based on the examination of adult specimens from the grasslands of the Mexican states of Chihuahua and Durango (n = 47; see Appendix I).

Head depressed, broader than long; snout short, but slightly protruding in some specimens; rostrofrontal profile rounded or angular with a steep incline (Fig. 33); dorsal surfaces of the head covered with small, irregular, convex scales with rugosities formed by granulations and irregular ridges; frontal rim well elevated above occipital shelf (Fig. 21D); superciliary ridges distinct, terminating posteriorly in a short, blunt spine; external nares laterally pierced in line of canthus rostralis; temporal shelf expanded, weakly to moderately convex, produced posteriorly, occipital emargination deep; usually three short temporal horns, most posterior (third) largest, 12.7% (7.3–18.2%) of head length; occipital shelf bears several small convex scales or tubercles which vary from low, rounded to moderately elevated and pointed; interoccipital spine small, blunt; one short occipital horn on each side, usually separated from temporal horn by one or two scales; supralabials small; infralabials small, slightly enlarged posteriorly and continuous with typically three enlarged postlabials 3.6 (3–4); postrictal spine 11.5% (9.0–14.1%) of head length; chinshields slightly enlarged posteriorly, separated from infralabials by usually two or three small sublabials; gular scales small, subequal; two prescapular dermal folds, upper row larger, more posterior, each bearing a row of several soft spines; transverse gular fold well developed; a weak longitudinal gular fold on left and right sides, ephemeral, usually with enlarged scales posteriorly; tympanum elliptic, relatively broad, exposed; anterior margin of ear opening with granular scales or with one to several slightly enlarged, dentate-like scales; dorsal scales heterogeneous, but generally small, not imbricate; usually six indistinct dorsal rows of enlarged, keeled, spinous scales, each set in a rosette of smaller, keeled scales; one row of slightly enlarged, soft scales form lateral abdominal fringe; ventral scales small, smooth, imbricate; tail short, 189% (149–238%) of head length in 14 males, 153% (117–193%) in 33 females; maximum snout-vent length = 108 mm.

Head uniform brown; a pair of darker brown to charcoal nuchal blotches not usually bordered by white; dorsum brown, usually with three or four pairs of darker brown to charcoal dorsal spots between neck and sacral areas; dorsal spots with a posterior white border, discrete or grading into dorsal field; anterior edges of dorsal spots usually grade into dorsal field; dorsal tail base with several pairs of dark spots, these becoming transverse bands distally on tail, or tail uniform brown distally; vertebral area uniform or with white spots and lines; concealed surfaces of lips white, pink or red; gular area white with melanistic spots and irregular lines forming a pattern of chevrons or irregular transverse bands (in melanin-disperse phase); chest and belly white with scattered dark flecks or small melanistic patches, rarely spots (melanin-dispersed phase); ventral tail unmarked (Figs. 34–35)

Variation. The occipital and temporal horns project upward (ca. 45°) to nearly vertical in 36 of 45 specimens (80.0%); in seven specimens (15.5%) the occipital horns project upward, but the temporal horns project horizontally; in two specimens (4.4%) both sets of horns are directed horizontally.

All specimens examined lack a white and/or yellow line along the medial edge of the dorsal spots, although one specimen from WNW of General Trías has partial development of the trait. The posterior white borders of the dorsal spots grade into the dorsal field in 14 individuals (31.1%); in 26 specimens (57.7%) the white borders are discrete and well defined, and in five examples (11.1%) the white borders are absent. The head is uniform, without light-colored flecks or spots in all specimens examined. In 11 specimens (24.4%) examined, the dorsal spots are wedge-shaped; in 12 specimens (26.7%) the spots are slightly rounded; 21 individuals (46.7%) have transverse bands, and one example (2.2%) lacks dorsal spots. The variation in the shape of the dorsal spots does not show any geographically correlated trend. In this subspecies dorsolateral white spots are usually lacking. However, a small number of specimens from several localities in Chihuahua have the white spots, including one specimen from San Diego, one from 41 km WNW of General Trías, and two among a series of 12 collected at San José de Babícora. Also, a single specimen examined from the Sierra Mojina has numerous white spots extending to near the vertebral area.

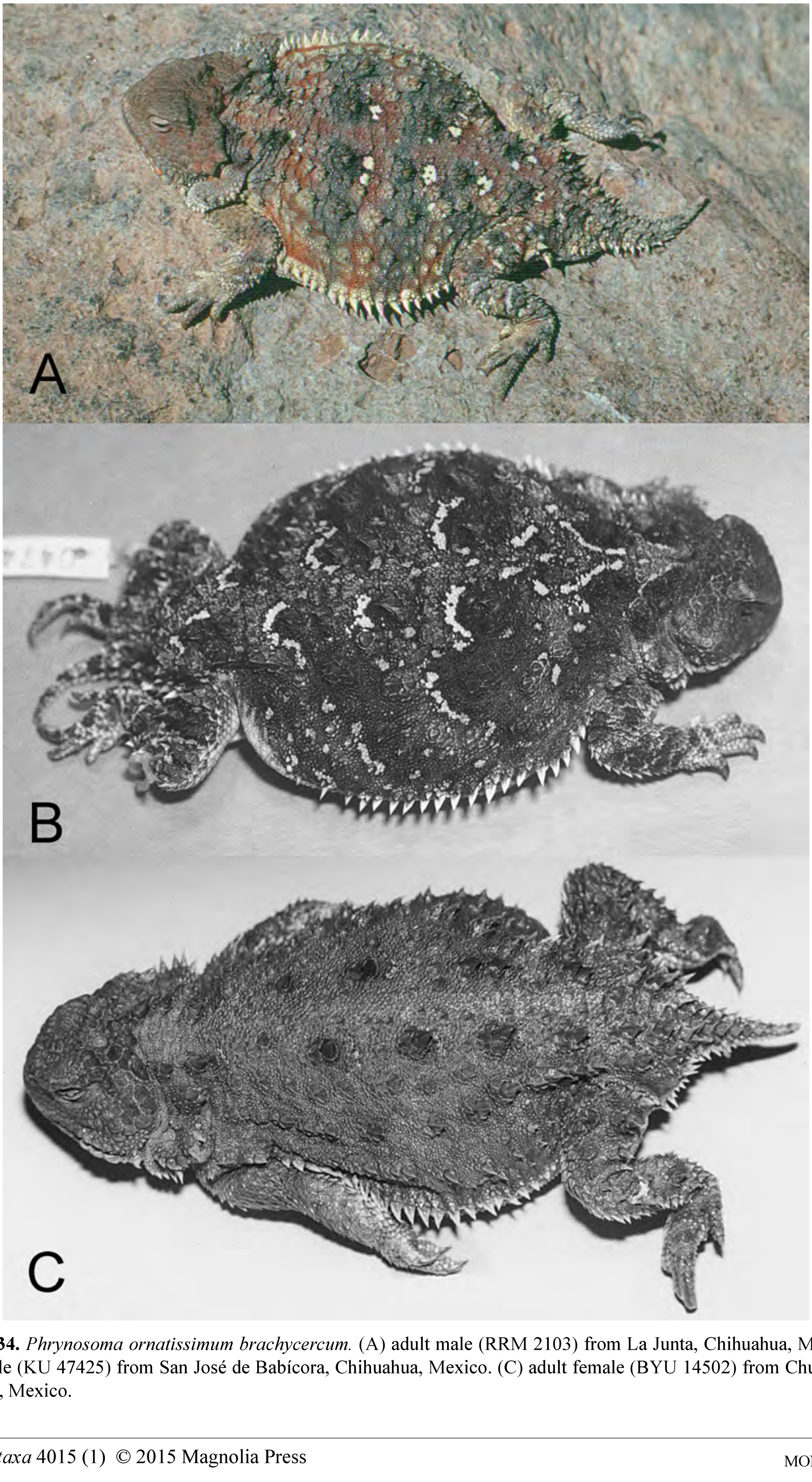

FIGURE 34. *Phrynosoma ornatissimum brachycercum.* (A) adult male (RRM 2103) from La Junta, Chihuahua, Mexico. (B) adult female (KU 47425) from San José de Babícora, Chihuahua, Mexico. (C) adult female (BYU 14502) from Chuhuichupa, Chihuahua, Mexico.

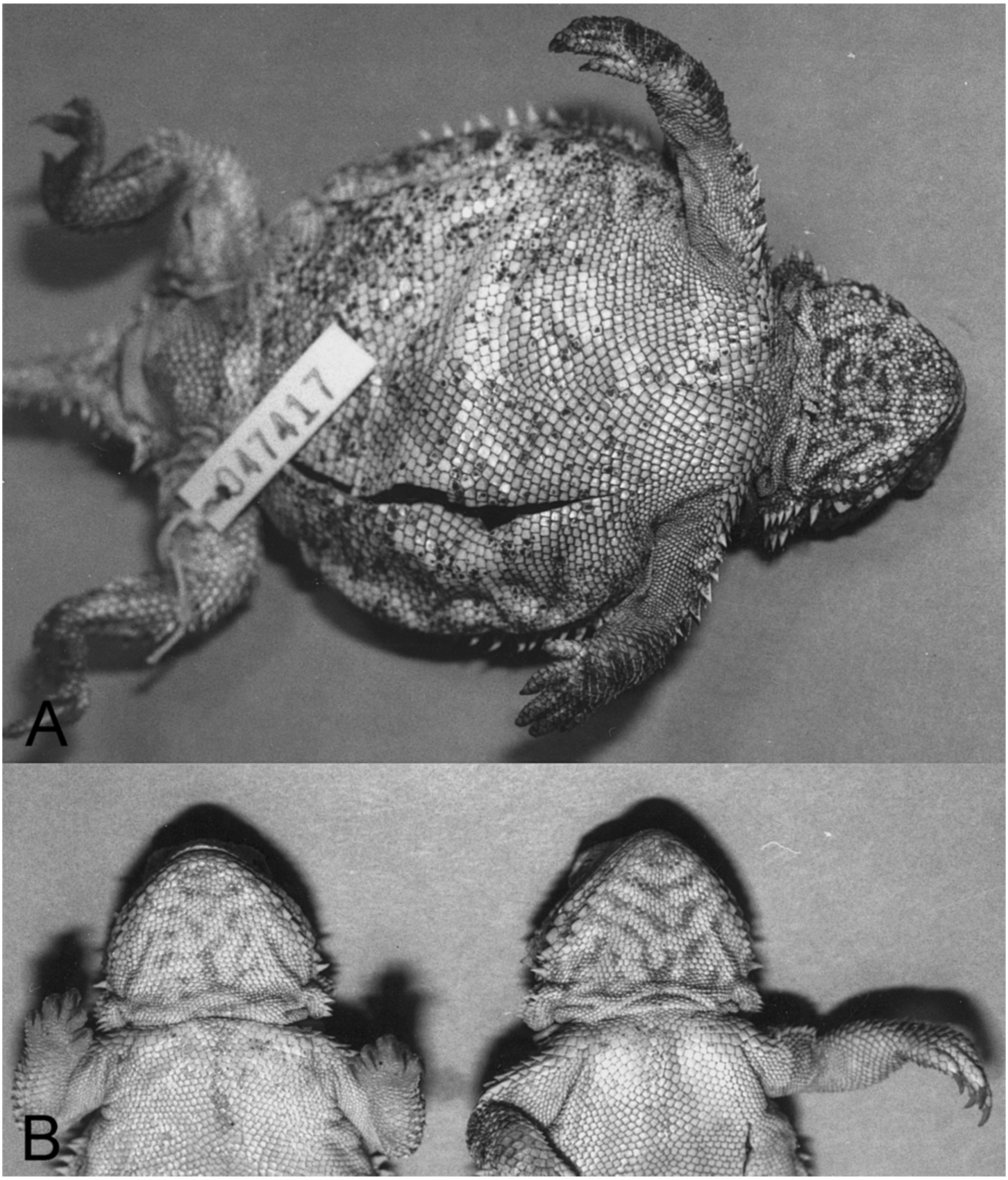

FIGURE 35. *Phrynosoma ornatissimum brachycercum.* (A) female with scattered flecks on abdomen (KU 47417, San José de Babícora, Chihuahua, Mexico); (B) gular patterns (KU 45315–16, Santo Tomás, Chihuahua, Mexico).

Distribution and habitat. *P. o. brachycercum* is distributed along the lower eastern slopes of the Sierra Madre Occidental and the adjacent plains encompassing the Mexican states of Chihuahua, Durango, and Zacatecas (see Appendix II, maps 3, 4, 6). The most northern locality known for this subspecies is Ramos (30˚ 36' N; 108˚ 05' W) in Chihuahua, based on MCZ 36888 which I have examined. Smith & Taylor (1950:100) and Reeve (1952:926) listed the Ramos specimen as *P. hernandesi*, but apparently the authors did not examine it. *P. o. brachycercum* ranges south through Durango to at least as far south as La Ordeña (22° 54' N; 102° 56' W), SSW of Fresnillo, Zacatecas (Smith & Flores-Villela, 1994).

In northern Chihuahua, *P. hernandesi* has been recorded from the Sierra de San Luis (31˚13' 41.1" N; 108˚ 44' 5.5" W) (Lemos-Espinal *et al*., 2004) and 11.3 km southwest of Colonia Pacheco, at 1,738 m (5,700 ft) (30˚ 03' N; 108˚ 26' W), based on MVZ 46655. *P. o. brachycercum* occurs at Colonia Juárez (30˚ 18' N; 108˚ 04' W), which lies northeast of Colonia Pacheco. At least one specimen in a series from Colonia Juárez is *P. hernandesi* (BYU 15201); it has a prognathous snout and gradually sloping rostrofrontal profile, horizontally directed cephalic horns, and the auricular border is serrate. Additionally, it has indications of large melanistic spots on the abdomen. If this specimen is correctly catalogued, it indicates contact between the two taxa in this area. Another specimen (BYU 15193) in the Colonia Juárez series is referred to *P. o. brachycercum*, but it has a rather prognathous snout which could indicate genetic influence from *P. hernandesi*; its snout length is 55.3% of orbit to rostral scale distance. Also *P. hernandesi* apparently occupies the mountains directly to the west of Colonia Juárez. *P. o. brachycercum* is sympatric with *P. orbiculare* near San José de Babícora (29˚ 14' 45" N; 107˚ 46' 30" W), and the two species probably coexist in other areas. However, no morphological evidence of hybridization between the two species has been detected. A specimen of *P. o. brachycercum* from the Sierra del Nido (UTEP 2520) also has a rather protruding snout (54.5% of orbit to rostral scale distance), raising the question whether *P. hernandesi* occurs in the upper reaches of this mountain range and perhaps is genetically interacting with *P. o. brachycercum*. Alternatively, it may simply be an aberrant specimen for this character.

The habitat of *P. o. brachycercum* can be generally characterized as "desert grassland", but it also occurs in oak and pine-oak associations. The climax vegetation and dominant fasciations in the grassland communities have not been thoroughly studied and categorized. It has been found in "grassland" habitat at the following localities in Chihuahua: southwest slope of the Sierra del Nido, SW of La Junta, 8 km S of San Buenaventura, and Yepómera, and in Durango: 19 km SE of Yerbaniz and 2 km N of Atotonilco. Grassland with scattered oaks has been recorded at 6.4 km NNE Boquilla, Durango, and pine-oak association has been noted at 25 km N of Gómez Farías, and 17 km SW of San Buenaventura, Chihuahua. Elevations recorded at various localities (n = 14) range from 1,730 m (5,674 ft) near La Resolana, Durango, to 2,194 m (7,196 ft) on the southwest slope of the Sierra del Nido, Chihuahua.

Remarks. Additional collecting is needed to obtain a clearer concept of the distribution limits of this race, particularly at the southern extreme of its range and along its eastern periphery. The potential interactions, both ecological and genetic, with *P. hernandesi and P. orbiculare* merit detailed study (see Montanucci, 1981). Although records are few in the northern part of Mexico, it appears that *P. hernandesi* ranges southward along the Sierra San Luis, flanked on the west (Sierra el Tigre) by *P. orbiculare* and on the east by *P. o. brachycercum*.

Cope (1900:417) listed USNM 206 (now lost) as *P. d. ornatissimum* from between Janos, Chihuahua (30˚ 53' 16" N; 108˚ 11' 24" W), and San Luis Spring (31˚ 19' 07.97" N; 108˚ 51' 28.98" W), Sonora. It was received from Lt. William H. Emory and collected by Dr. Kennerly during the U.S.–Mexico Boundary Survey. A photographic voucher of a live specimen from near Janos exhibits characteristics of nominotypical *P. ornatissimum* (dorsolateral white spots) and *brachycercum* (wedge-shaped dorsal spots with posterior light borders and light medial borders virtually absent). The region north of Janos as well as much of northern Chihuahua requires additional field work to understand the distributional relationships of *P. hernandesi*, *P. o. ornatissimum*, and *P. o. brachycercum.*

Lemos-Espinal *et al.* (2004) reported on a collection of lizards from the state of Chihuahua made by the senior author in 2002. Described therein is a series of specimens of *Phrynosoma hernandesi* from three localities categorized as northern, central, and southern. The specimens (which I have not examined) were deposited in the collection of Unidad de Biologia, Technologia y Prototipos (UBIPRO), Universidad Nacional Autonoma de Mexico (UNAM).

The northern locality is Cañón de la Madera in the Sierra de San Luis, 1638 m., (31˚ 13' 41.1" N; 108˚ 44' 5.5" W). Two specimens (UBIPRO 10400–01) have a tail length ratio in the range of 33% to 37% of SVL, but the gender of the specimens is not given (males and females differ in proportional tail length). UBIPRO 10400 is a subadult, 55 mm SVL with faint subcaudal bands. The other specimen is a juvenile between 26 and 30 mm SVL and has dark melanistic subcaudal bands. Based on this description the specimens are probably *P. hernandesi*. The only other species with prominent tail bands is *Phrynosoma orbiculare* which has been recorded from the Sierra el Tigre (Montanucci, 1981) to the west southwest of the Sierra de San Luis.

The central locality is La Quebrado del Mesteño, 2,248 m. (29˚ 27' 37.2" N; 106˚ 51' 5.5" W). One specimen, 43 mm SVL, was collected (UBIPRO 10139); its gender is not given; no tail bands are present, and the authors state that its tail ratio falls within the limits of the northern sample. The locality is near the southwestern slope of the Sierra del Nido, and based on locality, is probably *P. o. brachycercum* (see Appendix I for additional records).

The southern locality is Mesa de Agostadero, Cerro Blanco, 2356 m., (26° 54' 38.7" N; 106° 47' 14.1" W). Seven specimens were collected, including juveniles with dark black tail bands (UBIPRO 9140–43, 9206–08). Tail ratios show wide limits from 36% to 59% of SVL, and the lower limit falls outside the range of variation for both sexes of *Phrynosoma orbiculare* and the upper limit falls outside the limit for *P. o. brachycercum* (Montanucci, unpublished data). Therefore both species are probably represented in the series. *P. orbiculare* was previously reported from this locality (Montanucci, 1981), and the assignment of these specimens to *P. hernandesi* is probably erroneous. Lemos-Espinal *et al*. (2004) stated that the tail banding is strictly a juvenile trait and is not a taxonomic character. On the contrary, the ventral tail pattern in the melanin-dispersed phase is taxonomically useful and informative for all age classes.

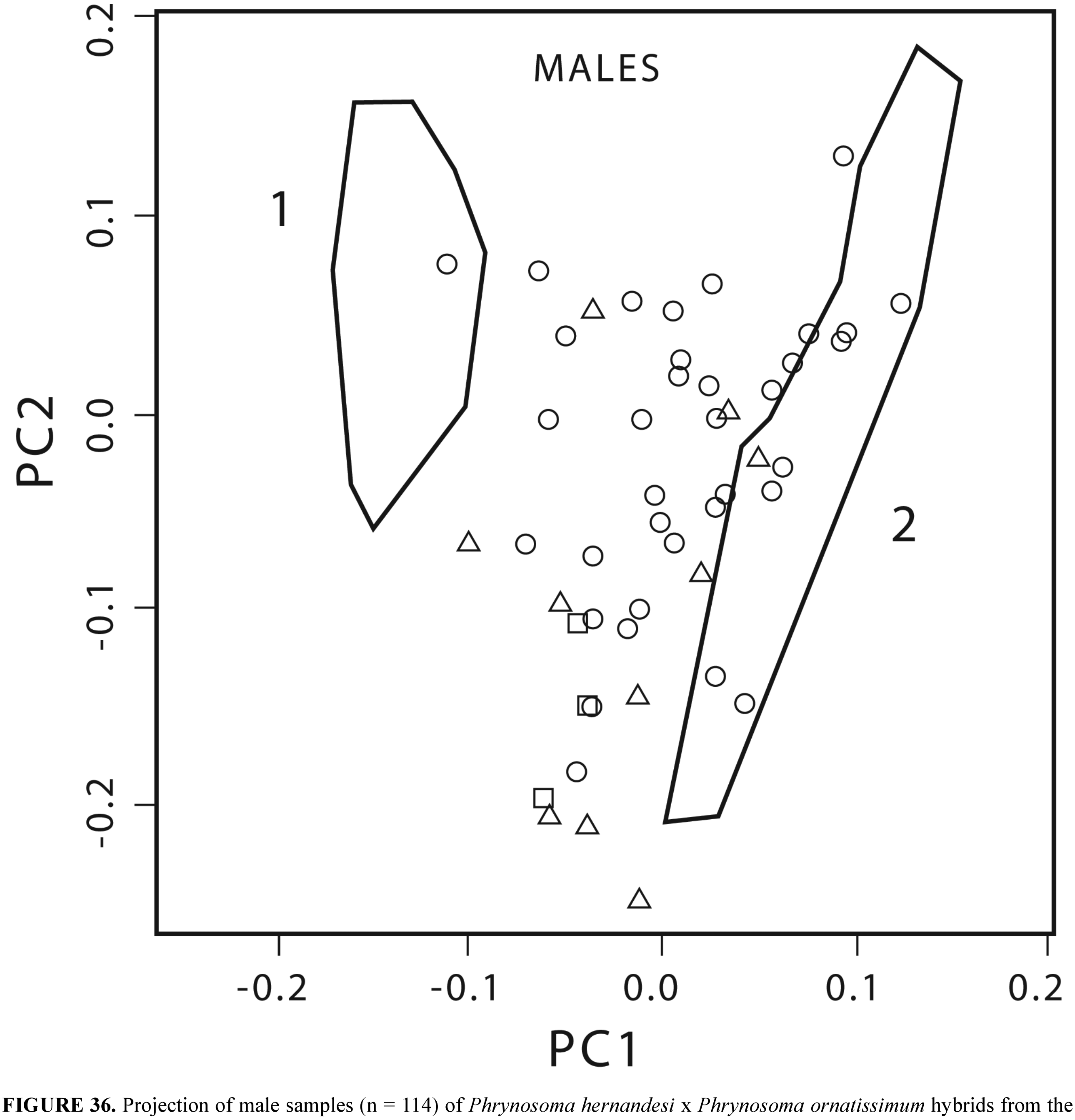

FIGURE 36. Projection of male samples (n = 114) of *Phrynosoma hernandesi* x *Phrynosoma ornatissimum* hybrids from the Colorado Plateau, on the first two principal components (PC1, PC2) of a 17-character correlation matrix. PC1 explains 40.5% and PC2 explains 17.9% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are 1. *Phrynosoma ornatissimum* reference sample, 2. *Phrynosoma hernandesi* reference sample. Presumptive hybrid samples are: Little Colorado River Basin, Arizona (open circles), San Juan-Mancos river basins, Colorado (squares), and Chaco Basin, Upper Rio San Jose, and the Malpais, New Mexico (triangles). See text for further discussion.

Hybridization between *Phrynosoma hernandesi* and *Phrynosoma ornatissimum*

This study has revealed areas of contact and hybridization between two morphologically defined species of short-horned lizards, *P. hernandesi* and *P. ornatissimum*. The following is a quantitative and descriptive analysis of the character variation in these hybrid zones based on the specimens examined. Heretofore, there have been no studies of hybridization between the two short-horned lizard taxa. With regard to the Colorado Plateau region, Stejneger (1890) presented comparative descriptions of what he believed to be *P. ornatissimum* and *P. hernandesi* from the Desert of the Little Colorado River and the San Francisco Mountains respectively. But data presented herein indicate that Stejneger's concept of the former taxon was based largely on specimens of hybrid origin. Eaton (1935) attempted to identify a small series of short-horned lizards from this region, but experienced difficulty because of their admixture of traits and because he was confused as to the diagnostic characters that distinguish the two species. My morphological analyses reveal Eaton's specimens to be presumptive hybrids. It is also worth noting that Gehlbach's (1965) conclusion that *P. hernandesi* and *P. ornatissimum* were conspecific was based on a series of morphologically variable specimens collected from the Colorado Plateau hybrid zone, near its eastern edge.

Colorado Plateau hybrid zone. An extensive area of northeastern Arizona, northwestern New Mexico, southwestern Colorado and southeastern Utah is occupied by populations of short-horned lizards displaying combinations of characters of *Phrynosoma hernandesi* and *P. ornatissimum*. The morphological heterogeneity exhibited by specimens from this region suggests a history of genetic interaction between the two taxa. Principal components analyses of male and female data sets reveal that individuals morphologically similar to the two presumptive parental species as well as an array of morphologically intermediate specimens comprise these samples. The hybrid clusters in both plots fall generally between the polygons for the parental reference samples and they show relatively greater dispersion along both PC axes (Figs. 36–37, Table 6).

TABLE 6. Character loadings from correlation matrices for the first and second principal components of the multivariate analyses of male and female data sets of the Colorado Plateau hybrid zone.

	Males		Females	
Character	**PC1**	**PC2**	**PC1**	**PC2**
FR	0.351880	0.107470	0.354537	0.137261
OO	0.336129	0.057705	0.311704	0.040236
OT	0.324392	0.027678	0.309932	-0.011423
RF	0.308385	0.098992	0.285716	0.030950
DS	0.313228	0.138032	0.291875	0.208449
EM	0.297148	0.156671	0.336117	0.176046
WS	0.312127	0.227231	0.301652	0.195285
FP	0.176766	0.190712	0.150856	0.203092
TL	-0.236000	-0.031544	-0.266580	-0.121004
SL	0.036698	0.237098	-0.027235	0.093265
FW	0.003105	0.212577	0.055493	0.284396
HW	-0.101917	0.450597	-0.116349	0.444222
TR	-0.137606	0.454751	-0.166197	0.429615
IOD	0.169692	-0.111795	0.178082	0.008841
OH	-0.095108	0.381133	-0.084726	0.342154
TH	-0.254903	0.344279	-0.265843	0.360554
SUP	-0.242067	0.233297	-0.248849	0.302252

TABLE 7. Summary of character states for putative hybrids and parental specimens from the Colorado Plateau hybrid zone. Characters and character states are: Orientation of occipital horns (OO), Orientation of third temporal horn (OT): E = slightly elevated, H = horizontally directed, U = upright; Rostrofrontal profile (RF): A = angular, R = rounded, S = sloping gradually; Dorsal spots (DS): LR = large, rounded, SR = small, rounded, TB = transverse bands, W = wedge-shaped; Extent of pale margins (EM): L = lateral margin, M = medial margin, P = posterior margin; Dorsolateral white spots (WS): + = present, 0 = absent; Gular pattern (GP): C = chevrons, HW = horizontal wavy bands, S = spots, SU = suffusion, V = vermiculations; Abdominal pattern (ABD): F = flecks, S = spots, SU = suffusion; Subcaudal bands (SCB): + = present, 0 = absent; Tail length (TL): I = intermediate length tail, L = tail long, S = tail short. Relative tail length based on *P. hernandesi* reference sample from San Francisco Peaks, Arizona, and *P. ornatissimum* from Albuquerque, New Mexico.

Museum Number	**Sex**	**OO**	**OT**	**RF**	**DS**	**EM**	**WS**	**GP**	**ABD**	**SCB**	**TL**
Arizona: Apache Co: Adamana											
MVZ 9014	F	E	H	R	SR	P	0	--	--	--	L 2.12
MVZ 9015	F	E	H	S	SR	P, M	0	--	--	--	S 1.88
RRM 3298	F	U	U	S	LR	P, M, L	0	S, V	S	+	L 2.06
RRM 3299	F	U	U	S	LR	P, M	0	S, V	S	--	L 2.35
USNM 82309	F	E	E	R	LR	P, L	0	S, V	--	--	S 1.52
Arizona: Apache Co: Chinle, 8 km SE											
USNM 44626	F	E	E	R	W	P	0	--	--	--	L 2.14
Arizona: Apache Co: Chuska Mts.											
UAZ 25324	F	U	E	S	SR, W	P	0	--	--	--	L 2.48
UAZ 33478	F	E	H	S	SR, W	P	0	S, V	S, SU, F	--	L 2.37
Arizona: Apache Co: Ganado, 6.4 km NW											
USNM 44627	F	U	H	R	SR	P	0	S, V	--	--	L 2.16
Arizona: Apache Co: Holbrook											
ANSP 19869	M	E	H	S	SR	P, M	0	V	--	--	L 2.30
Arizona: Apache Co: Holbrook, 90 mi. NNE											
UF 23053	F	E	E	S	SR	P	+	--	--	--	L 2.56
Arizona: Apache Co: Little Colorado River											
UAHC 66-220	F	H	H	R	LR	P, L	+	--	--	--	I 1.98
UMMZ 85018	M	E	H	S	SR	P	0	--	--	--	S 1.80
Arizona: Apache Co: Sanders, 16 km S											
UCM 24268	M	E	H	R	LR	P, M	+	S, V	--	--	L 2.50
Arizona: Apache Co: Sanders, 19 km S											
UCM 24269	M	E?	H?	S	SR	P, M, L	0	S, V	S	+	--

......*continued on the next page*

TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Arizona: Apache Co: St. Johns											
MVZ 9021	F	H	H	R	SR, W	P	0	--	--	--	L 2.42
MVZ 9022	M	E	E	R	SR	P	+	--	--	--	I 2.38
MVZ 9024	M	E	E	R	LR	P, M	0	--	--	--	I 2.50
MVZ 9025	F	H	H	R	W	P	+	--	--	--	I 2.03
MVZ 9026	F	H	H	R	SR, W	P	0	--	--	--	L 2.27
MVZ 9027	F	H	H	R	LR	P	0	--	--	--	L 2.07
TNHC 07437	F	H	H	S	TB	P	0	--	--	--	L 2.34
UAZ 36012	F	H	H	S	TB	P	0	S, V	S	+	L 2.35
Arizona: Apache Co: St. Johns, 6.4 km N											
UAZ 36011	F	U	U	R	SR	P, L	0	S, V	--	--	S 1.86
Arizona: Apache Co: St. Johns, 9.6-12.8 km S											
MVZ 9016	F	E	E	R	SR, W	P	+	--	--	--	I 2.03
MVZ 9017	M	E	E	S	LR	P, M	0	--	--	--	I 2.54
Arizona: Apache Co: St. Johns, 24 km S											
UCM 24270	F	H	H	S	W	P	0	S, SU	S	+	L 2.40
Arizona: Apache Co: Tsaile Lake											
UAZ 33632	F	E	H	R	SR, W	P, L	0	S, SU, V	S, SU	--	L 2.20
Arizona: Apache Co: Zuni River											
UCM 24271	M	E?	E?	R?	SR	P, M, L	+	V, HW	S	+	--
USNM 3219	M	E	H	R	W	P	0	S	--	--	I 2.50
USNM 293248	F	H	H	S	W	P	0	S	--	--	L 2.26
USNM 293249	F	E	E	S	W	P	0	--	--	--	L 2.10
Arizona: Coconino Co: Black Tank Lava Beds											
MVZ 16023	M	E	E	S	SR, W	P	0	--	--	--	I 2.28
MVZ 16024	F	E	E	S	W	P	0	--	--	--	L 2.18
Arizona: Coconino Co: Deadman Flat											
MVZ 8668	M	H	H	S	W	P	0	--	--	--	I 2.56
MVZ 8670	M	E	E	S	TB	P	0	--	--	--	I 2.35
UAZ 1976	M	H	H	S	SR, W	P	0	S, V	S, SU	+	I 2.58
UMMZ 74029	M	E	E	S	W	P	0	SU	SU?	--	I 2.50
UMMZ 74030	M	E	H	R	TB	P	0	SU, V	S	+	I 2.44

......*continued on the next page*

TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Arizona: Coconino Co: Flagstaff, 40 km NE											
UMMZ 223395	F	H	H	S	SR	P	0	S	S	0	L 2.08
UMMZ 223396	F	H	H	S	W	P	0	S, SU	S	+	L 2.07
Arizona: Coconino Co: Gray Mtn. lava field											
MVZ 8671	F	E	E	R	SR	P	0	--	--	--	I 1.97
MVZ 8672	M	H	H	S	TB	P	0	--	--	--	I 2.42
MVZ 8688	F	H	H	S	TB	P	0	--	--	--	L 2.20
RRM 2106	M	E	E	S	SR	P	0	SU	S	+	I 2.48
RRM 2122	M	E	H	S	LR	P	0	S, V	S, SU	+	I 2.56
RRM 2147	M	E	E	S	SR	P	0	S, C	S	+	I 2.26
RRM 2167	M	E	E	A	SR	P	0	SU	S	0	I 2.30
RRM 2263	F	H	H	S	SR	P	0	S?	S	+?	I 1.98
RRM 2268	M	H	H	S	TB	P	0	S, SU	S	+	I 2.43
RRM 2326	F	E	H	A	TB	P	0	S, HW	S	+	S 1.94
Arizona: Coconino Co: Lava Field East of San Francisco Mts.											
USNM 15814	M	H	H	S	W	P	0	--	S	+	I 2.48
Arizona: Coconino Co: Little Colorado River											
USNM 4580	F	U	H	R	SR	P	+	S	--	--	S 1.87
USNM 4599	M	E	E	R	SR	P	0	V	--	--	I 2.31
Arizona: Coconino Co: Lockett Tank, 8 km W Tappan Spring											
USNM 60188	F	H	H	S	W	P	0	S, V	S	+	L 2.09
USNM 60189	M	H	H	S	SR	P	0	--	--	--	L 2.73
USNM 60191	F	H	H	S	W, TB	P	0	S, V	--	--	L 2.10
USNM 60192	M	H	H	S	SR	P, L	0	--	S	+	I 2.32
Arizona: Coconino Co: Meteor Crater											
LACM 101536	M	E	E	S	LR	P	0	C	--	--	I 2.25
LACM 121576	F	E	E	S	SR, W	P	+	S	--	--	S 1.92
RRM 3297	F	H	E	S	LR, TB	P	0	S	--	--	S 1.83
Arizona: Coconino Co: Painted Desert											
USNM 15816	M	E	U	S	SR	P	0	--	--	--	--
USNM 15817	M	H	H	R	SR	P	0	S, SU	S	+	I 2.39
USNM 15818	F	U	H	S	SR	P	0	V, C	F	+	S 1.63
USNM 15819	F	E	E	R	SR	P	0	S	S	--	S 1.84

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Arizona: Coconino Co: Sunset Crater											
TNHC 11604	F	E	E	S	TB	P	0	--	--	--	L 2.12
Arizona: Coconino Co: The Gap, 8 km N											
MVZ 65809	F	E	E	S	W	P	0	--	--	--	S 1.85
MVZ 65810	M	E	E	S	W	P, M	0	--	--	--	S 2.10
Arizona: Coconino Co: Tuba City											
BYU 807	M	H	H	S	SR	P, L	0	S, V	S	--	I 2.42
MVZ 17866	F	E	E	A	LR	P	0	--	--	--	S 1.84
MVZ 17867	F	E	E	R	SR, W	P	0	--	--	--	L 2.28
UAZ 871	M	U	U	S	SR	P	0	S, V	S	+	--
Arizona: Coconino Co: Winona, NW											
RWA 4861	F	H	H	R	SR	P	0	--	--	--	L 2.25
USNM 60177	F	H	H	S	W	P	0	S, SU	S, SU	--	L 2.33
USNM 60178	F	H	H	S	W	P	0	S, SU	S, SU	+	L 2.25
Arizona: Coconino Co: Winslow, 16 km W											
UNLV 2152	F	U	U	R	SR	P, L	0	S	S	--	L 2.61
Arizona: Coconino Co: Wupatki Nat. Mon.											
UAZ 1984	F	E	E	S	W	P	0	S, SU	S	+	L 2.15
UMMZ 223402	F	H	H	S	W	P	0	S, C	S	+	I 1.98
Arizona: Navajo Co: Bidahochi											
MPM 1634	F	H	H	R	SR, W	P, M	+	HW	S	0	L 2.44
MPM 1635	F	E	H	S	SR	P, M	+	S, V	--	--	I 2.05
Arizona: Navajo Co: Black Mesa											
FMNH 23046	F	E	E	S	W	P	0	S, V	S	--	I 1.98
Arizona: Navajo Co: Heber, 1.6 km E											
UMMZ 79196	F	H	H	S	LR, TB	P	0	SU	S	--	I 2.00
Arizona: Navajo Co: Hotevilla											
UAZ 1991	M	E	H	R	SR	P	0	S, V	--	--	S 2.10
Arizona: Navajo Co: Kayenta											
MVZ 17868	F	U	E	R	LR	P, M	0	--	--	--	S 1.94
MVZ 17869	F	E	E	A	LR	P, M	0	--	--	--	I 2.01

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Arizona: Navajo Co: Kayenta, 19 km SW at Marsh Pass											
UU 2170	F	U	E	S	W	P	0	V	S, SU	--	L 2.41
Arizona: Navajo Co: Oraibi											
FMNH 51832	M	E	H	R	SR	P, M, L	0	S, V	--	--	S 2.19
FMNH 51833	F	E	H	R	SR	P	0	S, V, C	S	--	L 2.42
LACM 19672	F	E	E	S	LR	P	0	S, C	--	--	I 2.02
MVZ 16025	F	E	E	S	SR	P, M	0	--	--	--	L 2.19
RRM 3306	M	E	E	S	SR	P, M, L	0	S	--	--	I 2.29
UAZ 867	F	E	H	R	LR	P	0	S, V	S	--	S 1.65
USNM 73749	F	E	H	S	SR	P, M, L	0	S	--	--	L 2.20
USNM 73750	M	E	H	S	SR	P, M, L	0	V, C	--	--	L 2.66
Arizona: Navajo Co: Seba Dalkai											
UTEP 12354	F	E	H	R	SR	P, L	0	--	--	--	L 2.20
Arizona: Navajo Co: Show Low, 6.4 km N											
UAZ 1986	F	H	H	S	TB	P	0	V	S	--	L 2.32
Arizona: Navajo Co: Skeleton Mesa											
FMNH 23557	M	E	H	S	SR, W	P	0	V	SU?	--	I 2.40
FMNH 23558	F	E	H	S	TB	P	0	S, V	S, SU	+	S 1.85
Arizona: Navajo Co: Snowflake, 10.7 km S											
UMMZ 124601	F	E	E	S	W	P	0	--	S, SU	--	L 2.28
Arizona: Navajo Co: Toreva											
MPM 1630	F	E	E	S	SR, W	P	+	S, HW	--	--	I 2.01
MPM 1631	F	H	H	R	SR	P, M, L	0	S	--	--	L 2.34
Arizona: Navajo Co: Winslow											
FMNH 218755	F	E	H	S	TB	P	0	S, SU	S	0	L 2.15
UAZ 39649	M	E	E	S	SR, W	P	0	V	--	--	I 2.39
UMMZ 74031	F	H	H	S	W	P	0	SU	--	--	L 2.23
UMMZ 223405	F	H	H	S	W	P	0	SU, V	S	+	L 2.08
Arizona: Navajo Co: Winslow, 32 km NE											
MVZ 8932	M	E	E	R	LR	P, M	0	--	--	--	I 2.39
Colorado: Archuleta Co: Pagosa Springs											
USNM 8443	F	E	E	R	W	P	0	--	--	--	S 1.80

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Colorado: Archuleta Co: Pagosa Springs, 32 km E											
MVZ 105115	F	E	E	A	W	P	0	--	SU?	--	L 2.33
Colorado: Archuleta Co: Chimney Rock											
UTEP 2160	F	E	E	R	W	P	0	--	--	--	L 2.20
Colorado: La Plata Co: Durango, 6.4 km S											
RRM 3294	F	U	U	S	W	P, M	0	S?	--	--	L 2.10
Colorado: La Plata Co: Durango, 19 km W											
LACM 101538		E	E	R	W	P	0	SU	--	--	L 2.29
Colorado: La Plata Co: Perins Peak											
RRM 3293	F	E	H	S	W	P, M	0	SU	SU	--	L 2.24
Colorado: Montezuma Co: Ackmen, SW of Pleasant View											
FMNH 29366	M	E	H	S	SR, W	P, M	0	S, SU	S, F	+	I 2.34
FMNH 29367	F	E	E	S	SR	P, M	0	S	S, SU	+	S 1.97
Colorado: Montezuma Co: Cortez											
UCM 51265	M	E	E	S	W	P	0	S	S	+	L 2.64
UCM 51267	F	E	H	S	W	P	0	S	S	--	L 2.08
Colorado: Montezuma Co: Mancos											
AMNH 13603	M	E	E	R	SR	P, M	0	--	--	--	L 2.84
TNHC 11927	M	E	E	A	SR	P	0	--	--	--	I 2.30
Colorado: Montezuma Co: Mesa Verde											
KU 105937	F	E	E	S	W	P	0	V	--	--	L 2.37
LACM 109550	M	E	E	S	W	P	0	SU	--	--	I 2.51
UCM 7458	F	U	H	S	SR, W	P	0	SU, V	S	+	L 2.42
UCM 32240	F	E	H	S	W	P	0	S	S	--	L 2.50
Colorado: San Miguel Co: Gypsum Creek											
UCM 447	F	U	H	S	W	P, M	0	SU, S	S	0	L2.50
New Mexico: Cibola Co: Blue Water Canyon											
CU 5707	F	E	E	S	W	P	0	S, SU, V	S	--	L 2.24
MSB 11514	M	E	H	S	SR, W	P	0	--	--	--	L 2.74

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: Cibola Co: Casa Blanca, S											
MSB 23285	F	E	E	S	SR, W	P	0	HW	--	+?	S 1.80
MSB 23286	M	U	E	R	LR	P, L	0	S, V	S, F	--	I 2.43
New Mexico: Cibola Co: La Mosca Lookout, Mount Taylor											
CU 5453A	F	E	E	R	W, LR	P, M	0	S, SU, V	S	+	L 2.17
CU 5453B	F	H	H	S	W	P	0	SU	S?, SU	+	L 2.43
KU 28062	F	E	E	S	W, TB	P	0	V, C	S	+	L 2.32
New Mexico: Cibola Co: Malpais lava field											
CU 5601A	M	E	E	S	SR	P, M, L	0	--	--	--	I 2.32
CU 5601B	M	E	H	S	W	P, L	0	--	--	--	S 2.11
CU 5601C	F	E	E	S	LR	P, L	0	S?	--	--	L 2.28
MSB 4335	M	E	E	R	W	P	0	--	--	--	I 2.43
NMSU 1511	F	E	H	S	LR	P, M, L	0	--	--	--	L 2.38
USNM 44702	M	H	H	A	W	P	0	S, V	S	+?	L 2.80
New Mexico: Cibola Co: McCarty's											
USNM 16000	M	U	U	R	SR, W	P	0	S, V	--	+?	I 2.39
USNM 16001	F	E	E	S	SR	P	0	V	--	+?	L 2.23
New Mexico: Cibola Co: Milan											
MSB 23096	F	E	E	S	SR, W	P, L	0	--	--	--	L 2.07
New Mexico: Cibola Co: Mount Sedgwick											
USNM 44566	F	H	H	S	W	P	0	V	S	0	S 1.92
New Mexico: Cibola Co: Quemado, 41.6 km N											
MSB 15533	F	E	E	S	W	P	0	--	--	--	L 2.20
New Mexico: Cibola Co: San Fidel Lake											
MSB 19984	M	E	E	S	SR, W	P	0	S, V	S	+?	I 2.35
New Mexico: Cibola Co: San Mateo											
CAS-SU 5061	M	E	E	S	SR	P	0	--	--	--	I 2.62
New Mexico: Cibola Co: Schuman's Ranch (34° 43' 5.9" N, 107° 55' 52.5" W)											
UMMZ 86617	F	E	H	S	LR	P	0	--	--	--	L 2.36

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: McKinley Co: Continental Divide											
AMNH 62853	F	E	E	S	SR	P, M	0	--	--	--	I 2.00
AMNH 62854	F	U	U	R	SR	P	0	--	--	--	S 1.93
New Mexico: McKinley Co: Fort Wingate											
USNM 14396	F	U	U	A	SR	P, M, L	+	S, SU	SU, F	0	L 2.55
New Mexico: McKinley Co: Gallup											
CU 5841	F	E	E	R	LR	P	0	V	F	--	L 2.56
New Mexico: McKinley Co: Gallup, 16 km N											
TNHC 11654	F	E	E	S	SR	P	0	S, HW	--	--	I 2.00
TNHC 11655	F	U	E	A	LR	P, L	0	--	--	--	L 2.15
New Mexico: McKinley Co: Mexican Springs, 12.8 km E, 6.4 km S											
MSB 3238	F	E	E	S	SR	P, L	0	--	--	--	L 2.19
MSB 3239	F	U	E	S	SR	P, L	+	S, V	S	--	L 2.08
New Mexico: McKinley Co: Seven Lakes											
CU 5620A	F	E	E	S	SR, W	P	+	S, V	--	--	S 1.94
CU 5620B	F	E	H	S	SR, W	P	+	S, SU, V	--	--	I 1.98
New Mexico: McKinley Co: Thoreau, 3.2 km S											
MSB 13722	F	E	E	S	W	P	0	V, HW	S, F	--	L 2.07
New Mexico: McKinley Co: Thoreau, 9.k km S											
CU 5103	F	E	H	R	LR, TB	P	0	V, HW	--	--	S 1.94
CU 5119	F	E	E	S	W	P	0	S, SU	--	--	L 2.13
CU 5233	F	H	E	S	W	P	0	S	--	--	I 2.00
CU 5447A	F	E	E	S	W, LR	P	0	--	--	--	L 2.15
CU 5709	F	E	E	R	W	P	0	S, V	S	--	S 1.91
MSB 47197	F	H	H	S	W	P	0	S	SU	+	L 2.13
MSB 47238	F	E	E	S	SR, W	P	0	C	--	+	S 1.59
New Mexico: Rio Arriba Co: SW corner of county											
UMMZ 97496	M	U	E	S	W	P	0	S, V	--	+	I 2.56
UMMZ 97496	F	E	E	S	LR	P	0	S	S, F	+	L 2.40
New Mexico: Rio Arriba Co: San Juan River, 6 km SE Allison											
MSB 2969	M	E	H	S	W	P	0	S	S	+?	L 2.73

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TABLE 7. (Continued)

Museum Number	**Sex**	**OO**	**OT**	**RF**	**DS**	**EM**	**WS**	**GP**	**ABD**	**SCB**	**TL**
New Mexico: Rio Arriba Co: San Pedro Mts.											
USNM 58419	F	E	E	R	LR	P	0	S, V	S	+	L 2.36
New Mexico: San Juan Co: Aztec											
AMNH 9683	F	U	E	R	SR	P, L	0	--	--	--	S 1.80
MSB 1340	F	U	E	S	SR	P	0	S, SU	S, F	+	L 2.59
New Mexico: San Juan Co: Chaco Canyon Nat. Mon.											
MCZ 161080	F	U	E	R	W	P	0	S, C	S	0	L 2.24
MSB 3390	F	E	H	R	SR	P, L	0	S, V	F	--	S 1.96
MSB 21715	F	E	E	S	SR	P	+	--	--	--	I 2.05
MSB 33349	F	E	E	R	SR	P	0	S	F	0	S 1.91
New Mexico: San Juan Co: Chaco River, W of Burnham											
MSB 3195	F	E	H	R	SR, W	P	0	C	F	0	L 2.18
New Mexico: San Juan Co: Cottonwood Canyon											
MSB 2965	F	E	H	S	SR, W	P	0	S, V	S	--	L 2.32
New Mexico: San Juan Co: Farmington, 56 km S											
UMMZ 127847	M	E	E	R	SR	P, M, L	+	--	--	--	I 2.31
New Mexico: San Juan Co: Nageezi											
MSB 4150	F	E	H	R	SR	P, L	0	S, SU	S, SU	--	L 2.22
New Mexico: San Juan Co: San Juan River, 7.4 km ESE Allison											
MSB 7386	M	E	E	S	W	P	0	--	--	--	S 2.06
New Mexico: San Juan Co: San Juan River at Los Pinos River											
MSB 2966	F	E	E	S	W	P	0	--	--	--	L 2.28
MSB 7544	M	E	E	S	LR	P	0	C	S	+	I 2.36
MSB 7545	M	E	H	S	W	P	0	--	--	--	S 2.19
New Mexico: San Juan Co: Sheep Springs, 22 km E											
MSB 60936	F	U	E	S	SR, W	P, M, L	0	S, SU	S, SU	0	L 2.11
New Mexico: Sandoval Co: Counselors											
MSB 60294	F	E	H	S	W	P, M, L	0	V	F	+	L 2.13

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TABLE 7. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: Sandoval Co: Cuba											
MPM 19987	M	H	H	S	W	P, L	0	S, V	F?	+	I 2.40
MPM 19992	M	H	H	S	SR	P, M, L	0	S, V	F?	+	L 2.64
MPM 19993	M	E	E	R	SR, W	P, M	0	C	F?	+	L 2.75
MPM 19994	F	E	H	S	W	P	0	V	SU?	+	L 2.22
Utah: San Juan Co: Dunn's Trading Post											
MVZ 17870	F	E	H	R	W	P	0	--	--	--	L 2.47
Utah: San Juan Co: Elk Ridge, Manti-La Sal Nat. Forest											
LACM 25386	F	E	E	R	W	P	0	--	--	--	I 1.98
MSB 21943	F	E	H	S	SR	P, L	0	--	--	--	L 2.38
UU 2830	F	E	H	S	W	P	0	SU	S	0	L 2.60
UU 2860	M	E	H	S	SR	P, L	0	SU	S, SU	0	I 2.57

The morphological characters inherited from *P. hernandesi* include a gradually sloping rostrofrontal profile, horizontally directed occipital and temporal horns, a relatively long tail, wedge-shaped dark dorsal spots or transverse bands with light-colored borders confined to their posterior edges, gular area with gray suffusion, and/or spots and vermiculations, abdomen with rows of large melanistic spots, and interrupted and /or complete melanistic subcaudal bands. The traits from *P. ornatissimum* include a rounded or angular and steeply inclined rostrofrontal profile, elevated to upright cephalic horns, a relatively short tail, large, rounded dorsal spots with narrow, discrete white and/or yellow lines bordering the medial and posterior edges, conspicuous white spots scattered over the dorsolateral surfaces of the body, gular area with a chevron pattern or transverse wavy lines, abdomen with scattered flecks, and no markings under the tail. The variation in rostrofrontal profile, cephalic horn orientation, dorsal and ventral pattern traits, and proportional tail length are tabulated for 106 specimens from northeastern Arizona, 63 specimens from northwestern New Mexico, 17 specimens from southwestern Colorado, and five specimens from southeastern Utah (Table 7). Additional specimens (juveniles and damaged road-killed specimens) from the region were studied, but little useful information was recorded.

The following summary of variation in short-horned lizards from the Little Colorado River region of Arizona is based on 100 of the 106 tabulated specimens. The cephalic horns are elevated above the horizontal plane or directed upward in 45 lizards (45%). Twenty-six lizards (26%) have elevated or upright occipital horns, but horizontally directed temporal horns. In twenty-nine lizards (29%), the occipital and temporal horns are directed horizontally. The rostrofrontal profile is nearly flat and gradually sloping in 64 lizards (64%), and rounded or angular with a steep incline in 36 lizards (36%). The dorsal pattern consists of dark, wedge-shaped spots or transverse bands in 33 lizards (33%); the spots are small and more or less rounded in 51 lizards (51%), and are large and rounded in 16 lizards (16%). In specimens with small, rounded spots, the spots typically have a paired arrangement on the dorsum. The light-colored borders of the dorsal spots are confined to the posterior margins in 71 lizards (71%); in eight lizards (8%) the light-colored borders extend from the posterior to the lateral margins of the spots. In 13 lizards (13%) the light-colored borders extend along the posterior and medial margins of the dorsal spots. In some lizards, the light-colored medial borders are not well defined, but rather faint. In other specimens, the light-colored borders are fragmented into dots or short lines. In eight specimens (8%), the dorsal spots have nearly encircling whitish borders (i.e. medial, posterior and lateral margins) producing an ocellus-like pattern (Fig. 38). In many specimens only a few of the dorsal spots have light-colored medial borders; the remaining spots have posterior and lateral borders only. Lizards with light-colored borders along the medial margins of the dorsal spots have been collected from Adamana, Bidahochi, Holbrook, Kayenta, Oraibi, Sanders, St. Johns, The Gap, Toreva, northeast of Winslow, and Zuni River. Dorsolateral white spots are present in 12 specimens (12%) and absent in the remaining 88 lizards (88%). Some specimens have only a few white spots more or less concentrated in the lateral areas of the dorsum. In three specimens (3%), the spots are numerous and scattered over nearly all of the dorsum. Specimens with white spots have been collected from Bidahochi, Little Colorado River, Meteor Crater, Sanders, St. Johns, Toreva, and Zuni River. The tail is long in 42 of 97 specimens (43.3%); it is short in 18 lizards (18.6%), and it is intermediate in length in 37 lizards (38.1%). Reference samples to determine proportional tail length are *P. hernandesi* from the San Francisco Peaks, Arizona, and *P. ornatissimum* from the Rio Grande Valley near Albuquerque, New Mexico.

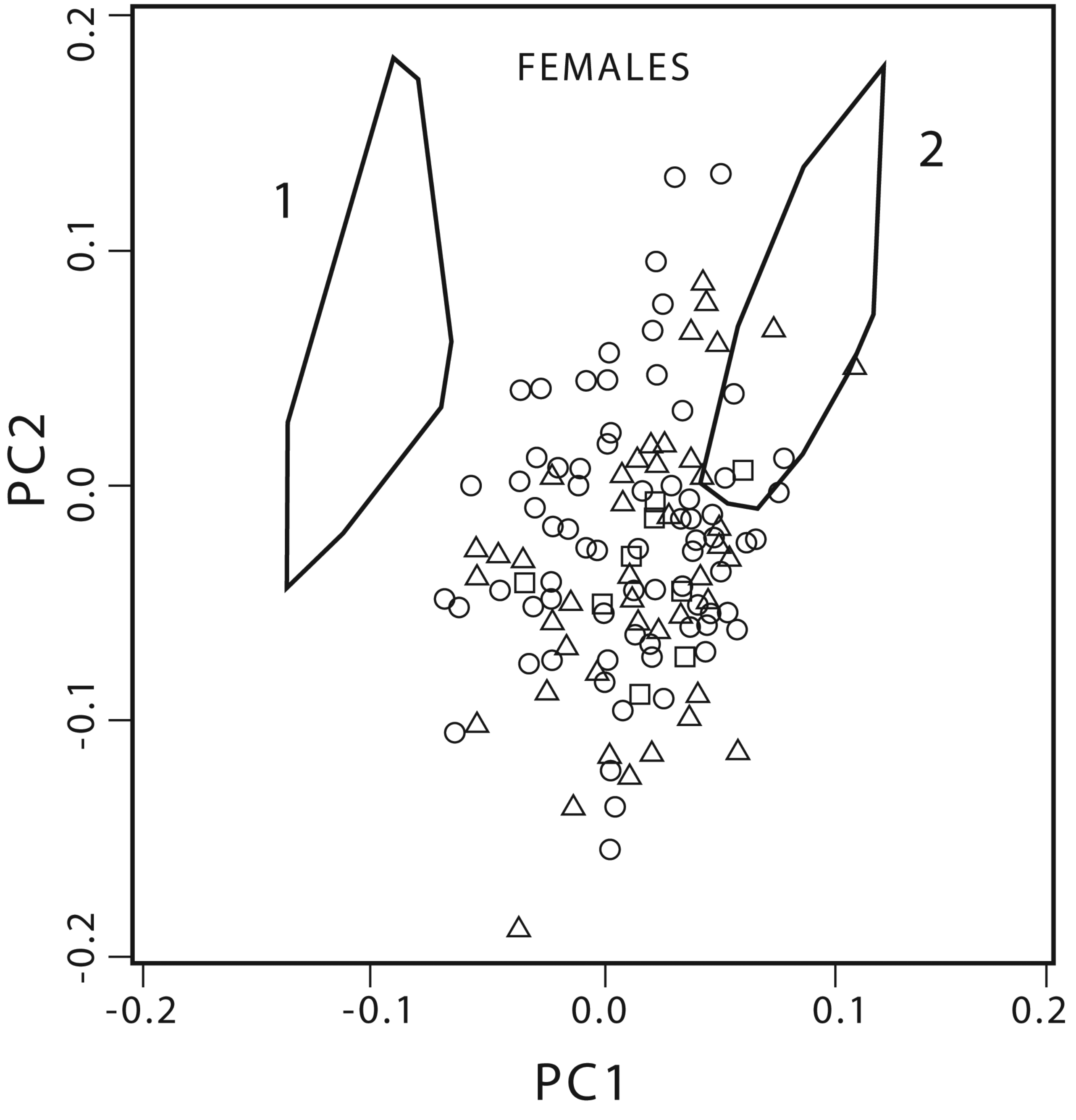

FIGURE 37. Projection of female samples (n = 235) of *Phrynosoma hernandesi* x *Phrynosoma ornatissimum* hybrids from the Colorado Plateau, on the first two principal components (PC1, PC2) of a 17-character correlation matrix. PC1 explains 34.9% and PC2 explains 18.3% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are 1. *Phrynosoma ornatissimum* reference sample, and 2. *Phrynosoma hernandesi* reference sample. Presumptive hybrid samples are: Little Colorado River Basin, Arizona (open circles), San Juan-Mancos river basins, Colorado (squares), and Chaco Basin, Upper Rio San Jose, and the Malpais, New Mexico (triangles). See text for further discussion.

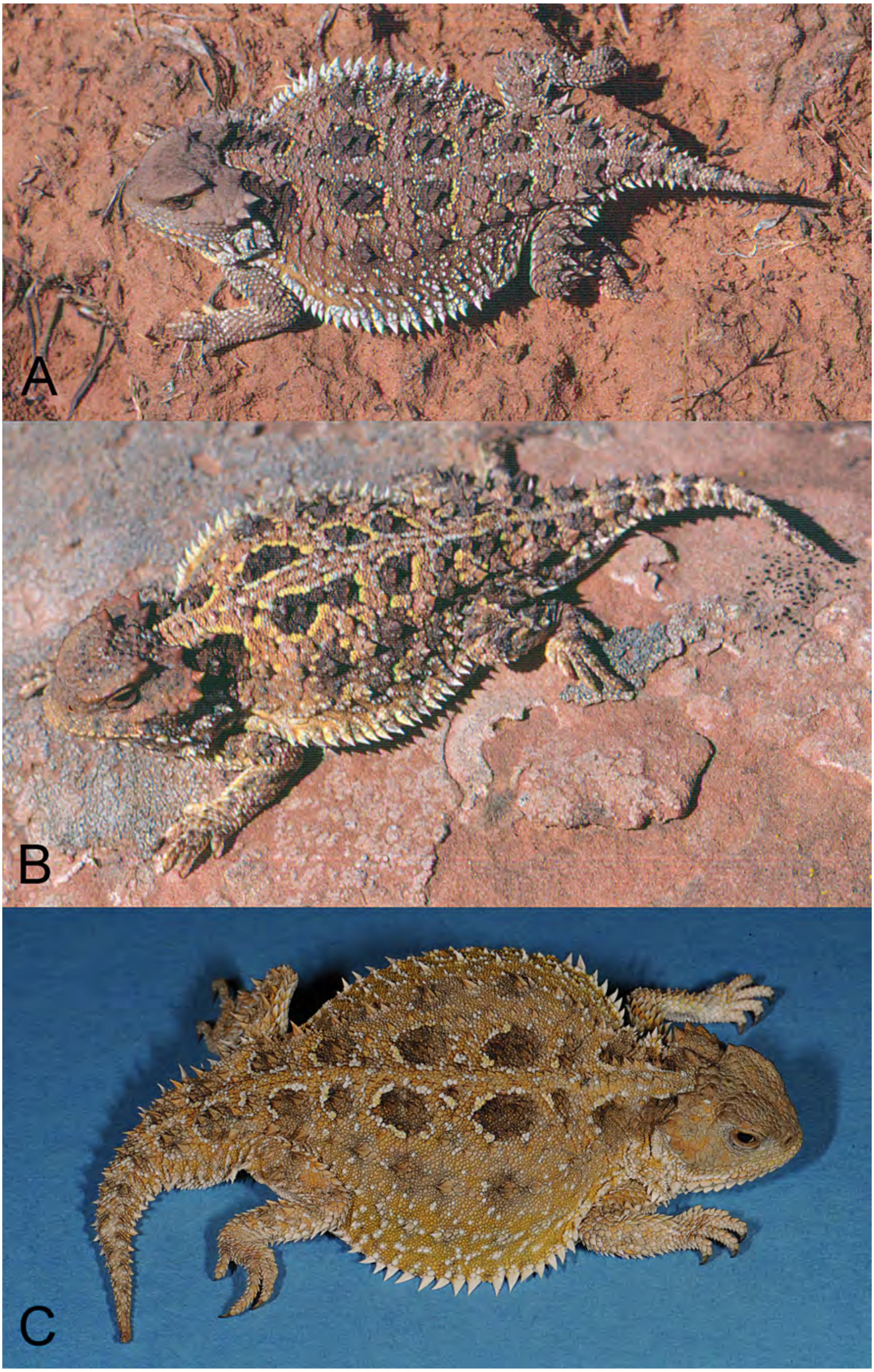

FIGURE 38. *Phrynosoma hernandesi x Phrynosoma ornatissimum* hybrids (A, B) from Kaibito, Coconino Co., and (C) from Oraibi, Navajo Co., Arizona. Note whitish margins encircling the dorsal spots. Photos A & B by Karl Switak.

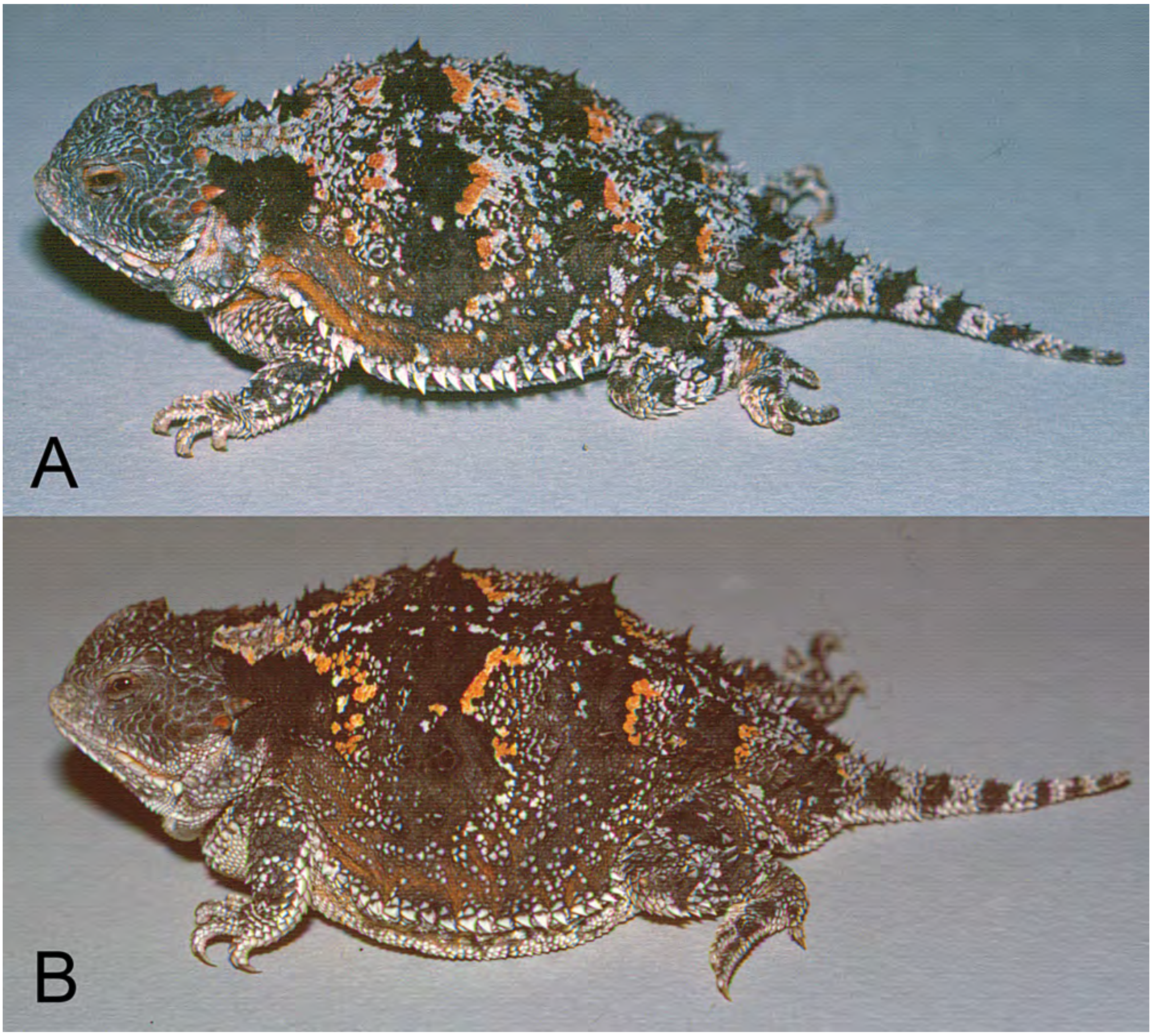

FIGURE 39. Hybrids (*Phrynosoma hernandesi* x *Phrynosoma ornatissimum*) morphologically similar to *P. hernandesi*. (A) RRM 2147 and (B) RRM 2326, from lava field 7 km S of Gray Mountain, Coconino Co., Arizona.

Phrynosoma hernandesi is known from the San Francisco Peaks and from the Mogollon Rim along the western perimeter of the Colorado Plateau hybrid zone. Specimens morphologically close to *P. hernandesi* have been collected from NW of Winona, Sunset Crater, Deadman Flat and Wupatki National Monument. Specimens from farther north in the San Francisco lava field are morphological intermediates or are similar to *P. hernandesi*. Short-horned lizards from the lava beds are more or less melanistic with reddish cephalic horns; the posterior margins of the dorsal spots vary from white, yellow, or orange to coral pink (Fig. 39). These lizards are well concealed against the black lava rocks on which white and yellow lichens grow. Presumptive hybrids that are morphologically close to *P. hernandesi* have also been collected from Black Mesa, Marsh Pass, Skeleton Mesa in Navajo County, and the Chuska Mountains which straddle the Arizona-New Mexico border region.

Morphologically intermediate hybrids as well as specimens resembling *P. ornatissimum* have been taken in Arizona from Adamana, Bidahochi, Kayenta, Oraibi, Little Colorado River, Painted Desert and Tuba City. One specimen (UCM 24268) from 16 km south of Sanders, Apache County, is quite remarkable in that it very closely resembles typical *P. ornatissimum* in dorsal pattern (Fig. 40A), more so than any of the other 189 specimens examined from the Colorado Plateau region. However, it bears similarity to *P. hernandesi* in having horizontally directed cephalic horns and a proportionally long tail (250% of head length). Additional collecting in the vicinity of Sanders is needed to gain a better understanding of the variation in the short-horned lizards occurring there.

Specimens from the vicinity of St. Johns, Apache County, include morphological intermediates as well as a few similar to *P. hernandesi.* Specimens from 24 km south of St. Johns and farther south, appear to be typical *P. hernandesi.*

The following summary of variation in morphology and color pattern of short-horned lizards (n = 63) from northwestern New Mexico includes samples from the Chaco River Basin, the San Juan River Basin, the Rio San Jose Basin, the Malpais lava field, and the San Mateo and Zuni mountains. In forty-two lizards (66.7%) the occipital horns are elevated or upright, but the temporal horns are directed horizontally. Fifteen lizards (23.8%) have both the temporal and occipital horns elevated or upright. In six lizards (9.5%), the occipital and temporal horns are directed horizontally. The rostrofrontal profile is nearly flat and gradually sloping in 43 lizards (68.3%); it is rounded or angular with a steep incline in 20 lizards (31.7%). The dorsal pattern consists of dark wedge-shaped spots or transverse bands in 23 lizards (36.5%); the dorsal spots are small and more or less rounded in 29 lizards (46%); the spots are large and rounded in 11 lizards (17.5%). In specimens with small, rounded spots, the spots typically have a paired arrangement on the dorsum. The light-colored borders of the dorsal spots are confined to the posterior margins in 42 lizards (66.7%); in 11 lizards (17.5%) the light-colored borders extend from the posterior to the lateral margins of the spots. In three lizards (4.7%) the light-colored borders extend along the posterior and medial margins of the dorsal spots. In seven specimens (11.1%), the dorsal spots are nearly encircled by whitish borders. In many specimens only a few of the dorsal spots have light-colored medial borders; the other spots have only posterior and lateral light-colored borders. Lizards with whitish borders along the medial margins of the dorsal spots have been collected from Bisti Trading Post south of Farmington, Continental Divide, Counselors, Cuba, Fort Wingate, La Mosca Lookout, Malpais lava field, and east of Sheep Springs. Dorsolateral white spots are present in six specimens (9.5%), three of which have the spots scattered throughout the dorsum; the white spots are absent in the remaining 57 lizards (90.5%) from the region. Specimens with dorsal and dorsolateral white spots have been collected from Bisti Trading Post south of Farmington, Chaco Canyon, Fort Wingate, southeast of Mexican Springs, and Seven Lakes. In 35 lizards (55.6%) the tail is long; in 13 lizards (20.6%) the tail is relatively short, and in 15 lizards (23.8%) the tail is intermediate in length.

In New Mexico, hybrids morphologically similar to *P. ornatissimum* have been collected at various localities in the Chaco Basin (Bisti Badlands, Chaco Canyon, southeast of Mexican Springs, and Seven Lakes) and at Fort Wingate along the upper reaches of the Puerco River (Fig. 41) Presumptive hybrid specimens morphologically similar to *P. hernandesi* have been collected in the San Mateo and Zuni mountains. Specimens that resemble *P. hernandesi* have also been collected from the upper reaches of the San Juan River near its confluence with the Los Pinos River near the Colorado border. Along the Rio San Jose apparent hybrids have been collected near McCarty's, San Fidel Lake, and near the east slope of Seama Mesa. A specimen from the latter locality (MSB 23286) is morphologically similar to *P. ornatissimum*, having short, upright occipital horns, a rounded rostrofrontal profile, large, rounded dorsal spots but with only posterior and lateral light-colored margins, and a relatively long tail (Fig. 40B). Seama Mesa is situated close to the presumptive western range limit of *P. ornatissimum*, based on a specimen collected about 16 km farther east (RRM 2234). At the eastern periphery of the hybrid zone near Cuba, Sandoval County, four specimens are quite similar to *P. hernandesi*, but show several traits indicating possible genetic influence from *P. ornatissimum* (Table 7). Specimens from localities farther east in the San Pedro Mountains and the Sierra Nacimiento are classified as *P. hernandesi.*

The summaries of morphological and color pattern variation in samples from southwestern Colorado and southeastern Utah are combined (n = 22) as the sampled localities are situated (with the exception of one specimen) from north of the San Juan River. Twelve specimens (54.5%) have the occipital and temporal horns elevated or directed upright. Ten specimens (45.5%) have elevated or upright occipital horns, but horizontally directed temporal horns. No specimens from the area have both sets of cephalic horns directed horizontally. The rostrofrontal profile is gradually sloping in 14 lizards (63.6%), but rounded or angular in eight lizards (36.4%). The dorsal pattern consists of dark, wedge-shaped spots or transverse bands in 15 specimens (68.2%), and small, rounded spots in seven specimens (31.8%). No specimens have large, rounded spots. Dorsal spots with whitish borders confined to the posterior margins are noted in 14 specimens (63.6%); whitish borders along the posterior and lateral edges of the spots are recorded from two specimens (9.1%); light-colored borders along the medial and posterior edges of the spots are present in six specimens (27.3%). An additional specimen (USNM 40138) from Ashbaugh's Ranch, Montezuma County, Colorado, has especially well-defined light-colored borders along the posterior and medial margins of the dorsal spots. Additional data were not tabulated for this specimen because it was damaged. No specimens have light-colored borders encircling the dorsal spots. All specimens lack dorsolateral white spots. The tail is relatively long in 15 specimens (68.2%); it is short in two specimens (9.1%), and it is intermediate in length in five specimens (22.7%).

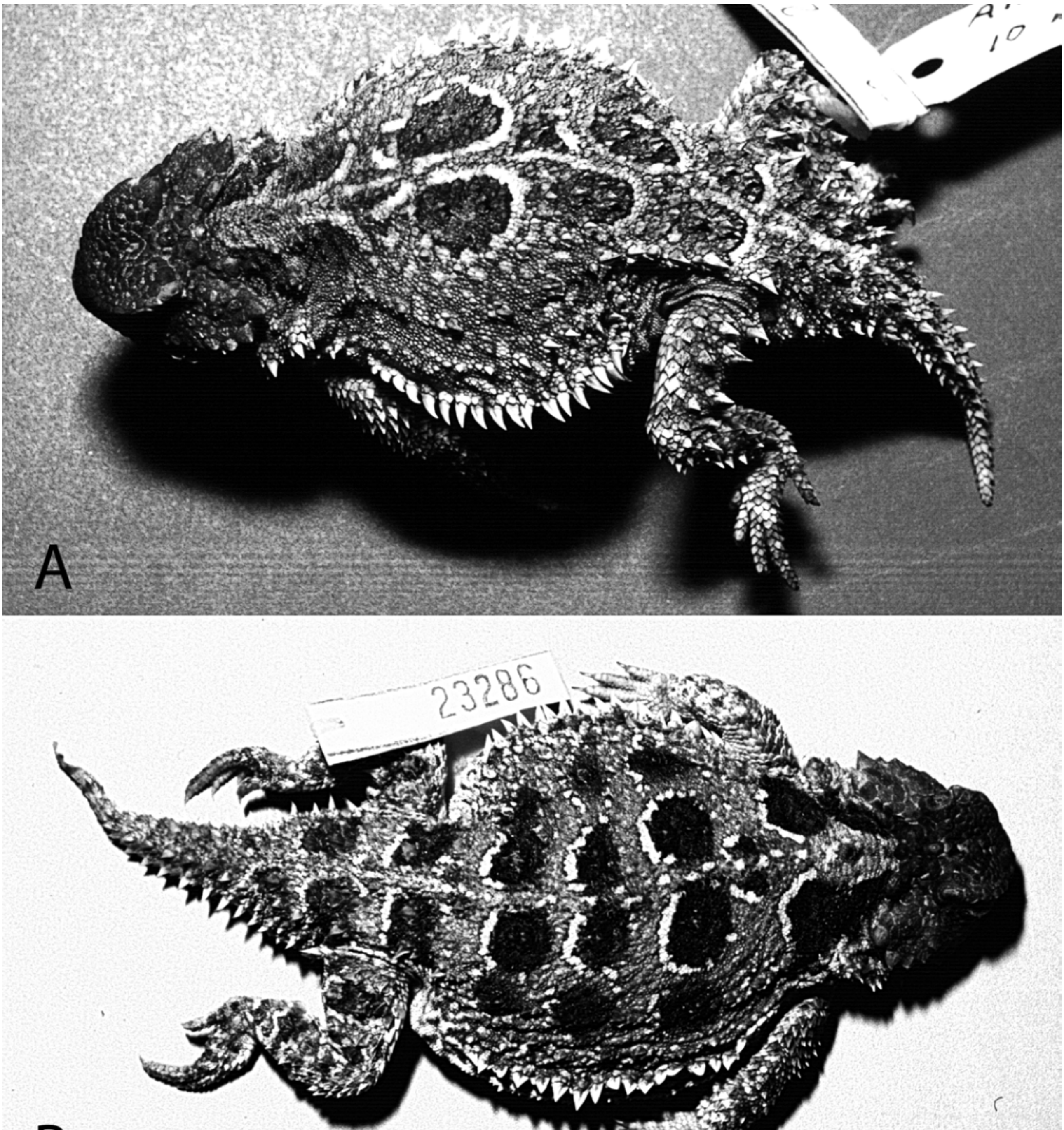

FIGURE 40. Hybrids (*Phrynosoma hernandesi* x *Phrynosoma ornatissimum*) morphologically similar to *P. ornatissimum*. (A) UCM 24268, 16 km S of Sanders, Apache Co., Arizona; specimen has large dorsal spots with light-colored medial borders; (B) MSB 23286, near east slope of Seama Mesa near Acoma Creek, Cibola Co., New Mexico; specimen has rounded dorsal spots but lacks light-colored medial borders and dorsolateral white spots; its tail is relatively long.

The putative hybrid specimens examined from southwestern Colorado are morphologically close to *P. hernandesi*, but as indicated above, display some traits that suggest genetic influence from *P. ornatissimum*. The most northern specimen with an admixture of traits is UCM 447 from Big Gypsum Creek, San Miguel County. A juvenile specimen (UCM 4509) from 3.2 km W of Gypsum Gap in Disappointment Valley appears to be *P. brevirostris.* Big Gypsum Valley is separated from the latter valley by only a low, narrow range of hills. Another juvenile specimen from Gypsum Gap (UCM 4510) appears to be *P. brevirostris*, but shows indications of traits from *P. hernandesi.* Potential genetic interactions between these taxa in this geographic area should be investigated.

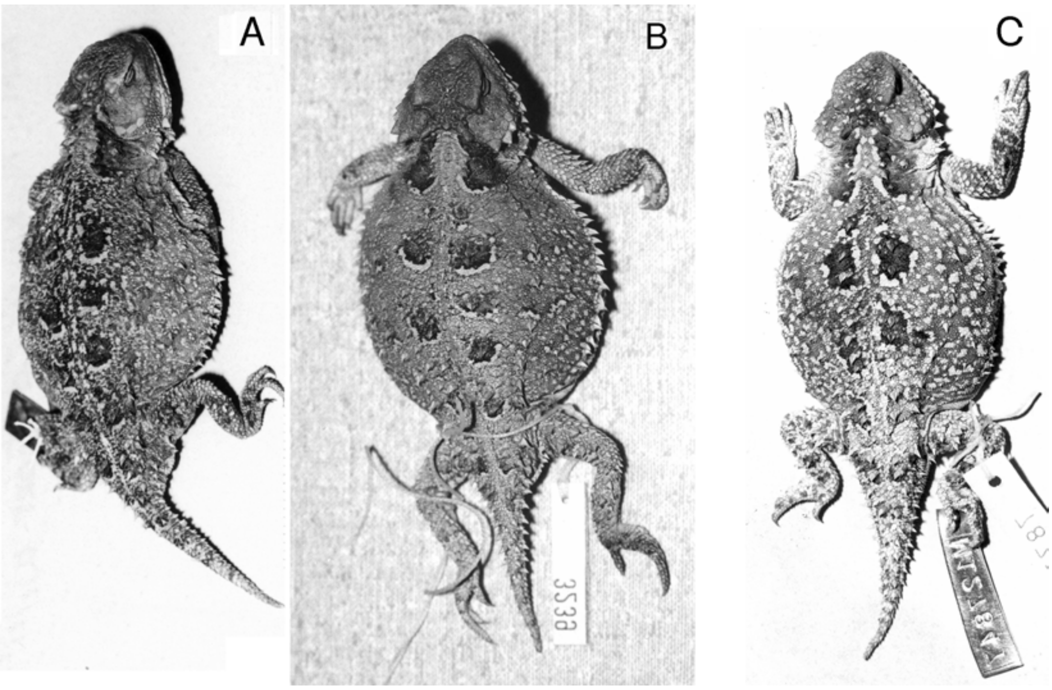

FIGURE 41. Hybrids (*Phrynosoma hernandesi* x *Phrynosoma ornatissimum*) morphologically similar to *P. ornatissimum* (A) USNM 14396 with rounded rostrofrontal profile, long tail, dorsal spots nearly encircled with light-colored borders, from Fort Wingate, McKinley Co., New Mexico; (B) MSB 3239 with dorsolateral white spots, from 13 km E and 6.4 km S of Mexican Springs, McKinley Co., New Mexico; (C) UMMZ 127847 with extensive white spotting, from Bisti Badlands, San Juan Co., New Mexico.

Available specimens from southeastern Utah are few. I examined four specimens from the mountainous region northwest of Blanding (Abajo Mountains, Elk Ridge), and all appear to be morphologically similar to *P. hernandesi*. No specimens have either dorsolateral white spots or light-colored borders along the medial edges of the dark dorsal spots. However, there is some variation in cephalic horn orientation and proportional tail length to suggest possible genetic influence from *P. ornatissimum*. There are no records for short-horned lizards from the lower segment of the San Juan River from near Aneth, Bluff and Mexican Hat to its confluence with the Colorado River. This area is dominated by Blackbrush (*Coleogyne*). One specimen from Dunn's Trading Post southeast of Navajo Mountain (MVZ 17870) is similar to *P. hernandesi*, but appears to be of hybrid origin. This locality, which is situated near the Arizona state line, lies in Great Basin sagebrush (*Artemisia*).

Mountains-plains hybrid zones. Montane populations of *P. hernandesi* occurring generally east of the Rio Grande in New Meixco and Texas are in parapatric contact with *P. ornatissimum* which occupies the surrounding short-grass plains. Where contact occurs, the two species readily hybridize as evidenced by specimens with various combinations of the diagnostic traits of the two species. Recorded elevations for presumptive hybrids range between 1,586 m (5,203 ft) and 2,135 m (7,005 ft), generally in the grassland-woodland ecotone, or at relatively low elevations in the juniper-pinyon woodland. Most specimens of *P. hernandesi* occur above this vertical range, from about 1,916 m (6,286 ft) to a maximum elevation of 3,475 m (11,400 ft). Recorded elevations for *P. ornatissimum* specimens are below this range, generally between 1,436 m (4,711 ft) and 2,134 m (7,001 ft).

Samples from the Sandia, Manzano, Sacramento, and Guadalupe mountains and the adjacent plains were subjected to Principal Components analysis. Scatterplots of the male and female data sets revealed morphologically intermediate specimens as well as specimens resembling the parental species (Figs. 42–43, Table 8).

TABLE 8. Character loadings from correlation matrices for the first and second principal components of the multivariate analyses of male and female data sets of the mountains-plains hybrid zones.

	Males		Females	
Character	**PC1**	**PC2**	**PC1**	**PC2**
FR	0.328374	0.146626	0.330236	0.109317
OO	0.320738	0.092893	0.299040	0.012031
OT	0.307497	0.077792	0.302050	0.006056
RF	0.323016	0.095227	0.325987	0.125501
DS	0.307323	0.117689	0.297362	0.168609
EM	0.282471	0.213314	0.298869	0.109464
WS	0.311307	0.114145	0.309945	0.119000
FP	0.156987	0.223824	0.105887	0.142130
TL	-0.280548	0.121359	-0.293090	-0.097789
SL	0.012212	0.325118	-0.035409	0.374607
FW	0.111311	0.231762	0.048859	0.389597
HW	-0.087510	0.431221	-0.092496	0.523817
TR	-0.134729	0.449579	-0.178788	0.424810
IOD	0.205217	-0.156690	0.178556	0.086761
OH	-0.108144	0.332877	-0.107283	0.123227
TH	-0.261675	0.283609	-0.290003	0.223542
SUP	-0.235097	0.232944	-0.247862	0.261028

The variation in rostrofrontal profile, cephalic horn orientation, dorsal and ventral pattern traits, and proportional tail length are tabulated for 31 specimens from the Sandia Mountains and vicinity, 19 specimens from the Manzano Mountains, 19 specimens from Carrizozo and the adjacent Sacramento Mountains, six specimens from the Guadalupe Mountains, eight specimens from the Chupadera Mesa, and nine specimens from the vicinity of Santa Fe, and several miscellaneous locations (Table 9). Data from an additional 65 specimens classified as *P. hernandesi* from the Sacramento Mountains are not tabulated, but are described below.

Putative hybrids have been collected from the west, north, and east slopes of the Sandia Mountains. Three specimens from the west slope are morphologically similar to *P. ornatissimum*, but display a few dorsal pattern traits suggesting genetic influence from *P. hernandesi*. Among four specimens from the north-slope near Placitas, two are similar to *P. hernandesi*, two others are more or less intermediate in morphology (Fig. 44). Three pecimens from the upper Cienega Canyon, one from 8 km NW of Sandia Park, one from Sandia Park, and another from Sulphur Canyon are morphologically close to *P. hernandesi*. A specimen from San Antonito (MSB 12901) agrees with *P. hernandesi* in color pattern, rostrofrontal profile, and proportional tail length, but has slightly elevated occipital horns. A series of specimens (MSB 1353-54, 1356-57) collected 11.2 km east of San Antonito are all typical *P. ornatissimum*. A specimen (MSB 1239) from 4.8 km north of San Antonito appears to be typical *P. hernandesi.* Another collected on NM 14 in extreme southeast Sandoval County (MSB 26362) appears to be a hybrid; it has the rostrofrontal profile, proportional tail length, and dorsal pattern of *P. hernandesi,* but it has dorsolateral white spots and upward directed occipital horns as in *P. ornatissimum*. Two specimens (MSB 11388-89) from near Zamora and a third specimen from east of Zamora at Barton, near the Bernalillo-Santa Fe County line are referable to *P. hernandesi*.

Only seven adult specimens (LACM 19704, MSB 1244–47, 8427, 16482) from higher elevations "crest areas" in the Sandia Mountains were examined. In terms of dorsal pattern, rostrofrontal profile and tail length, they are close to *P. hernandesi.* However, two specimens have upward directed occipital horns, and two others have the temporal as well as occipital horns directed upward, suggesting possible genetic influence from *P. ornatissimum*, although the evidence is not unambiguous.

TABLE 9. Summary of character states for putative hybrids and parental specimens from the mountains-plains contact areas in New Mexico and Texas. Characters and character states are: Orientation of occipital horns (OO), Orientation of third temporal horn (OT): E = slightly elevated, H = horizontally directed, U = upright; Rostrofrontal profile (RF): A = angular, R = rounded, S = sloping gradually; Dorsal spots (DS): LR = large, rounded, SR = small, rounded, TB = transverse bands, W = wedge-shaped; Extent of pale margins (EM): L = lateral margin, M = medial margin, P = posterior margin; Dorsolateral white spots (WS): + = present, 0 = absent; Gular pattern (GP): C = chevrons, HW = horizontal wavy bands, S = spots, SU = suffusion, V = vermiculations; Abdominal pattern (ABD): F = flecks, S = spots, SU = suffusion; Subcaudal bands (SCB): + = present, 0 = absent; Tail length (TL): I = intermediate length tail, L = tail long, S = tail short. Relative tail length based on *P. hernandesi* reference sample from Grant County, New Mexico, and *P. ornatissimum* from Albuquerque, New Mexico.

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: Bernalillo Co: Manzano Mountains											
MSB 5	F	H	H	S	TB	P	0	--	--	--	L 2.21
MSB 97	F	E	E	S	LR	P, M	0	SU	S	--	L 1.98
MSB 1250	F	E	H	S	TB	P	0	SU	S	+	L 2.41
MSB 4344	F	E	H	S	W	P	0	--	--	--	L 2.01
MSB 10560	F	E	H	S	TB	P	0	--	--	--	L 1.97
MSB 10970	M	E	E	S	W	P	0	--	--	--	L 2.42
MSB 11014	M	E	H	S	TB	P	0	--	--	--	L 2.48
MSB 11015	F	E	E	S	TB	P	0	S, V	S	--	L 2.04
MSB 11384	M	H	H	S	W	P	0	--	--	--	L 2.42
MSB 11501	F	U	E	R	LR	P, M	+	S	F	0	S 1.49
New Mexico: Bernalillo Co: Sandia Mountains (crest areas)											
LACM 19704	M	H	H	S	TB	P	0	SU	--	--	L 2.28
MSB 1244	F	E	H	S	LR	P	0	--	--	--	L 2.14
MSB 1245	M	H	H	S	W	P	0	--	--	--	L 2.34
MSB 1246	F	E	E	S	SR	P	0	--	--	--	L 2.29
MSB 1247	F	E	H	S	TB	P	0	--	--	--	L 2.03
MSB 8427	F	E	E	S	TB	P	0	SU	SU	+	L 2.15
MSB 16482	F	E	H	S	TB	P	0	--	--	--	L 2.20
New Mexico: Bernalillo Co: Sandia Mountains (east slope), Barton											
MSB 82954	M	E	H	R	TB	P	0	--	--	--	L 2.45
New Mexico: Bernalillo Co: Sandia Mountains (east slope), San Antonito											
MSB 12901	M	E	H	S	TB	P	0	--	--	--	L 2.57
New Mexico: Bernalillo Co: Sandia Mountains (east slope), San Antonito, 4.8 km N											
MSB 1239	F	H	H	S	TB	P	0	--	--	--	L 1.99

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TABLE 9. (Continued)

Museum Number	**Sex**	**OO**	**OT**	**RF**	**DS**	**EM**	**WS**	**GP**	**ABD**	**SCB**	**TL**
New Mexico: Bernalillo Co: Sandia Mountains (east slope) San Antonito, 11.2 km E											
MSB 1353	F	U	E	R	LR	P, M	+	--	--	--	S 1.49
MSB 1354	F	U	U	R	LR	P, M	+	--	--	--	S 1.68
MSB 1356	F	E	E	A	LR	P, M	+	--	--	--	S 1.75
MSB 1357	F	E	E	A	LR	P, M	+	--	--	--	S 1.74
New Mexico: Bernalillo Co: Sandia Mountains (east slope), Sandia Park											
MSB 1268	F	E	H	S	TB	P	0	--	--	--	L 2.05
New Mexico: Bernalillo Co: Sandia Mountains (east slope), Sandia Park, 8 km NW											
LACM 19703	F	E	E	S	TB	P	0	--	--	--	S 1.86
New Mexico: Bernalillo Co: Sandia Mountains (east slope), Sulphur Canyon											
MSB 124	F	H	H	S	TB	P	0	--	--	--	I 1.96
New Mexico: Bernalillo Co: Sandia Mountains (east slope), Upper Cienega Canyon											
MSB 2	F	E	H	A	TB	P	0	V	S	+	L 1.99
MSB 1344	F	H	H	S	TB	P	0	V	S	0	S 1.74
MSB 1345	F	E	E	S	TB	P	0	--	--	--	S 1.75
New Mexico: Bernalillo Co: Sandia Mountains (east slope), near Zamora											
MSB 11388	F	H	H	S	SR	P	0	--	--	--	L 2.30
MSB 11389	M	E	H	S	TB	P	0	S, V	S, F	+?	L 2.47
New Mexico: Bernalillo Co: Sandia Mountains (west slope)											
LACM 4350	M	H	H	R	LR	P, M	+	--	--	--	I 2.00
MSB 1259	F	U	U	R	LR	P, M	0	--	--	--	S 1.38
MSB 14435	F	U	E	R	--	P	+	C	F	0	S 1.74
New Mexico: Eddy Co: Guadalupe Mountains											
MSB 4340	M	E	E	S	TB	P	0	--	--	--	L 2.26
USNM 32983	M	E	E	S	W	P	+	S	S	--	L 2.30
New Mexico: Lincoln Co: Capitan Mountains, Capitan, 3.2 km E, 6.4 km N											
MSB 39680	M	H	H	S	TB	P	+	S	S	+	I 2.10
New Mexico: Lincoln Co: Sacramento Mountains, Capitan, 9 km NW											
MSB 22490	M	H	H	S	W, TB	P	+	S, V	S	--	I 2.08

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TABLE 9. (Continued)

Museum Number	**Sex**	**OO**	**OT**	**RF**	**DS**	**EM**	**WS**	**GP**	**ABD**	**SCB**	**TL**
New Mexico: Lincoln Co: Carrizozo											
UNLV 7235	F	E	E	R	LR	P	+	--	--	--	S 1.75
New Mexico: Lincoln Co: Carrizozo, 2 km N											
UNLV 305	M	E	E	R	LR	P, M	+	--	--	--	I 2.18
New Mexico: Lincoln Co: Carrizozo, 1.6 km S											
UNLV 306	F	U	E	R	LR	P, M	+	--	--	--	S 1.75
New Mexico: Lincoln Co: Carrizozo, 6.4 km S											
MSB 30297	M	E	E	R	LR, TB	P, M	+	--	--	--	I 2.09
New Mexico: Lincoln Co: Carrizozo, 7.4 km E											
MSB 30294	M	U	E	R	W, SR	P	+	--	--	--	S 1.72
New Mexico: Lincoln Co: "Carrizozo" (Bradt series)											
UMMZ 67852A	M	U	U	R	TB	P	+	--	--	--	S 1.79
UMMZ 67852B	F	U	E	R	TB	P	+	--	--	--	S 1.51
UMMZ 67852C	F	H	H	S	TB	P	0	S, HW	S	+	L 2.15
UMMZ 67852D	F	H	H	S	W	P	0	V, C	S	+	L 2.22
UMMZ 67852E	F	U	E	S	LR, TB	P	+	HW?	--	--	S 1.46
UMMZ 67852F	F	E	H	S	W	P	0	S	S	--	L 2.37
UMMZ 67852G	F	U	E	R	LR, TB	P, M	+	C	F	0	L 2.07
UMMZ 67852H	F	U	U	R	LR	P	+	HW	S, SU	0	I 1.88
UMMZ 67854	F	U	E	R	LR	P, M	+	--	--	--	S 1.63
UMMZ 67855	F	U	U	R	LR, TB	P, M	+	C	S	--	S 1.79
UMMZ 67856	F	U	U	A	LR	P	+	C	F, SU	0	S 1.82
UMMZ 67857	F	U	E	R	TB	P	+	S, C	F, SU	0	S 1.77
New Mexico: Lincoln Co: Sacramento Mountains, Alto											
TNHC 70977	F	E	H	S	W	P	+	S, V	S	+	L 2.08
TNHC 70979	M	H	H	S	W	P	+	--	S	--	--

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TABLE 9. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: Otero Co: Sacramento Mountains, Cloudcroft											
ANSP 15210	F	H	H	S	LR, TB	P, M	0	SU	S, SU	+	L 2.40
New Mexico: Sandoval Co: Sandia Mountains (north slope), Placitas											
MSB 22139	M	E	H	R	TB	P	+	--	--	--	I 2.19
New Mexico: Sandoval Co: Sandia Mountains (north slope), Placitas, 1.6 km W, 1.6 km S											
MSB 26231	F	H	H	S	W	P	0	S	S	+	I 1.91
New Mexico: Sandoval Co: Sandia Mountains (north slope), Placitas, 6.4 km E											
MSB 12694	M	E	E	S	LR	P	+	--	--	--	L 2.58
MSB 12695	F	E	E	S	W	P	0	V	S	--	L 2.02
MSB 26139	F	E	E	S	W, SR	P, M?	0	--	--	--	L 2.13
New Mexico: Sandoval Co: NM 14											
MSB 26362	F	E	H	S	W	P	+	V	S, F	--	L 2.10
New Mexico: Santa Fe Co: Santa Fe											
AMNH 112194	M	E	E	S	SR	P	0	--	--	--	L 2.47
RRM 2343	M	U	E	A	LR	P	+	C	F	0	S 1.93
New Mexico: Santa Fe Co: Santa Fe, 12.8 km SW											
KU 11288	M	U	E	R	LR	P, M	+	C	--	--	S 1.85
KU 11289	F	E	E	R	LR	P, M	+	V, C	--	--	S 1.74
KU 11290	M	E	E	R	LR	P, M	+	C	--	--	S 1.64
KU 11292	F	U	E	R	LR	P, M	+	--	--	--	S 1.81
KU 11294	M	U	E	R	LR	P	0	V, C	--	--	S 1.79
KU 11295	M	U	U	R	LR	P, M	+	--	--	--	S 1.87
KU 11297	M	E	E	R	SR	P	+	C	--	--	I 2.13
New Mexico: Sierra Co: San Andres Mountains, Bear Den Canyon											
MSB 60489	M	E	H	R	W, SR	P	+	S, SU, C	S	+	L 2.56
New Mexico: Socorro Co: Augustine, 16 km E Datil											
MSB 4348	F	U	E	R	LR	P	--	S	--	--	S 1.71

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TABLE 9. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
New Mexico: Socorro Co: Chupadera Mesa, Adobe Ranch											
LACM 19688	M	E	E	R	TB	P	0	C	--	--	S 1.82
New Mexico: Socorro Co: Chupadera Mesa, Bingham, 10.4 km N											
LACM 62556	M	E	H	A	LR	P	+	S, HW?	--	--	I 1.95
New Mexico: Socorro Co: Chupadera Mesa, Bingham, 25.6 km E, 16 km S											
NMSU 5686	F	U	E	R	TB	P	+	--	--	--	S 1.72
New Mexico: Socorro Co: Chupadera Mesa, Chicken Spring, 2.4 km E											
LACM 19689	M	U	U	A	LR	P	0	--	--	--	S 1.91
New Mexico: Socorro Co: Chupadera Mesa											
LACM 19690	F	E	E	R	SR	P	+	HW	--	--	S 1.65
LACM 19691	F	U	U	R	LR	P, M	+	C	--	--	S 1.35
New Mexico: Socorro Co: Chupadera Mesa, Cooper's Well, 4.8 km N											
LACM 19686	F	E	E	R	LR	P, M	+	S, C?	--	--	S 1.78
New Mexico: Socorro Co: Chupadera Mesa, White Store											
LACM 19687	F	E	E	R	TB	P	+	C	--	--	S 1.44
New Mexico: Taos Co: Taos											
CU 5106	M	E	E	R	W	P, M	0	V, HW	--	--	I 2.09
New Mexico: Torrance Co: Manzano Mountains											
AMNH 111149	M	E	E	S	TB	P	0	--	--	--	L 2.33
MSB 6865	F	E	E	S	TB	P	0	--	--	--	I 1.96
MSB 6868	F	H	H	R	W	P	0	--	--	--	L 2.18
MSB 10248	M	E	E	S	W	P	0	--	--	--	L 2.47
MSB 13925	M	H	H	S	W	P	0	--	--	--	I 2.14
MSB 121698	F	E	H	S	W	P	0	SU	S, SU	--	L 2.46
RRM 2315	M	H	H	S	W	P	0	--	--	--	L 2.27
RRM 2318	F	E	E	S	W	P	0	SU	SU	--	L 2.15
UMMZ 121698	F	E	H	S	W	P	0	--	--	--	L 2.46

......*continued on the next page*

TABLE 9. (Continued)

Museum Number	Sex	OO	OT	RF	DS	EM	WS	GP	ABD	SCB	TL
Texas: Culberson Co: Guadalupe Mountains											
SRSU 869	F	H	H	S	SR	P	0	--	--	--	L 2.14
TNHC 70983	F	H	H	S	W	P	0	--	--	--	L 1.96
TNHC 70985	F	H	H	S	TB	P	0	--	--	--	L 2.10
USNM 32984	F	H	H	S	LR	P, M	0	S	S	+	--

In the Manzano Mountains, *P. ornatissimum* has been collected from the west slope in Coyote Canyon (MSB 11501). Eighteen specimens from the eastern slopes of the mountain range (Bernalillo and Torrance counties) are all morphologically close to *P. hernandesi*. In the majority of these specimens the cephalic horns are more or less elevated and two specimens have an "intermediate" proportional tail length; these traits may indicate genetic influence from *P. ornatissimum.* One noteworthy specimen (MSB 97) from the Pine Flats area of Cedro Canyon has large rounded dorsal spots with traces of the light-colored medial borders characteristic of *P. ornatissimum.*

Specimens from near Santa Fe and to the southwest are morphologically close to *P. ornatissimum*, but all show partial or complete absence of the light-colored medial borders of the dorsal spots. One specimen from near Taos (CU 5106) has a dorsal pattern similar to that of *P. hernandesi* but some of its dorsal spots have whitish medial borders. There are no records for *P. ornatissimum* near Taos, but it has been collected near Abiquiu (USNM 8451) along the Rio Chama drainage; its northern extent along the Rio Grande has yet to be determined. *P. hernandesi* has also been recorded from near Abiquiu (USNM 293374) and upper elevation areas along the Rio Chama drainage, as well as the mountains adjacent to Taos.

Phrynosoma hernandesi was sampled from two general areas in the Sacramento Mountains, from Cloudcroft and localities to the south, and from Ruidoso and west of Alto in the Sierra Blanca. Among 39 adult specimens from the Cloudcroft area, all have a gradually sloping rostrofrontal profile. The dorsal pattern consists of dark transverse bands (25 specimens; 64.1% of sample) or dark wedge-shaped dorsal spots (14 specimens; 35.9%) with distinct, white and/or yellowish posterior borders. The nuchal blotches also have a discrete white line along the medial and posterior edges in many specimens. Only one specimen (2.5% of sample) from the vicinity of Cloudcroft (ANSP 15210) has discrete, narrow, white borders along the medial and posterior edges of the dorsal spots, reminiscent of the pattern in *P. ornatissimum.* This hybrid phenotype suggests that alleles from *P. ornatissimum* may occur at low frequency in the *P. hernandesi* population and are infrequently expressed through genetic recombination. In 25 specimens (64.1%) the cephalic horns are directed horizontally. Although no specimens have vertically directed horns, in 13 specimens (33.3%) the occipital horns are directed slightly upward, and in one specimen (2.5%) the temporal as well as occipital horns are oriented slightly upward.

In 26 specimens from the Alto-Ruidoso-Sierra Blanca area, all have a gradually sloping rostrofrontal profile. The dorsal pattern consists of dark transverse bands (12 specimens; 46.2%) or dark wedge-shaped dorsal spots (14 specimens; 53.8%) with distinct, white and/or yellowish posterior borders. No specimens have white medial borders. The nuchal blotches have narrow white lines along the medial and posterior edges in some specimens. In 11 lizards (42.3%) the cephalic horns are directed horizontally; in 13 specimens (50%) the occipital horns are directed slightly upward, and in two specimens (7.7%) both the occipital and temporal horns are directed slightly upward. Among a series of ten specimens from the vicinity of Alto, evidence of genetic influence from *P. ornatissimum* is noted in one specimen (TNHC 70977). Although it is morphologically close to *P. hernandesi*, it has dorsolateral white spots. A second specimen (TNHC 70979) from this locality has a few white spots on the flanks. Two other specimens (MSB 22490, 39680) from the Capitan area also have white spots, flecks, and vermiculations.

Among a series of 17 specimens from the vicinity of Carrizozo, Lincoln County, some show morphological evidence of hybridization. Eleven of the specimens (MSB 30294, 30297, UMMZ 67852 G, H, UMMZ 67854–57, UNLV 305, 306, 7235) resemble *P. ornatissimum* in morphology and color pattern. However, of the eleven, five lack the white medial borders of the dorsal spots (MSB 30294, UMMZ 67852 H, UMMZ 67856–57, and UNLV 7235). In three specimens (UMMZ 67852 G, UMMZ 67854–55), the medial borders are absent from some of the dorsal spots; the medial borders are present in three specimens (MSB 30297 and UNLV 305–06). Two juvenile specimens (UMMZ 67852 A, B) are morphologically close to *P. ornatissimum*, but have transverse dorsal bands with whitish posterior borders. Three specimens (UMMZ 67852 C, D, F) are close to *P. hernandesi* in morphology and color pattern. One specimen (UMMZ 67852 E) is more or less intermediate between the two species. The occipital and temporal horns are directed upward, and the tail is relatively short, but the rostrofrontal profile is gradually sloping. The dorsal pattern is similar to that of *P. hernandesi*, but with dorsolateral white spots.

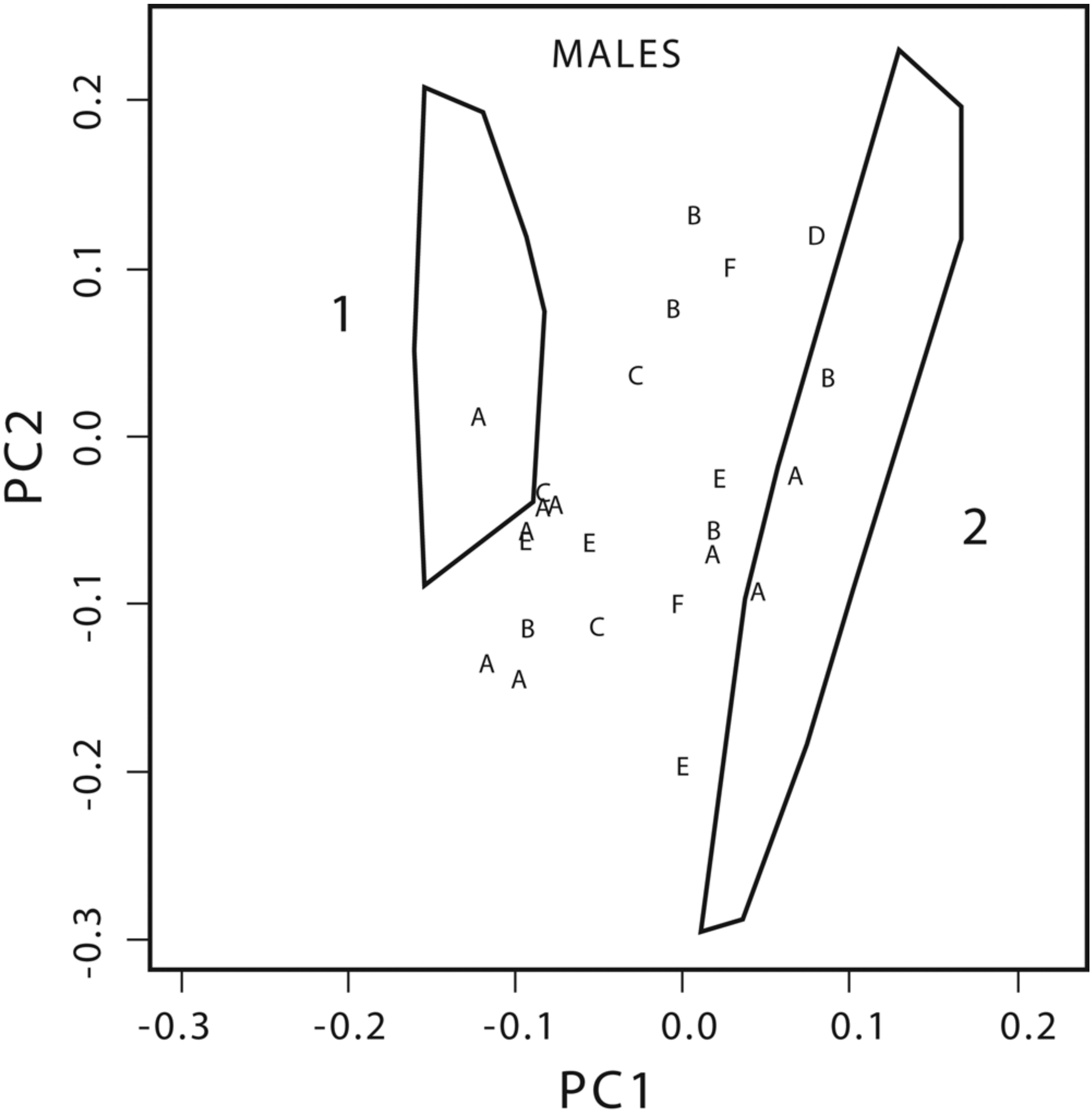

FIGURE 42. Projection of male samples (n = 95) of *Phrynosoma hernandesi* x *Phrynosoma ornatissimum* hybrids from mountains-plains contact areas in New Mexico and Texas on the first two principal components (PC1, PC2) of a 17-character correlation matrix. PC1 explains 46.7% and PC2 explains 16.2% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are 1. *Phrynosoma ornatissimum* reference sample, 2. *Phrynosoma hernandesi* reference sample. Presumptive hybrid samples are labeled as follows: (A) SSW of Santa Fe; (B) Sandia-Manzano Mts.-adjacent plains; (C) Chupadera Mesa; (D) San Andres Mts.; (E) Sacramento Mts.-Carrizozo; (F) Guadalupe Mts. See text for further discussion.

Eight specimens under UMMZ 67852 were collected from the vicinity of Carrizozo by L. Bradt in 1929. Although locality information in his field notes is imprecise, taking into consideration the habitat preferences of the two species, it is likely that Bradt's specimens were collected at various points east of Carrizozo as he ascended the Sierra Blanca. MSB 30294 was collected 7.4 km east of Carrizozo and it closely resembles *P. ornatissimum* (except for the dorsal spots and white borders). This suggests that Bradt's morphologically intermediate specimens and specimens morphologically similar to *P. hernandesi* were probably taken east of that point. The next entry in Bradt's field notes is "Bonito Canyon" (= Bonito Creek Canyon) in the Sierra Blanca where he collected *P. hernandesi*.

The absence of the white medial borders in some of the *P. ornatissimum*-like lizards from Carrizozo is probably due to genetic introgression from *P. hernandesi,* as other features of the color pattern and morphology in the material from this area point to hybridization. However, it should be noted that about 2.8% of the *P. ornatissimum* examined from outside of hybrid zones lack the white medial borders for some or all of the dorsal spots.

Eight specimens examined from the Chupadera Mesa (LACM 19686–91, 62556, NMSU 5686) are morphologically close to *P. ornatissimum*. However, only one specimen has medial white borders for all the dorsal spots; another specimen lacks the medial white borders for some of the dorsal spots, and six specimens completely lack the medial white borders. Two of the eight specimens also lack dorsolateral white spots. Regarding the orientation of the cephalic horns, rostrofrontal profile and proportional tail length, the specimens generally agree with *P. ornatissimum*. Whether the dorsal pattern traits in these specimens reflect genetic introgression from *P. hernandesi* is uncertain. There are no nearby records of *P. hernandesi*, but the Chupadera Mesa is more or less continuous with the Sierra Oscura-San Andres Mountains axis. Much of this elevated region, which has yet to be explored for short-horned lizards, may support populations of *P. hernandesi*. One specimen (MSB 60489) from Bear Den Canyon (33° 11' 03" N, 106° 38' 52" W) in the San Andres Mountains, about 82 km to the south of Chupadera Mesa, appears to be of hybrid origin. This specimen has a proportionally long tail and in other morphological features is close to *P. hernandesi*. However, it has dorsolateral white spots, indications of chevrons on the gular area, and the occipital horns are directed slightly upward.

Six adult specimens from the Guadalupe Mountains were examined. Two specimens from the "Bowl" (SRSU 869; TNHC 70983) and one from "Pine Top" (TNHC 70985) are *P. hernandesi* and show no morphological evidence of genetic influence from *P. ornatissimum*. One specimen from Dark Canyon (MSB 4340) is close to *P. hernandesi* in dorsal color pattern but it has upward directed occipital and temporal horns. Two others with imprecise locality data from the mountain range also show mixed characteristics and are judged to be of hybrid origin. One (USNM 32984) has horizontally directed horns and a gradually inclined rostrofrontal profile as in *P. hernandesi*, but the dorsal spots are large with discrete medial and posterior white borders as in *P. ornatissimum* (Fig. 44). The other (USNM 32983) has a rostrofrontal profile like *P. hernandesi*, but it has upward directed horns, dorsal spots with traces of white medial borders, and a few dorsolateral white spots.

One emaciated specimen allegedly from the vicinity of Carlsbad Caverns, Eddy County, New Mexico (UCM 52169) exhibits an unusual combination of traits. It has upright occipital horns, slightly elevated temporal horns, but a more or less sloping rostrofrontal profile. The frontal rim is not elevated above the occipital shelf. It has longitudinal gular folds bearing slightly enlarged, pointed scales. The proportional tail length falls within the limits of *P. hernandesi*. The dorsal spots are small, rounded to wedge-shaped, with narrow, posterior whitish borders. There are no dorsolateral white spots. The specimen was apparently a long-term captive, which renders the locality data suspect.

In the Gallinas Mountains, a small range in Torrance and Lincoln counties, a lizard similar to *P. ornatissimum* was photographed in conifer forest at 2,622 m (8,600 ft) where *P. hernandesi* would be expected to occur. The plant community consists of Ponderosa Pine, Douglas fir, Limber Pine and Gambel Oak (Robert Sivinski, personal communication). Based on the photograph, the lizard is an apparent hybrid male with a proportionally long tail, faint dorsal spots nearly forming transverse bands, and with mostly fragmented yellowish medial borders. The question arises whether a montane isolate of *P. hernandesi* may have previously existed in this mountain range and was eventually genetically swamped by surrounding *P. ornatissimum* populations. The Gallinas Mountains are situated north of, and on the same trend line, as the Sacramento Mountains. The short-horned lizard populations there warrant detailed study.

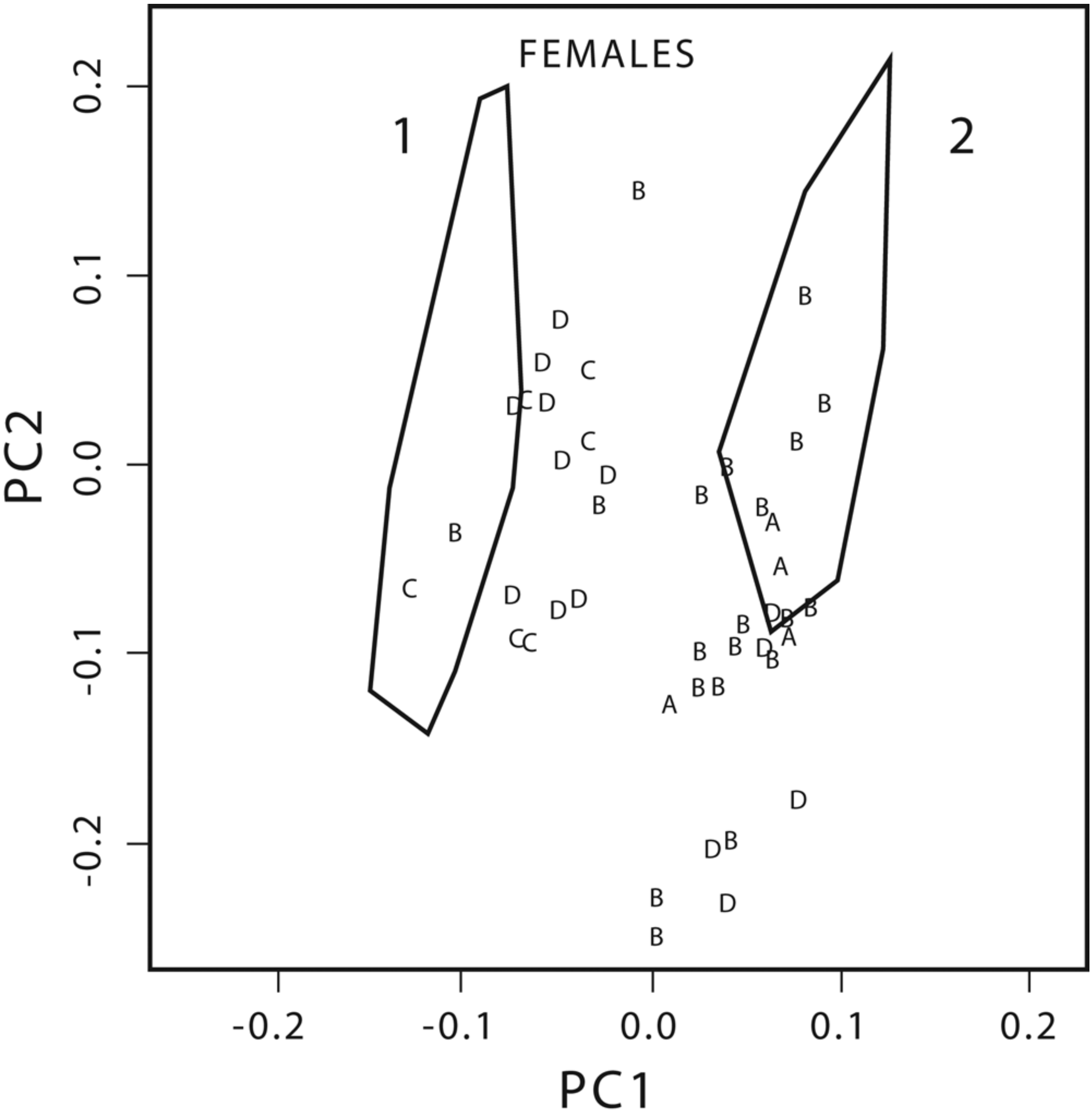

FIGURE 43. Projection of female samples (n = 146) of *Phrynosoma hernandesi* x *Phrynosoma ornatissimum* hybrids from mountains-plains contact areas in New Mexico on the first two principal components (PC1, PC2) of a 17-character correlation matrix. PC1 explains 46.7% and PC2 explains 14.2% of the total variance. The dispersion polygons show the boundaries of the population clusters by linking all outermost data points. Dispersion polygons are 1. *Phrynosoma ornatissimum* reference sample, 2. *Phrynosoma hernandesi* reference sample. Presumptive hybrid samples are labeled as follows: (A) SSW of Santa Fe; (B) Sandia-Manzano Mts.-adjacent plains; (C) Chupadera Mesa; (D) Sacramento Mts.-Carrizozo. See text for further discussion.

In comparing the character variation of the hybrids from the mountains-plains contact areas with the Colorado Plateau hybrid zone, several points can be made. The levels of morphological heterogeneity are similar based on the extent of dispersion of the hybrid clusters in the multivariate scatter plots (Figs. 36–37 and 42–43). In the mountains-plains contact areas parental phenotypes may occur proximate to one another and to morphologically intermediate hybrids. In the Colorado Plateau region, parental *P. ornatissimum* is apparently absent, although lizards closely resembling *P. ornatissimum* occur south of Sanders, Apache County, Arizona. In other areas, intermediate hybrids or hybrids similar to *P. hernandesi* are prevalent. There is also a difference in the frequencies of alternative dorsal-spot phenotypes. The frequencies of dorsal pattern phenotypes are similar in the Arizona and New Mexico portions of the Colorado Plateau hybrid zone. The percentages for Arizona and New Mexico, respectively, are: transverse bands and wedge-shaped spots (33% vs. 36.5%), small, rounded dorsal spots (51% vs. 46%), large, rounded dorsal spots (16% vs. 17.5%). In the mountains-plains contact areas, the percentages are: transverse bands and wedge-shaped spots (58.7%), small, rounded dorsal spots (6%), and large, rounded dorsal spots (35%). The difference in frequency of lizards with small dorsal spots in the mountains-plains contact areas (6%) compared with the Colorado Plateau region (up to 51%) is clearly significant. Hybrid lizards with the "ocellus-like" pattern trait appear to be unique to the Colorado Plateau hybrid zone; this phenotype has not been observed at any of the mountains-plains contact sites. Lizards with the ocellus-like pattern occur at a frequency of about 8% in the Little Colorado River basin region and about 11.1% in the San Juan and Chaco river basins.

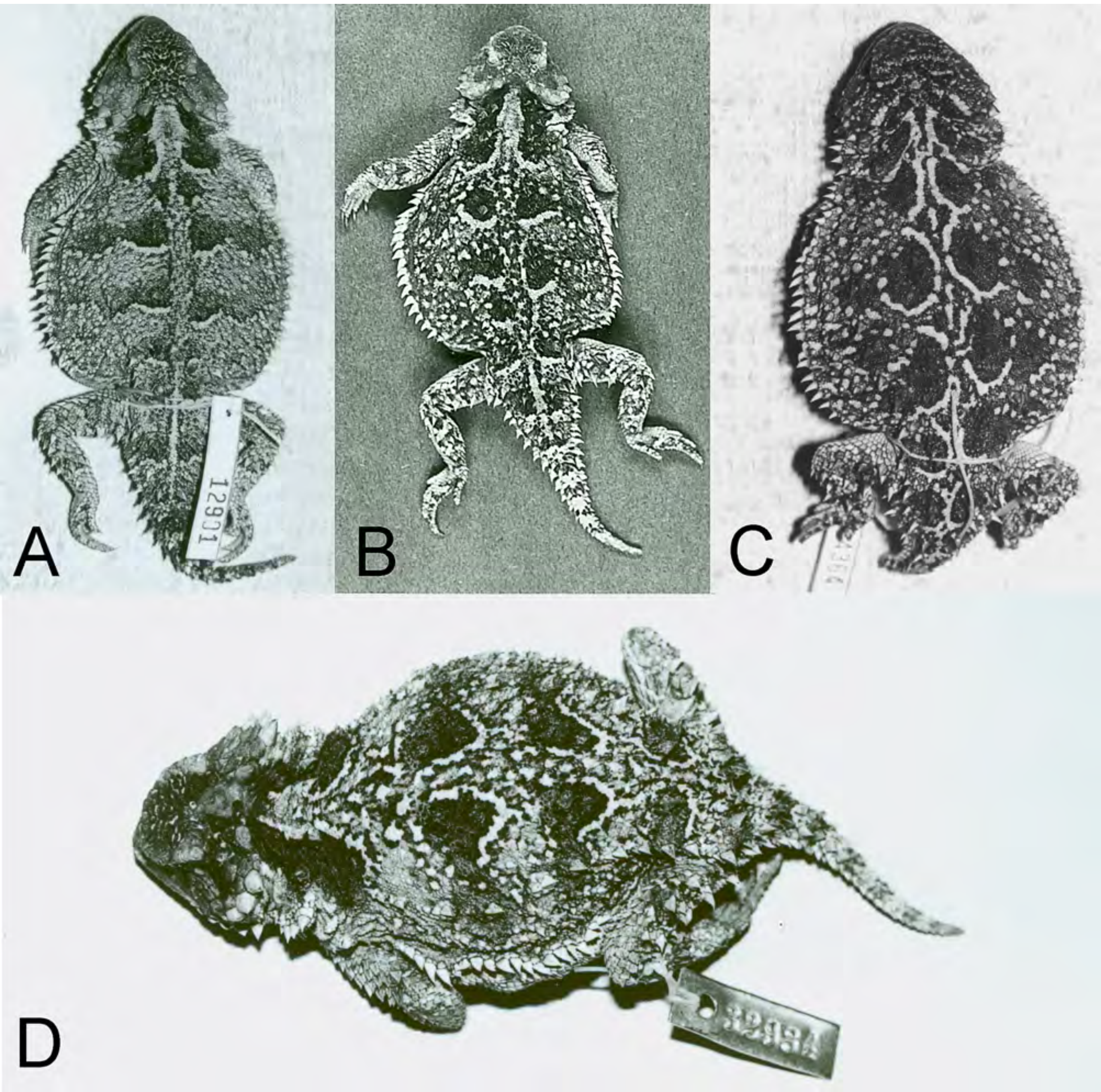

FIGURE 44. Putative hybrid and parental specimens from mountains-plains contact areas. (A) *Phrynosoma hernandesi* (MSB 12901, San Antonito, Bernalillo Co., New Mexico); (B) *P. hernandesi* x *P. ornatissimum* hybrid (MSB 12694, 6.4 km E Placitas, Sandoval Co., New Mexico); (C) *Phrynosoma ornatissimum* (MSB 4364, Bernalillo Co., New Mexico); (D) *P. hernandesi* x *P. ornatissimum* hybrid (USNM 32984, Guadalupe Mountains, Culberson Co., Texas), showing dorsal spots with white medial borders; specimen has gradually sloping rostrofrontal profile and horizontally directed cephalic horns.

Summary

Multivariate and univariate statistical analyses of the *Phrynosoma douglasii* species complex support the recognition of *P. douglasii* (Bell), and the resurrection of *P. brevirostris* Girard and *P. ornatissimum* Girard as species distinct from *P. hernandesi* Girard. Two new species allied to *P. brevirostris* are described: *P. bauri* **sp. nov.** from the eastern plains of Colorado, southeastern Wyoming and southwestern Nebraska south of the North Platte River, and *P. diminutum* **sp. nov.** endemic to the San Luis Valley of southern Colorado and northern New Mexico. The northern Mexican taxon *brachycercum* Smith is reassigned as a subspecies of *P. ornatissimum* Girard, being morphologically very close to it. The taxon *ornatum* Girard, although sharing several traits with *P. brevirostris*, is morphologically close to *P. hernandesi*, and it is treated taxonomically as a subspecies of *P. hernandesi*.

P. brevirostris is characterized by relatively short, usually upright cephalic horns, weak development or absence of the frontal rim, a low number of enlarged frontal rim scales, a truncate snout and a rounded or angular and steeply inclined rostrofrontal profile, a relatively short temporal shelf, a relatively long tail, small, wedge-shaped or slightly rounded dorsal spots with white or yellow borders along the posterior edges only, grey flecks and patches on the abdomen, and absence of melanistic subcaudal bands. *P. bauri* **sp. nov.** differs discretely from *P. brevirostris* in having dorsolateral white spots, and large melanistic spots on the abdomen (in the melanin-dispersed phase). Also, the frontal rim is typically elevated and rather well defined as compared with that of *P. brevirostris*. *P. bauri* **sp. nov.** differs statistically (observed limits overlapping) from *P. brevirostris* by having a longer third temporal horn, higher number of frontal rim scales, and longer temporal shelf. *P diminutum* **sp. nov.** differs discretely from *P. brevirostris* in having irregular rows of large, melanistic spots or extensive dark suffusion on the abdomen and interrupted subcaudal bands (melanin-dispersed phase). It further differs statistically (observed limitis overlapping) by having a shorter, more convex temporal shelf and a proportionally shorter tail. *P. diminutum* **sp. nov.** differs discretely from *P. bauri* **sp. nov.** by the absence of am elevated frontal rim, and by lacking dorsolateral white spots. It differs statistically (observed limits overlapping) from *P. bauri* **sp. nov.** by a shorter temporal shelf, shorter third temporal horn, and a lower number of frontal rim scales.

Phrynosoma douglasii is characterized by minute, typically upright cephalic horns, weak development or absence of the frontal rim, a low number of enlarged frontal rim scales, a truncate snout and a rounded or angular and steeply inclined rostrofrontal profile, a short, convex or rounded temporal shelf, a narrow and elliptic, or small and rounded, tympanum exposed or concealed by granular scales, a moderately short tail, small, wedge-shaped or rounded dorsal spots with white or yellow borders along the posterior edges, gray suffusion or flecks and patches on the gular area and abdomen, and absence of melanistic subcaudal bands (melanin-dispersed phase).

Nominotypical *P. hernandesi* is characterized by relatively long, horizontally directed cephalic horns, an elevated frontal rim with enlarged frontal rim scales, a prognathus snout and gradually sloping, rather flattened, rostrofrontal profile, a relatively long tail, wedge-shaped dorsal spots or transverse bands with light-colored borders along the posterior edges, large melanistic spots on the abdomen and yellow, orange or red pigment on the abdominal and gular surfaces, and complete and/or interrupted melanistic subcaudal bands (melanin-dispersed phase). The subspecies *P. h. ornatum* differs primarily in having a less prognathus snout and an obtusely angular or somewhat rounded rostrofrontal profile, a shorter temporal shelf, a frontal rim that is weakly developed or absent, and a low number of enlarged frontal rim scales.

Nominotypical *P. ornatissimum* is characterized by relatively short, typically upright cephalic horns, a strongly elevated frontal rim with enlarged and conspicuous frontal rim scales, a relatively short snout and a rounded or angular and steeply inclined rostrofrontal profile, large, rounded dorsal spots with discrete, narrow white and/or yellow borders along the medial and posterior edges, dorsolateral white spots, a gular pattern with chevrons or wavy transverse lines, grey flecks and patches on the abdomen, absence of melanistic subcaudal bands (melanin-dispersed phase), and a relatively short tail. Its subspecies, *brachycercum*, is virtually identical in habitus, but differs in that its dorsal spots lack the narrow white or yellow medial borders; the dorsal pattern is polymorphic and may consist of small, wedge-shaped to large, rounded spots or transverse bands; it further differs by the absence of dorsolateral white spots in most specimens.

The ranges of *P. hernandesi* and *P. ornatissimum* broadly overlap in central New Mexico; the former taxon occupies the coniferous forests of disjunct mountain ranges, the latter occurs in the surrounding desert grasslands. Principal components analysis has revealed morphological evidence of hybridization where the two taxa meet, generally within ecotones between montane forest associations and grasslands. Gehlbach's (1965) concept that the

two taxa represent clinal forms of one variable species is dismissed (see **Remarks** under *P. o. ornatissimum*). Principal components analysis has also revealed considerable morphological heterogeneity in populations occupying the Colorado Plateau of northeastern Arizona, northwestern New Mexico, extreme southwestern Colorado and adjacent Utah. These populations presumably arose through past hybridization between the two taxa, and although an array of phenotypes occurs at some localities, hybrids morphologically similar to *P. ornatissimum* tend to be prevalent at the lowermost elevations in the Little Colorado and San Juan-Chaco basins whereas hybrids similar to *P. hernandesi* predominate in the adjacent high mesas and mountains. Although parental *P. hernandesi* occurs in proximity to hybrids at some localities, the parental species *P. ornatissimum* is apparently absent from most of the plateau region.

Morphological evidence supports the hypothesis that *P. h. ornatum* is of hybrid origin, with one parent clearly being *P. hernandesi*. Traits from this parent include red pigmentation on the temporal and occipital horns, a red border above the lateral fringe row, large melanistic spots on the abdomen and partial and/or complete subcaudal bands (melanin-dispersed phase). Morphometric data from the head and micrornamentation of the cephalic lepidosis (moderately broad ridges and granulations on the cephalic scales) suggest that *P. brevirostris* was the other parent involved in the origin of *ornatum*. The mean number of enlarged frontal rim scales in *P. h. ornatum* is more or less intermediate between that of the putative parental taxa. *P. h. ornatum* also displays a higher coefficient of variation than either of the parental taxa for this character. Moreover, the rostrofrontal profile of *P. h. ornatum* varies from nearly flat and gradually sloping to more rounded or angular within local populations. The morphological variability observed in *P. h. ornatum* seems to support the postulated hybrid origin of this taxon.

A substantial percentage of specimens in samples of *P. hernandesi* from the Wasatch Range, the Henry Mountains, and the Kaibab Plateau have upward directed cephalic horns, relatively short temporal horns, a relatively short temporal shelf, and a tendency toward a rounded rostrofrontal profile. The variation in these characters suggests that *P. hernandesi* in eastern Utah experienced a history of genetic interaction with *P. brevirostris*. However, only limited samples have been analyzed and additional specimens are needed to gain a better understanding of the morphological variation and relationships of *P. hernandesi* from southern and eastern Utah.

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Appendix I

The following locality records are organized alphabetically by taxon, except the two new species, which are inserted after *P. brevirostris.* Also specimens from the Colorado Plateau hybrid zone and the New Mexico–Texas mountains–plains hybrid zones are listed under those headings. The listings include parental as well as hybrid specimens. Consult the text and tables 7 and 9 for their description and classification. The few specimens considered hybrids between *P. bauri* **sp. nov.** and *P. hernandesi* are listed under the former taxon. See text for their description. Specimens not studied but used only for plotting distributions are marked with an asterisk (*). Geographical coordinates are given for some localities that are difficult to find or for historical settlements no longer in existence. See **Acknowledgements** section and Leviton *et al.* 1985 for museum acronyms.

Phrynosoma brevirostris

Canada: Alberta Province
Audet Ranch (Powell & Russell, 1998)
Bear Gulch (Powell & Russell, 1998)
Bow Island RRM 2273
Bow Island, 9 km NW (Powell & Russell, 1998)
Comrey CMNAR 1859.1, 1859.2
Foremost CMNAR 1147.1, 1147.2, 1830.1, 1830.2
Foremost, 3 km E at Chin Coulee (Powell & Russell, 1998)
Forty-Mile Coulee (Powell & Russell, 1998)
Grassy Lake (Powell & Russell, 1998)
Lecuyer's Coulee (Powell & Russell, 1998)
Manyberries CMNAR 1284, 1921.1, 1921.2, 1921.3, 3482, UAHC 53.679
Manyberries, 20 km SE (Powell & Russell, 1998)
McDonald Coulee (Powell & Russell, 1998)
McKinley's Ranch (Powell & Rusell, 1998)
Medicine Hat CMNAR 35b, MCZ 31784, 32517–18
Medicine Hat, 16 km NE (Powell & Russell, 1998)
Milk River Canyon, north edge (Powell & Russell, 1998)
Nemiskam Community Pasture (Powell & Russell, 1998)
Nemiskam National Park (Powell & Russell, 1998)
Onefour (Powell & Russell, 1998)
Onefour, NW at Lost River Ranch CMNAR 7333.1, 7333.2
Onefour, W at Lost River Canyon (Powell & Russell, 1998)
Onefour, 8 and 9 km S (Powell & Russell, 1998)
Redcliff (Powell & Russell, 1998)
Redcliff, 11 km W (Powell & Russell, 1998)
Second Laidlaw (Powell & Russell, 1998)
Suffield, 20 km S (Powell & Russell, 1998)
Wildhorse (Powell & Russell, 1998)
Wildhorse, 30.4 km W, 2.4 km N CMNAR 13496
Writing On Stone CMNAR 1829

Canada: Saskatchewan Province
Coal Creek, SE of Killdeer (Powell *et al.*, 1998)
Frenchman River Valley near 49th parallel (Powell *et al.*, 1998)
Gergovia CMNAR 1634
Killdeer, 8 km W at Butte Creek Coulee CMNAR 15499
Rock Creek and Butte Creek coulees, between (Powell *et al.*, 1998)
Rosefield CMNAR 5680*
Seventy-Mile Butte (Powell *et al.*, 1998)
Val Marie, 11 km SE CMNAR 35199

United States
Colorado: Delta Co:
Crawford, 6.4 km W UCONN 2241–52
Delta, 4.8 km E USNM 88579–82
Delta, Dry Mesa OSUS 1151, UCM 6714–18

Colorado: Garfield Co:
Baxter Pass (Cary, 1911)
Book Cliffs (Cary, 1911)
Mesa County line, 91.4 m N UCM 52757
Rifle, 12.8 km W MVZ 16471

Colorado: Mesa Co:
Badger Wash Experimental Area MSB 82951–53
Fruita, 9.6 km S UCM 2793
Grand Junction DSC 1065–66, FMNH 931 (2),1118,1135
Grand Junction, 9.6 km N UCM 15299–301
Grand Junction, 14.4 km SW UCM 52141–42
Mack USNM 40142
Utah state line, 8 km E UCM 52168
Whitewater UCM 21534

Colorado: Moffat Co:
Cold Spring Mountain UCM 2313–19
Cross Mountain FMNH 22676(11)
Dinosaur National Monument, Blue Mountain UCM 5298*
Dinosaur National Monument, Harding Hole Overlook UCM 3662
Dinosaur National Monument, Harpers Corner UCM 2865–73, 5299–5302
Dinosaur National Monument, Round Top Mountain UCM 5297
Elk Springs, NE UTA 1653*, 2239*
Elk Springs, 32 km W UCM 2320
Godiva Rim USNM 40140*
Irish Lakes, 10.4 km N, 5.6 km W MSB 82673
Lay USNM 40144
Little Snake River, 32 km WSW Baggs USNM 40141
Middle Mountain, NE slope MSB 84003

Colorado: Montrose Co:
Bedrock (Ellis & Henderson, 1913)
Black Canyon of the Gunnison National Park, Serpent Point UCM 13684
Coventry (Ellis & Henderson, 1913)
Naturita UCM 446 (2)

Colorado: Ouray Co:
Colona, 4.8 km SW UCM 56608

Colorado: Rio Blanco Co:
Cathedral Bluffs UCM 56174
Cathedral Creek UCM 56175
Colorow Mountain, 39.4 km SW UNCMNH 4*, 1100*
Meeker AMNH 13604–05, UCM 50*
Meeker, 3.2 km SE UCM 51*, 1069
Wet Swizer Creek MSB 82948–50

Colorado: San Miguel Co:
Gypsum Gap UCM 4510
Gypsum Gap, 3.2 km W UCM 4509

Montana: Big Horn Co:
Fort Custer, near Hardin USNM 14523
Tongue River Reservoir MSBU 5955*

Montana: Carbon Co:
Bear Canyon drainage, on Gyp Spring Road IMNH 1634*
Belfry, 8.8 km SSW OMNH 41775*
Bighorn Basin, Sage Creek USNM 47701*
Bridger, near MSBU 5434*
Bridger, 8.6 km ENE OMNH 41749
Bridger, 11.1 km S OMNH 41750
Bridger, 12.5 km S OMNH 41748
Bridger, 22.9 km S OMNH 41746–47
Dry Head Creek Valley KU 182301–02
Pryor Mountains MSBU 1551*
Warren, near RRM 3310–11

Montana: Chouteau Co:
Fort Benton USNM 9414

Montana: Custer Co:
Miles City, near UCM 721*

Montana: Dawson Co:
Camp Thorne (historical; 46° 55' 36" N, 104° 52' 10" W) ANSP 12799–809, 12810 (2), 34885 (2)

Montana: Gallatin Co:
Gallatin Station USNM 17415
Logan USNM 32652
Logan, 16 km SW MSBU 1556*
Yellowstone National Park, near West Entrance Checking Station MVZ 72271
No specific locality USNM 14641*, 293446*

Montana: Garfield Co:
Cohagen, 24 km SE USNM 61405*
Cohagen, 48 km SW USNM 61404*
No specific locality AMNH 141114*

Montana: Glacier Co:
Cut Bank, 17.2 km SW (Werner, 1974)

Montana: Golden Valley Co:
Barber, 4.8 km S MSBU 1564*
Painted Robe Creek USNM 45299

Montana: Hill Co:
Milk River at 49° N latitude (Coues & Yarrow, 1878)

Montana: McCone Co:
Circle, 8 km N MSBU 1552*
Dreyer Ranch IMNH 1545*
Fort Peck Reservoir, Rock Creek MSBU 5436*

Montana: Musselshell Co:
Roundup, east of MSBU 1565*

Montana: Powder River Co:
Broadus AMNH 79131
Broadus, 32 km N IMNH (UI 102)*
Powderville CAS–SU 7772
Powderville, 12.8 km SW USNM 54593
Powderville, 19.2 km W USNM 54591–92

Montana: Prairie Co:
Terry USNM 335120*
Terry, 40 km N USNM 44931

Montana: Richland Co:
Yellowstone River, near mouth USNM 9198, 293391–96

Montana: Rosebud Co:
Forsyth CAS–SU 7768
Forsyth, north of MSBU 4433*
Forsyth, 8 km W MVZ 35196
Rosebud CAS 20997–98
Rosebud Creek USNM 45300–01

Montana: Silver Bow Co:
Butte, northwest of (Photo voucher)

Montana: Stillwater Co:
Abasarokee USNM 45298*
Columbus, 9.6 km N MSBU 1570*
Hailstone National Wildlife Refuge RRM 3308–09

Montana: Sweet Grass Co:
Big Timber MSBU 1555*

Montana: Teton Co:
Choteau, 11.2 km S, 19.2 km W (Photo voucher)
Dutton USNM 335121*
No specific locality YPM 9270–73*

Montana: Toole Co:
Sweet Grass Hills USNM 11924*, 293436*

Montana: Wheatland Co:
Harlowton UMMZ 75699

Montana: Yellowstone Co:
Billings CAS-SU 7769–71, 7782, 10186–87, MSBU 1554*, USNM 44705, 44929–30
East Pryor Creek USNM 28443–45
Pompey's Pillar MSBU 1569*
Shepherd, 17 km WNW OMNH 41751

Nebraska: Box Butte Co:
Agate, 35.2 km E UCM 50533*
Hemingford UNSM 983*, 1081*, 1208–09*, 1897–1904*
Hemingford, 8 km N UNSM 1200–01*
Marsland, 25.6 km SW KU 21451–52
Running Water Quarry UCM 50530–32*
Sand Canyon Creek, near mouth UNSM 1844–49*

Nebraska: Dawes Co:
Chadron, 12.1 km NNW UNSM 15873
Chadron, 16 km S UMMZ 79612
Crawford UNSM 1190–91*
Dunlap (historical), 22.4 km W AMNH 60054–58, 143114–16, 143118–28
Fort Robinson YPM 712, 989–91
Pebble Creek, near mouth UNSM 15578–79*
Pine Ridge UNSM 1198*
Wayside KU 23082

Nebraska: Sheridan Co:
Hay Springs AMNH 58966*, 60296*, 143141–57*
Hay Springs, 19.2 km SW UNSM 1197*
Sand Hills and Running Water, between (= Running Water Station?, historical, cf. Perkey, 2003) USNM 4585, 293251–59

Nebraska: Scotts Bluff Co:
Gering AMNH 64738–40

Nebraska: Sioux Co:
Agate UMMZ 79702–04, UNSM 1580–82*, 1896*
Agate, north of UMMZ 136156 (4), UTA 7444*
Agate, 8 km E FMNH 35804–06
Agate, 9.6 km E UMMZ 79610
Agate, 40 km S UMMZ 79611
Agate Fossil Beds National Monument BYU 5679–80*, 5779*, 5791–92*
Agate Springs MCZ 29330*
Andrews UNSM 1891–95
Crawford, 8 km NW UNSM 1884–86*
Crawford, 23.2 km NW UCONN 4768
Crawford, 24 km NW UCONN 2448
Harrison UCM 51820–44*
Harrison, 14.4 km N UMMZ 115770
Harrison, 16 km SW UCM 44054*
Henry, 28.8 km N UNSM 1215*
Niobrara River AMNH 64714, 64751–57, 143158–60
Niobrara River, 14.4 km N AMNH 64750
Orella UNSM 1189*
Soldier Spring Creek UNSM 15580*

North Dakota: Billings Co:
McCutcheon Ranch, presumably near Mikkelson (Wheeler & Wheeler, 1966)
Medora, 3 km NNW (Jundt, 2000)
Medora, 3 km NNE (Wheeler & Wheeler, 1966)
Medora, 4.1 km ENE UNSM 16790*
Medora, 5.1 km NNE Medora (Wheeler & Wheeler, 1966)
Medora, 7.2 km E Medora (Wheeler & Wheeler, 1966)
Medora, 9.3 km SSE (Wheeler & Wheeler, 1966)
Medora, 26.2 km S (Jundt, 2000)
Mikkelson (Wheeler & Wheeler, 1966)
Peaceful Valley Ranch, 3 km NNE Medora UMMZ 56917

North Dakota: Bowman Co:
Bowman, 20.8 km S, 41.6 km W KU 130273
Marmarth, 24.1 km S (Jundt, 2000)
No specific locality UMMZ 58654
Rhame, 19.7 km SSW (Jundt, 2000)

North Dakota: Dunn Co:
Dunn Center, 22.1 km N (Jundt, 2000)
Manning, 15.7 km WNW (Jundt, 2000)
Watford City, 91.7 km SSE (Jundt, 2000)

North Dakota: Golden Valley Co:
Beach JFBM 1157

North Dakota: McKenzie Co:
Cartwright, 28.6 km S (Wheeler & Wheeler, 1966)
Grassy Butte (Wheeler & Wheeler, 1966)
Grassy Butte, 4.2 km WSW (Jundt, 2000)
Sentinel Butte, 64 km N (Wheeler & Wheeler, 1966)

North Dakota: Morton Co:
No specific locality FMNH 20889*

North Dakota: Slope Co:
Amidon, 16.5 km NW (Jundt, 2000)
Little Beaver Creek, near Marmarth (Wheeler & Wheeler, 1966)
Marmarth, 5.2 km WNW (Jundt, 2000)

North Dakota: Williams Co:
Fort Union, 3.8 km W Buford (Wheeler & Wheeler, 1966)

South Dakota: Butte Co:
Belle Fourche (Peterson, 1974)

South Dakota: Fall River Co:
Ardmore USNM 63047
Edgemont, 9.6 km NW (Platt *et al*., 2006)
Edgemont, 12.8 km W UNSM 23857*

South Dakota: Harding Co:
Buffalo, 3.2 km N UNSM 16825, 16827–28*
Crow Buttes UNSM 16831*

South Dakota: Meade Co:
Mud Butte, 16 km SE near Sulphur Creek UNSM 16826, 16833*

South Dakota: Perkins Co:
No specific locality UNSM 16832*

South Dakota: Shannon Co:
Oglala, 3 km W at Blacktail Creek (Platt *et al*., 2006)
Wounded Knee Creek (Over, 1923)

South Dakota: Undetermined Co:
Southwest region MCZ 5061, 169814–16

Utah: Box Elder Co:
Box Elder Creek Canyon USNM 5321, 293322–24

Utah: Carbon Co:
Castle Gate, 14.4 km N on US 191, and 4.8 km E on Nine Mile Canyon Road
LACM 101548–49
Price BYU 8033, 11980, BYU 30027, DSC 160, FMNH 26408*, UU 1378–81, 1391

Price, 36.8 km S RRM 2214
Sunnyside, near Mud Spring LACM 101550

Utah: Carbon–Utah Co:
Kyune, near BYU 2118, 2809

Utah: Daggett Co:
Manila, 10.4 km E KU 79478

Utah: Duchesne Co:
Duchesne, 22.4 km S BYU 39440–41
Indian Canyon Summit BYU 38032
Roosevelt BYU 13010–14
Roosevelt, 4.8 km S BYU 11254, 12889–92
Talmage, 3.2 km SW BYU 2810, 3956

Utah: Emery Co:
Buckhorn Wash BYU 2364, 2366–68
Cleveland Lloyd Dinosaur Quarry BYU 32244
Goblin Valley RRM 3283
Green River, near UMMZ 34403–06
Green River, 9.6 km W AMNH 64829
Huntington Canyon BYU 30028
Iron Wash BYU 48200*
San Rafael Reef, near Goblin Valley BYU 22817*, 22828–29
Wellington, 9.6 km S UU 1385–90
Woodside, 14.4 km NW USNM 88583*

Utah: Grand Co:
Cisco BYU 44385, 44387
Crescent Junction, 16 km S BYU 32090
Thompson CAS 38342, 41138
Thompson, 0.8 km S RRM 2341

Utah: Uintah Co:
Bitter Creek Canyon BYU 45650
Bonanza, 2.4 km E, 1.6 km S CWU 1278
Bonanza, 24 km N BYU 14170
Bull Canyon, 54.4 km S Ouray BYU 46031–33, 46096
Dinosaur National Monument MSB 82028
Hardscrabble Mountain, trail north of UCM 3185
Jensen USNM 66181–82*
Jensen, 20.8 km E BYU 13009, 13061
Kennedy's Hole, between Jensen and White River AMNH 46992–93
Leota, ca. 14 km N Ouray MCZ 46051
Leota, SE YPM 713, 992
Lone Spring Ridge, 3.2 km W Colorado state line BYU 45649
Myton, 9.6 km S YPM 711
Myton, 11.2 km E KU 56098
Ouray National Wildlife Refuge (Photo voucher)
Vernal DSC 978–80, UMMZ 204949–52, UU 49
Willow Creek, south of Ouray UU 791

Utah: Wayne Co:
Hanksville BYU 8393–95
Hanksville, 40 km NE UU 3043*

Wyoming: Albany Co:
Como Ridge UWYMV 355
Laramie UWYMV 187
Laramie, 59.2 km N KU 79477
Split Rock UCM 50535–38*

Wyoming: Big Horn Co:
Greybull, 9.6 km NE UMMZ 69022–24
Greybull, 16 km N UMMZ 69025
Otto, 14.4 km S UMMZ 69021

Wyoming: Campbell Co:
Rockypoint, 3.2 km S, 2.4 km W KU 27819

Wyoming: Carbon Co:
Aurora Lake AMNH 515–18
Bridger Pass USNM 9308, 9313, 16018, 227699–701
Dad (41° 19’ 34” N, 107° 45’ 30” W) KU 51380
Fort Fred Steele USNM 48154
Medicine Bow AMNH 528–30
Rawlins AMNH 513–14
Saratoga USNM 48110–11
Saratoga, 8 km N UWYMV 353
Saratoga, 16 km N UWYMV 354
Saratoga, 19.2 km N AMNH 58842
Shirley Basin UCM 47601–02*
Sinclair, 40 km N UTA 24769–71*
Stratton Ranch (41° 07' 41" N, 107° 10' 15" W) MSB 82955–56

Wyoming: Converse Co:
Bill, 19.2 km N, 9.6 km W KU 27818
Douglas, 28.8 km W UCM 14106*
Douglas, 32 km N UWYMV 430

Wyoming: Crook Co:
Moskee, 4.8 km SE UIMNH 52482–83

Wyoming: Fremont Co:
Bison Basin, 31 km WSW Jeffrey City MCZ 62484–86*, 166743*
Fort Washakie ANSP 12825, USNM 44788–92
Lander, 8 km W FMNH 55872*
Lander, 72 km SE UWYMV 163 (3)
Riverton UWYMV 476*
Riverton, 4.8 km W MCZ 65974*, 157358*, 166739*
Riverton, 32 km SE MCZ 139423*
Sheep Creek, at southeast base of Owl Creek Mountains USNM 48122*
Shoshoni TNHC 70974–76
Sweetwater Station, 1.6 km N UMMZ 128168 (2)

Wyoming: Goshen Co:
Fort Laramie USNM 4604, 293260*
Rawhide Buttes, 21.4 km S Lusk FMNH 1894*

Wyoming: Hot Springs Co:
Willow Creek, 24 km SW Thermopolis USNM 48123

Wyoming: Lincoln Co:
Kemmerer MCZ 62421–22*
Opal, 7.6 km ENE YPM 10176

Wyoming: Natrona Co:
Beulah Belle Lake UWYMV 412 (2)
Casper CU 1160 (2)
Cloud Creek ANSP 8708–22
Efell Mine USNM 40189*

Wyoming: Niobrara Co:
Hat Creek region (historical; ca. 42° 56' 22" N, 104° 22' 11" W) MCZ 161020–57
Indian Creek (42° 55' 43" N, 104° 13' 37" W) MCZ 4673
Lance Creek FMNH 35807

Wyoming: Park Co:
Badland Hills, 14.9 km SSE Clark USNM 266090*
Burlington, 16 km W USNM 48181–82
Cody USNM 48178
Cody, 32 km E USNM 48179–80
Germania (= Emblem), 16 km W USNM 48177*
Powell, 9.6 km W, 6.4 km N MCZ 150345–46*, 166745*

Wyoming: Platte Co:
Guernsey UWYMV 530

Wyoming: Sheridan Co:
No specific locality UWYMV 386
Sheridan USNM 47704, UWYMV 248 (6)
Sheridan, 40 km NE MCZ 29331*

Wyoming: Sublette Co:
Farson, 21 km N, 12 km E MSB 84374
Tabernacle Butte, 13.8 km NNE Big Sandy Reservoir MCZ 65975

Wyoming: Sweetwater Co:
Bitter Creek, 28.8 km S KU 23091
Bitter Creek, 36.8 km SW MVZ 18266
Bitter Creek, 38.4 km S AMNH 46994
Bitter Creek, 51.2 km S FMNH 46058*
Black’s Fork UWYMV 160
Black Rock Butte UWYMV 162, USNM 49666
Eden Valley UWYMV 176 (2)
Flaming Gorge Reservoir, near UCM 58937*
Flaming Gorge Reservoir, east side UCM 58973–74*
Green River ANSP 17958, KU 79476
Green River, 14.4 km S UU 3450
Green River, 17.6 km S UU 3449
Henry’s Fork UWYMV 161
Linwood, 24 km N UMMZ 66744
Rock Springs, 54.4 km NW UMMZ 124640
Rock Springs, 40 km N, 54.4 km E KU 29400
Rock Springs, 43.2 km N, 59.2 km E KU 29401

Sand Dunes, 8 km SE KU 63766–67
Table Rock, 32 km N UMMZ 72602
Undetermined locality UU 3451–53

Wyoming: Teton Co:
Hoback Canyon, 17.9 km S Jackson UWYMV 367* (Photo voucher)

Wyoming: Uinta Co:
Bear River, 22.4 km N Evanston USNM 48686
Evanston UWYMV 175 (2)*
Fort Bridger ANSP 8741–44, KU 23595, USNM 16199–200*, 44913, 45047*, 47703, 131659
Fort Bridger Reservation USNM 5455, 293325–28

Wyoming: Washakie Co:
Ten Sleep, 32 km W USNM 48124, 48183–84
Worland, 6.4 km S, 11.2 km W KU 29402

Wyoming: Weston Co:
Newcastle, 36.8 km S KU 23680–81

***Phrynosoma bauri* sp. nov.**

United States
Colorado: Adams Co:
Byers, 12.8 km NE UCM 11351*
Commerce City UCM 32237*

Colorado: Alamosa Co:
Mosca Pass, west slope MEL 1001–02

Colorado: Arapahoe Co:
Englewood UMMZ 43882–83, 43885–86
Fort Logan CAS 14495

Colorado: Boulder Co:
Boulder AMNH 17837, BYU 21861, UCM 218–19, 221, 277, 414, 520, 1937, 3184, 20121, 21533, USNM 34569–70*
Boulder, east of UCM 220*
Boulder, north of UCM 2557*
Boulder, 4 km N UCM 7436*
Boulder, 4.8 km N UCM 11352–53, 13676–83
Boulder, 6.4 km N UCM 11354*
Boulder, 8 km N UCM 43405
Boulder, 8 km NE LACM 62557
Boulder, Four-Mile Mesa OSUS 2257, UCM 51819
Eldorado Springs, 3.2 km E UCM 9697*
Flagstaff Mountain, at base UCM 278*
Lyons, 4.8 km SE OSUS 2256
Marshall UCM 10841*
Marshall, south of UCM 282*
Owens Lake (Ellis & Henderson, 1913)
Sixmile Reservoir, 0.8 km N UCM 2903*
Valmont Butte UCM 20434
White Rocks UCM 1070*

Colorado: Cheyenne Co:
Kit Carson, 23.1 km N UNCMNH 728*
Wild Horse, 9.6 km NW UCM 52753*

Colorado: Clear Creek Co:
Snyder Mountain, SE base on Witter Gulch Road SIU 1

Colorado: Costilla Co:
Fort Garland, ca. 8.8 km NE MEL 1017–18
Russell, 11.2 km SE CU 3723 (8)

Colorado: Crowley Co:
Ordway, 9.6 km N UCM 19687*

Colorado: Custer Co:
Silver Cliff UCM 7437–55
Westcliffe FMNH 22855

Colorado: Denver Co:
Denver CU 3902, MPM 810*, 1683*, OSUS 1141–42, UCM 10048–56*, 20435*, UMMZ 43881, 43884, USNM 29601, 30915–20, 293450–52
Englewood UMMZ 43887–94
Globeville MSB 82947

Colorado: Douglas Co:
Larkspur FMNH 94951*

Colorado: Elbert Co:
Agate, 24 km SE UCM 56095*
Cedar Point, 8 km WNW UNCMNH 130*
Kiowa FMNH 21483*
Limon, 9 km WNW MEL 1004
Limon, ca. 14.9 km NW MEL 1003, 1005–07
Matheson, 5.4 km S UNCMNH 129*
Matheson, 6.4 km S UNCMNH 126*
Matheson, 17.6 km SSE UNCMNH 447*
River Bend, 8 km NW UCM 19688*

Colorado: El Paso Co:
Colorado Springs ANSP 12826–27, KU 88150–56, MVZ 7586–87, UMMZ 71429 (7), UNSM 1080*, USNM 8444*, 8514*, 9263*, 293351–55*
Colorado Springs, 8 km N MSB 4466
Fountain, 20.8 km E CAS 102047
Rush, 0.8 km W UCM 25643*

Colorado: Huerfano Co:
Aguilar, 15.8 km NNW MVZ 49831
East Spanish Peak, north slope, on Sporleder Ranch UMMZ 62239
Gardner, 3.2 km N UCM 17861
Gardner, 3.2 km SE UCM 20120
Gardner, 4.8 km SE UCM 43323–24
Gardner, 8 km S UCM 20119
La Veta Pass (Ellis & Henderson, 1913)
Muddy Creek, 4.8 km away (N?) on CO 69 (Ellis & Henderson, 1913)
No specific locality UCM 48463
Walsenburg UMMZ 62240

Walsenburg, ca. 15 km ESE MEL 1009–10
Walsenburg, 24 km NE UCM 2312

Colorado: Jefferson Co:
Golden, 4.8 km S UCM 52717*, 54214*
Ken–Caryl Ranch (Ludlow, 1981).
Rocky Flats, 12.8 km S Boulder UCM 43406–07

Colorado: Kiowa Co:
Arlington, south of UNCMNH 767*
Arlington, 1.3 km S, 0.3 km E UNCMNH 973*

Colorado: Kit Carson Co:
Flagler, ca. 3.2 km E UNCMNH 37–40* (Photo voucher)

Colorado: Larimer Co:
Fort Collins, 6.4 km SW UCM 51232
Fort Collins, 8 km SW UCM 51238
Fort Collins, 16 km S UCM 11355
Laporte, 8 km N UCM 51233–37
Wellington, 6.4 km E (Ellis & Henderson, 1913)
Wellington, 19.2 km NE UCM 51223–31
No specific locality UCM 51227

Colorado: Las Animas Co:
Aguilar UCM 1107*
Kim, 1.6 km N UCM 25696
Trinidad UCM 7072–76, USNM 80294–95*
Trinidad, 19.2 km S near Raton Pass KU 68087
Trinidad, 20.8 km ESE UCM 7077
Trinidad, 43.2 km E, near Purgatoire River UCM 9430
Walsenburg, 19.3 km SE MEL 1011

Colorado: Lincoln Co:
Boyero, 10.9 km SSW UNCMNH 643*
Boyero, 11.4 km SSW UNCMNH 646*
Boyero, 11.8 km W UNCMNH 640*
Boyero, 12.8 km W UNCMNH 637*
Boyero, 13.6 km SW UNCMNH 632*
Boyero, 14.2 km SW UNCMNH 1019*
CO 71, just E on county road 3T UCM 61523*
Forder, 0.8 km W UCM 19689*
Hugo (Ellis & Henderson, 1913)
Hugo, 1.7 km S UNCMNH 1029*
Karval, 9.4 km NNE UNCMNH 569*
Karval, 9.6 km NNE UNCMNH 131*
Karval, 13.9 km NNE UNCMNH 1011*
Karval, 14.4 km W UNCMNH 996*
Karval, 17.5 km NNE UNCMNH 1015–16*
Karval State Wildlife Area, 5.1 km S UNCMNH 1*
Punkin Center, 5.9 km N UNCMNH 135*
Punkin Center, 16.3 km E UNCMNH 2*
Punkin Center, 28.6 km E UNCMNH 128*
Punkin Center, 30.8 km E UNCMNH 1098*
Punkin Center, 32.5 km E UNCMNH 127*, 1030*
Punkin Center, 33.2 km E UNCMNH 3*

Colorado: Logan Co:
Clyde Ward Ranch UMMZ 107977, 125426
Martin Canyon LACM 19681
No specific locality UMMZ 96055 (4)
Peetz, 13.6 km W, 7.2 km S KU 51377–79
Peetz, 14.4 km W, 8 km S SIUC 1073, 1076, 1086, 1090
Peetz, 17.6 km W, 6.4 km S SIUC 1074, 1077
Peetz, 17.6 km W, 8 km S SIUC 1078, 1084, 1091
Peetz, 19.2 km W, 8 km S SIUC 1080–81, 1088–89
Peetz, 22.4 km W, 3.2 km S SIUC 1079
Peetz, 28.8 km W SIUC 1082, 1085
Peetz, 32 km W SIUC 1075, 1083, 1087
Sterling, 19.2 km NW UF 16757, 16759, 16763
Willard, 6.4 km N UCM 19690*

Colorado: Morgan Co:
Cottonwood Spring, 24 km N Weldona UCM 223
Fort Morgan, 4.8 km NE UCM 51239
Fort Morgan, 19.2 km NE UCM 51240–43
Fort Morgan, 20.8 km N, 9.6 km E UCM 11785*
Orchard, 12.8 km N UCM 11356–59
Pawnee Buttes KU 370
Weldona, 2.4 km W, 12.8 km N UCM 11786–87

Colorado: Otero Co:
Rocky Ford SIUC 686

Colorado: Pueblo Co:
Colorado City MCZ 2449*
Pueblo, 24 km E UCM 19691

Colorado: Weld Co:
Avalo USNM 40139*
Chalk Bluffs at head of Gerry Creek UWYMV 381
Greeley USNM 37035*
Greeley, 32 km NE UCM 20118
Grover, 14.4 km E, 1.6 km N UCM 32239, 51250–52
New Raymer, 16 km N UCM 17871–73, 43026
New Raymer, 16–28.8 km N UCM 17862–66
No specific locality KU 23571–73
Nunn, 12.8 km N, 8 km E RRM 2113–14, 2204, 2210, 2112
Pawnee Buttes AMNH 46999–7000, KU 371
Pawnee Buttes, 6.4 km SE UCM 17874–75
Pawnee National Grasslands BYU 5673–8*
Stoneham, 1.6 km NNE UCM 17867–70
Stoneham, 35.2 km N UCM 2311
Stoneham, 38.4 km N UCM 2310
Stoneham, at Stoneham Hogbacks RRM 2413
Wellington, 6.4 km E UCM 222
Wellington, 12.8 km NE RWA 3250
Wellington, 16.5 km NE UCM 51244–49

Nebraska: Cheyenne Co:
Potter, 1.6 km S UNSM 6658–61, 7374
Potter, 19.2 km S UNK 487 (4)*
Sidney ANSP 18029, CU 1525, UNSM 15418, USNM 10786

Sunol, 2 km N, 3.2 km W UNSM 7844
Sunol, 1.6 km N, 4.8 km W UNSM 7845–47

Nebraska: Deuel Co:
Big Springs (Photo voucher)

Nebraska: Kimball Co:
Bushnell, 9.6 km W UNSM 8986–87
Dix UNSM 1204–07
Kimball (Photo voucher)
Kimball, 8 km S UNSM 8984–85
Kimball, 1.6 km S, 12.4 km W UNSM 9710–11

New Mexico: Colfax Co:
Cimarron USNM 22666
Farley, 9.6 km SW TNHC 70982
Philmont Scout Ranch MSB 5263, UMMZ 230427
Philmont Scout Ranch, at Headquarters MSB 5265
Philmont Scout Ranch, at Ponil Base Camp FWM 2743, RRM 3312
Philmont Scout Ranch, on Training Center Road MSB 5264
Raton LACM 4348, NMSU 1503–06

New Mexico: Harding Co:
Roy, 16 km N, 6.4 km W MSB 7138

New Mexico: Mora Co:
Fort Union USNM 9196, 293389–90
Mora OMNH 25207
Wagon Mound AMNH 62857

New Mexico: San Miguel Co:
Las Vegas MPM 1532, TNHC 7262, OMNH 25205, 25208–12, 25214, 27467–68
Las Vegas, W AMNH 62859

New Mexico: Union Co:
Capulin Volcano National Monument ENMU 3422, 4224
Grenville BYU 43673

Wyoming: Laramie Co:
Carpenter, 19.2 km WNW UCM 51253–61
Cheyenne, 24 km ESE KU 63765
Pine Bluffs, 8 km S KU 79475

Wyoming: Platte Co:
Cassa USNM 40190
Wheatland UWYMV 169, 247 (4)

***Phrynosoma diminutum* sp. nov.**

United States
Colorado: Alamosa Co:
Alamosa LSUMZ 13839
Blanca, 8 km NW UCM 3894–95
Medano Ranch, near UCM 61895–97
Zapata Ranch, ca. 15.6 km WNW Blanca Peak MEL 1013, 1015–16

Colorado: Conejos Co:
Antonito USNM 44888
Antonito, 4.8 km S UCM 9698–99*
Antonito, 19.2 km E USNM 44889–90
Mesita, 14.4 km SW LSUMZ 13834–35
Mesita, 14.4 km W LSUMZ 13836
Mogote, southwest of UCM 55605*
Rio Grande River, 1.6 km W on CO 142 UCM 43553*
San Antonio MVZ 27042

Colorado: Costilla Co:
Fort Garland USNM 8256, 8558
Medano Ranch, 3.2 km SE (*fide* Ellis & Henderson, 1913; see Alamosa Co.)
Mesita, 1.6 km W LSUMZ 13840, UCM 3896–98
Mesita, 14.4 km W LSUMZ 13837

Colorado: Rio Grande Co:
Monte Vista UMMZ 62241–68

Colorado: Saguache Co:
Mineral Hot Springs, near UCM 51268
Mineral Hot Springs, 4.8 km SW UCM 48464*
Mineral Hot Springs, 7.2 km SW UCM 48465–66

Phrynosoma douglasii

United States
California: Lassen Co:
Bieber USNM 44887*

California: Siskiyou Co:
Brewer Creek PSM 3895*, 4885*
Clear Lake, Klamath Mountains (Marble Mtn. Wilderness) USNM 45138*
Grasshopper Flat MVZ 215589*, 218110–17*, 218222–26*, 219609–12*,
223192–212*, 223426–34*, 230682*
Little Glass Mountain, 4.8 km SE (Photo voucher)
Macdoel (Photo voucher)
Medicine Lake CAS 84693
Mount Hebron CAS 84694, USNM 60180–83*
Mount Shasta, east slope near Brewar Creek PSM 3895*, 4885*
Mount Shasta, west base (*fide* Townsend, 1887) USNM 13792*, 293438–39*
Mount Shasta, northeast slope on Military Pass Road MVZ 92521*
Mount Shasta, 32 km E MVZ 158992*
Sheep Mountain (Sight record; J. Shedd, personal communication)

Idaho: Bannock Co:
Pocatello CAS-SU 1944, USNM 48665*

Idaho: Bingham Co:
Aberdeen UU 177*, 180–81*
Blackfoot USNM 16771*
Fort Hall (Cope, 1872), CAS 41305*
Middle Butte, 1.6 km NNW IMNH 957*
Springfield ANSP 17566–67*

Idaho: Blaine Co:
Craters of the Moon National Monument KU 50439, IMNH (UI 36)*
Magic Reservoir PSM 10839*

Idaho: Bonneville Co:
Idaho Falls, 20.8 km S IMNH 864*

Idaho: Butte Co:
Arco, near BYU 30754–69*, CAS-SU 2840, 2842, IMNH 1037–38*
Arco, 16 km S IMNH (UI 300)*
Arco, 19.2 km E RRM 2361
Big Butte, near IMNH 779*, USNM 16772–73*
Big Lost River, at sink IMNH 954*, USNM 16318–19*
Howe, 16 km N MVZ 80249
Idaho Falls, northwest of BYU 5793–94*
Idaho National Engineering Laboratory IMNH 955–56*, UTA 45277–78
Idaho National Engineering Laboratory, Tractor Flat Road UTA 45232
US 20 & 26 jct., 8 km W, 3.2 km S RRM 2363–64, 2390
US 20 & 26 jct., 16 km NW RRM 2393

Idaho: Butte–Custer Cos:
Big Lost River USNM 16774–75*

Idaho: Cassia Co:
Bridge, ca. 6 km WSW UMMZ 107238–39
Conant CAS-SU 2801
Cottonwood Creek CAS-SU 2816
Malta, 4.8 km E IMNH (UI 25 [2])
Raft River Valley BYU 42042–43

Idaho: Custer Co:
Little Lost River, Summit Creek IMNH 778*, 787*
Little Lost River, Summit Creek, 1.6 km SW Barney Hot Springs IMNH 861*
Upper Pahsimeroi Valley IMNH 776*, 781–86*, 790–92*

Idaho: Elmore Co:
Mountain Home (Evender, 1946)

Idaho: Fremont Co:
Egin BYU 8178

Idaho: Latah Co:
Moscow OSUS 1585–89

Idaho: Lemhi–Clark Co. line:
Birch Creek, near head USNM 16315–17*

Idaho: Lincoln Co:
Shoshone CAS-SU 1950*

Idaho: Madison Co:
Rexburg BYU 8054

Idaho: Minidoka Co:
Rupert, 20 km W, 5.6 km N UMMZ 133797

Idaho: Nez Perce Co:
Clearwater River, 11.2 km above Lewiston USNM 21473*
Lewiston, near IMNH (UI 68)*

Idaho: Owyhee Co:
Three Creek, 50.3 km NNW (T. Jezkova, unpublished data)
Murphy Hot Springs, 18 km WSW of Three Creek IMNH 1254–55

Idaho: Power Co:
American Falls CAS-SU 2837*, IMNH 860*
Crystal Ice Caves MVZ 80250
Rock Lake, 27.7 km NW Aberdeen IMNH 793*

Montana: Beaverhead Co:
Centennial Valley MCZ 42197

Nevada: Humboldt Co:
Badger Flat UMMZ 173661
Black Rock Range near head of Craine Creek (Photo voucher)
Blowout Mountain (T. Jezkova, unpublished data)
Summit Lake UMMZ 91863

Nevada: Washoe Co:
Fish Creek Mountain (T. Jezkova, unpublished data)
Painted Point (T. Jezkova, unpublished data)
Round Mountain (Photo voucher)

Oregon: Crook Co:
Buck Creek USNM 44974*
Prineville, 6.4 km SW MVZ 26921
Prineville, 40 km S USNM 44907*

Oregon: Deschutes Co:
Bend and Sisters, between (Photo voucher)
Brothers (Photo voucher)
Brothers, 14.4 km SE PSM 4143*
Bull Flat, west of Bend (Photo voucher)
Cache Mountain UMMZ 173629, 173633
Deschutes National Forest UMMZ 173631
Fryrear Butte, 22.3 km W Redmond (Photo voucher)
La Pine (Photo voucher)
Millican Valley (Photo voucher)
Mount Washington, east slope UMMZ 173627–28
Mount Washington, E at lava field RRM 2321, 2327, 2357, 2366
Sisters (Photo voucher)

Oregon: Harney Co:
Burns, southwest of (Photo voucher)
Burns, 24 km NW BYU 49552–54*
Frenchglen, 16 km N UMMZ 173648
Hines UMMZ 173654
Malheur National Wildlife Refuge MVZ 146089, USNM 312993–94*
Squaw Butte Research Station UMMZ 173634–38
Steens Mountain, on lava plateau FMNH 46059–61*
Stone House Creek, 36.5 km NNE Steens Mountain (Photo voucher)
US 20 & OR 78 jct., 40 km SE RRM 2316, 2320, 2322

Voltage (historical; 43° 15' 41" N, 118° 48' 26" W) USNM 63264–65*
Wagontire PSM 3025*
Wagontire, 4.8 km NE UMMZ 92239 (2)

Oregon: Jefferson Co:
Black Butte, E slope UMMZ 173630
Culver, 8 km E UMMZ 133082
Jack Lake UMMZ 176346
Madras, south of UMMZ 173639
Santiam Pass UMMZ 170332–48

Oregon: Klamath Co:
Bly, 7.7 km NNW UMMZ 133788 (2)
Crater Lake, 8 km N MVZ 40761
Jamison Meadow, 15.6 km E Chemult (Photo voucher)
Klamath Falls USNM 59288*, 312995*
Olene USNM 25911*

Oregon: Lake Co:
Alkali Lake (Photo voucher)
Cabin Lake UMMZ 153176–77, 174112–51, 174152–61, 174173, 174176, 174211–98
Chewaukan Valley USNM 10797, 293407–09
Coglan Butte, near Paisley (Photo voucher)
Fort Rock, 1.6 km W UMMZ 173649–50
Fort Rock, 9.6 km E UMMZ 173583, 173655
Fort Rock, 33.2 km NE UMMZ 173632
Fort Rock State Park MSB 33004
Fossil Lake UMMZ 144150
Hart Mountain USNM 312996*
Hart Mountain National Antelope Refuge BYU 4086, 4087, 4088, 4089*
Hart Mountain National Antelope Refuge, 2.4 km S UMMZ 173652–53
Hart Mountain National Antelope Refuge Headquarters UMMZ 173651
Hart Mountain National Antelope Refuge Headquarters, 0.4 km E UMMZ 173601–04
Hart Mountain National Antelope Refuge Headquarters, 0.8 km S UMMZ 173624
Hart Mountain National Antelope Refuge Headquarters, 1.6 km S UMMZ 173618–19
Hart Mountain National Antelope Refuge Headquarters, 1.6 km NE UMMZ 173621
Hart Mountain National Antelope Refuge Headquarters, 2.4 km SE UMMZ 173584–87
Hart Mountain National Antelope Refuge Headquarters, 2.8 km S UMMZ 137554, 173588–95, 173626
Hart Mountain National Antelope Refuge Headquarters, 3.2 km S UMMZ 173596–600, 173609–12
Hart Mountain National Antelope Refuge Headquarters, 3.2 km SE UMMZ 173605–08
Hart Mountain National Antelope Refuge Headquarters, 4.8 km S UMMZ 173613–17
Hart Mountain National Antelope Refuge Headquarters, 19.2 km S UMMZ 173620
Hart Mountan National Antelope Refuge, Lookout Point UMMZ 137553
Lake Abert CAS–SU 5767–805
Lyon's Ranch, 3.2–4.8 km N UMMZ 86090
No specific locality UMMZ 173569–77
Plush USNM 25909–10*
Plush, 6.4 km W UMMZ 173623
Plush and Blue Creek, between USNM 25912–13, 25923–33*
Silver Lake Desert MVZ 14990
Warner Lakes and Goose Lake, between ANSP 12793–98*
Warner Peak (Photo voucher)
Warner Valley, 9.6 km N CCC Camp UMMZ 173622, 173625
Warner Valley, at Honey Creek UMMZ 173582

Oregon: Linn Co:
Big Lake, 1.6 km W MSB 33003
Big Lake and US 20, between UMMZ 173640–47
Sand Mountain UMMZ 137442 (5), 173578–81
Santiam Junction BYU 49558–60*, UMMZ 133796 (2), 137412, 137413 (4), 137414–16, 137417 (2), 137418 (6), 137419–20, 137421 (5), 137424–31, 137433 (4), 137434 (8), 137435 (5), 137436 (8), 137437 (4), 137438 (4), 137439 (17), 137440 (6), 137441 (11), 137443 (10), 137444 (10), 137445 (5), 137446 (5), 137447 (9), 137448 (8), 137449, 137450 (4), 137451, 137452 (2), 172634–41, 174162–72, 174174–75, 174177–210, 174299–307

Oregon: Morrow Co:
Boardman, 9.6 km SW BYU 49555–57*
Cecil CAS 71419–22
Heppner USNM 44971–73*
Pine City, 9.6 km up North Fork of Butter Creek PSM 3715*, 3720*

Oregon: Umatilla Co:
Cold Springs Landing, 4.8 km S MVZ 16800–01
Cold Springs Landing, 8 km S MVZ 16797–99
Cold Springs Landing, 11.2 km S MVZ 16796
Cold Springs Landing and Holdman, between MVZ 16795*
Hermiston, 9.6 km N PSM 3726*
Pendleton, 24 km SW MVZ 16802–05

Oregon: Wasco Co:
Antelope USNM 45186*
Antelope, NE PSM 3558–59*

Utah: Box Elder Co:
Snowville BYU 14755

Washington: Adams Co:
Benge PSM 6381*
Cow Lake PSM 3890*
Lind PSM 4637*
Twelve Mile Slough CRCM 51.116

Washington: Asotin Co:
No specific locality CRCM 63.85

Washington: Benton Co:
Horse Heaven Hills, Gwiren's Hills Ranch PSM 8263*

Washington: Chelan Co:
Chelan PSM 3139*, 3142*

Washington: Douglas Co:
Bridgeport CRCM 39.43
Del Rio, 4.8 km E OMNH 28193
Withrow, 8 km E PSM 3475*

Washington: Franklin Co:
Kahlotus, 24 km SW IMNH (UI 323, 403)*
Pasco CRCM 64.66, 64.67, 75.886, 75.887, PSM 8375*
Pasco, 1.6 km E CRCM 58.314

Washington: Grant Co:
Beverly, 1.6 km E LACM 64264
Lind Coulee CRCM 58.526
Moses Lake PSM 3143–44*
O'Sullivan Dam CRCM 58.579
Ruff CRCM 50.244, 58.528
Soap Lake, 3.2 km N PSM 3013*
Vantage, 16 km NE PSM 4353*

Washington: Kittitas Co:
Colockum Pass, NNE of Ellensburg MVZ 223227*
Ellensburg, near UTA 5695*
Ellensburg, 14.4 km N CWU d
Ellensburg, 16 km E CWU e, f
Ellensburg, 17.6 km E CWU c
Ellensburg, 17.6 km NW MVZ 52082*
Ellensburg, 19.2 km E CWU a, b
Ellensburg, 27 km E PSM 6376*
Ellensburg, 28.8 km E PSM 4810*, 4969*
Ellensburg, 32 km E PSM 6377*
Vantage, 11.8 km W MEL 1000
Vantage, 16 km W LACM 26969

Washington: Klickitat Co:
Grand Dalles, at sand dunes PSM 3298*
Smithville, 1.6 km SE PSM 3390*

Washington: Lincoln Co:
Odessa, 19.2 km W PSM 4065*
Wilbur, 9.6 km N BYU 49561–63*

Washington: Okanogan Co:
Coulee Dam, 16 km N PSM 3539*
Pateros FMNH 115998*

Washington: Spokane Co:
Medical Lake UMMZ 173665
Spokane MVZ 43506, 43508*
Spokane Falls MVZ 43507*

Washington: Walla Walla Co:
Attalia UMMZ 173663
Fort Walla Walla USNM 10918 (5)*
Wallula MVZ 5578, UMMZ 173662
Wallula, 3.2 km NE UMMZ 173664

Washington: Whitman Co:
Almota (Svihla & Svihla, 1933)
Central Ferry, 8 km below Snake River PSM 4601*
Rock Lake (Svihla & Svihla, 1933)

Washington: Yakima Co:
Selah (Owen, 1940)
Sunnyside FMNH 784–86*
Sunnyside, 8 km E PSM 4257*
Toppenish, 24 km SW PSM 6029*
Yakima, north of LSU 86010, RRM 2513

Wyoming: Teton Co:
Upper Firehole River Basin USNM 9458

Phrynosoma hernandesi

Mexico
Chihuahua:
Colonia Pacheco, 11.2 km SW MVZ 46655

Sonora:
Arroyo Cajón Bonito USNM 21018
Cananea AMNH 67531, UAZ 875–906, 1995–2011*
Cananea, 3.2 km W LACM 101558
Cananea, 8 km NW LACM 101559
Cananea, 13.4 km E UAZ 32375*
Cananea, 22.7 km SE, south side Sierra de los Ajos UAZ 32454*
Cananea, 25.1 km E UAZ 32453*
Cananea, 29.7 km E UAZ 32456*
Imuris, 54.5 km E LACM 101560
Mexico Highway 2, near km post 111 RRM 2266–67, 2296, 2314
Mexico Highway 2, near km post 98 RRM 2365
Naco, 0.8 km S RRM 2344
Naco and Rancho Romo, between UAZ 48695*
Naco, 5.8 km SW UAZ 32382–83*, 32388–404*, 32457–58*, 32622–23*, 33659–64*, 33695*, 34040*, 48693–94*, 48696–702*, 49289–308, UTEP 2998
Sierra de la Madera, ENE of Moctezuma (Photo voucher)
Sierra de Los Ajos UAZ 34467*
Sierra de Los Ajos, north slope UAZ 34700*
Sierra San Luis, N of Cañon Diablo UTA 23535–36

United States
Arizona: Apache Co:
Alpine UAZ 36732
Black River, below Ten of Diamond Ranch MSB 17933
Black River, north side, 0.5 km below Whites Crossing UAZ 46120*
Bush Valley, near Alpine, Apache–Sitgreaves National Forest USNM 47090*
Carnero Lake UAZ 43867
Diamond Rock Lodge LACM 62555
Eagar BYU 932
Eagar, ca. 11.8 km SW at Mexican Hay Lake UAZ 56719*
Escudilla Mountain UAZ 37476, 43868
Fort Apache Reservation, Baldy Peak, northeast slope UAZ 45061
Fort Apache Reservation, base of Kinney Lookout UMMZ 105788
Greer UAZ 39645, 40793
Jackson Box, 21.4 km N Blue UAZ 48289
McNary, 1.6 km NE UMMZ 223384
McNary, 6.4 km SSE UAZ 32621
Nutrioso, 8 km NE KU 61496
Porter Spring, 3.2 km N UAZ 870
Springerville UAZ 847, 4234
Springerville, 1.6 km S UAZ 32745
Springerville, 3.7 km N, 4 km E UAZ 42534
Springerville, 5.6 km S UMMZ 79193 (2)
Springerville, 6.4 km N UAZ 32977
Springerville, 11.2 km N UMMZ 121703
Springerville, 16 km N UAZ 36010

Springerville, 20.8 km N UAZ 46150, UMMZ 85015
Springerville, 32 km N UMMZ 59806
White Mountains USNM 9637*, 56840*, 293399–400*
White Mountains, south of Big Lake UAZ 55423*
White River, North Fork at confluence with No Name Creek MSB 17931–32

Arizona: Cochise Co:
Apache, 13.9 km SW on AZ 80 UAZ 40791–92*
Benson MCZ 62348
Bisbee ANSP 17931*, UAZ 28669*
Chiricahua, 0.3 km SW UAZ 32586*
Chiricahua Mountains AMNH 80888, MVZ 7858
Chiricahua Mountains, Barfoot Lookout AMNH 80885
Chiricahua Mountains, Cave Creek at South Fork KU 47377
Chiricahua Mountains, Onion Saddle UF 78839–40
Chiricahua Mountains, Pinery Canyon ANSP 21254–56*, 21286*, MVZ 7853–56
Chiricahua Mountains, Reed Ranch UMMZ 114157
Chiricahua Mountains, Rucker Ranger Station, 2.4 km S MVZ 67081
Chiricahua Mountains, White River Canyon (= Rucker Canyon) UAZ 40795*, USNM 10191*, 293401–06*
Chiricahua Mountains, Whitetail Canyon MVZ 7860
Chiricahua National Monument INHS 7550–51, 7939, LACM 101535
Chiricahua National Monument, 0.8 km W UCM 40853*
Chiricahua National Monument, 0.9 km E entrance on Pinery Canyon Road UAZ 46853*
Chiricahua National Monument, 3.2 km W Ranger Station UNK 375*
Chiricahua National Monument, ca. 3.4 km W UAZ 28047*
Chiricahua National Monument, ca. 6.4 km W, 0.8 km N UAZ 18727*
Chiricahua National Monument, ca. 6.4 km W, 1.4 km N UAZ 46897*
Chiricahua National Monument, ca. 6.4 km W, 1.4 km S UAZ 54689*
Coronado National Memorial UAZ 43082–84*
Dos Cabezas (ghost town) MVZ 13843
Dos Cabezas (ghost town), 1.6 km SE UAZ 28746*, 39643*
Dos Cabezas (ghost town), 4.8 km SE UAZ 21343*
Dos Cabezas (ghost town), 32 km SE UAZ 40790*
Dos Cabezas Mountains USNM 312976–92*
Dos Cabezas Mountains, NE slope USNM 246153*
Dos Cabezas Mountains, W slope (Mitchell, 1975)
Dos Cabezas Mountains, SW slope, 19.2 km SE Willcox USNM 246152*
Elfrida, 20.8 km N UAZ 49287*
Fairbank CAS-SU 2603–04, FMNH 683*
Fivemile Creek, 4 km N on AZ 181 UAZ 28668*
Fort Bowie National Historic Site UAZ 42411*
Fort Huachuca UAZ 843*, UMMZ 75775, USNM 17783–84*, 18009*, 19681–83*, 21727*, 22232–34*, 22316*, 42136*
Hereford, 5.6 km SE UAZ 47047*
Huachuca Mountains CAS 35001, 35004, 48859–60, 48862, CAS-SU 86–87, MCZ 14907*
Huachuca Mountains, Carr Canyon AMNH 15051, 63492–93, ANSP 16495–98, CU 1775, LACM 75242, UAZ 11242*, 30962*, 39642*, 40798*, UMMZ 69746 (2)
Huachuca Mountains, Carr Peak MSB 6008
Huachuca Mountains, Miller Canyon UAZ 2102*
Huachuca Mountains, Montezuma Canyon AMNH 15047, CAS 84130
Huachuca Mountains, Nicksville Airport MVZ 44737
Huachuca Mountains, Ramsey Canyon CU 3535, MCZ 31686–89*, UAZ 43573*, UMMZ 86064
Huachuca Mountains, Reef Mine LACM 101534
Huachuca Mountains, Reef Road UAZ 40797*
Huachuca Mountains, Scotia Canyon UAZ 44503*
Huachuca Mountains, Sunnyside UAZ 1983*

Huachuca Mountains, Sunnyside Canyon UAZ 51946*
Mule Mountains, Moore Canyon AMNH 15052
Mustang Mountains, Schock Ranch UAZ 39644*, 55130–45*
Paradise CAS 35098
Paradise, 1.6 km S AMNH 63491
Portal UCM 20009*
Rodeo, 4.8 km N, 6.4 km W OMNH 37981*
Silver Creek, at AZ 80 MSB 36447
Southwestern Research Station AMNH 109090, CU 10680
Southwestern Research Station, 3.2 km SW LACM 107275, MVZ 67016
Southwestern Research Station, 5.9 km W NMSU 2380
Tombstone FMNH 542*, TNHC 15336, UAZ 869*
Whetstone Mountains, Cottonwood Canyon UAZ 51727–28*
Whetstone Mountains, Kartchner Caverns State Park UAZ 56058*

Arizona: Coconino Co:
Buckskin Mountain MCZ 9150–59*, 166741–42*,
Buckskin Mountain, V. T. Ranch UMMZ 73403 (3)–04, 73406–08, 73410
Buffalo Range Road, 6.2 km S Interstate 40 UAZ 47826
Elden Mountain RRM 2275, 2310–11
Elden Mountain, W side UMMZ 223387
Elden Mountain, S side LACM 19658–71, UAZ 10979
Elden Spring UAZ 2103
Flagstaff BYU 49539, FMNH 208099, KU 381–93, LACM 19654–55, 19660, MCZ 6847*, TNHC 11653, UMMZ 223385–86, 223388–91, USNM 56841, 60173, 82000, UU 207*
Flagstaff, 7.7 km N RRM 2350
Flagstaff, 8 km S UMMZ 223398
Flagstaff, 8 km W UMMZ 223392
Flagstaff, 9.6 km NE TNHC 7438
Flagstaff, 11.2 km NE MVZ 59444–45
Flagstaff, 11.2 km NW LACM 4340
Flagstaff, 12.8 km NW USNM 82000*, 312975*
Flagstaff, 12.8 km NE UMMZ 223393
Flagstaff, 16 km SSW UMMZ 218778
Flagstaff, 16 km NW UAZ 858
Flagstaff, 16 km W UAZ 1972
Flagstaff, 19.2 km N, 9.6 km W UMMZ 223400
Flagstaff, 22.4 km NW at Hart Prairie LACM 19656–57, USNM 60171*
Flagstaff, 24 km NNW UMMZ 223394
Flagstaff, 28.8 km NW UMMZ 79197
Flagstaff, 30.4 km N at Dove Tank Canyon UAZ 2098
Flagstaff, 32 km NW UMMZ 74032 (5), 79194
Flagstaff, 48 km NW UMMZ 223397
Grand Canyon (village) ANSP 21101–02, CAS 63845–46, LACM 101537, UAZ 864–65, 1981, 39646*, UMMZ 64939
Grand Canyon (village), 4.8 km W CAS 64965
Grand Canyon (village), 40 km NW USNM 59838
Grand Canyon, North Rim ANSP 21103–07, BYU 43254, FMNH 21482*, LACM 61490, MVZ 65671–73, UAZ 863, 874, 19121, UCM 7579–80, UMMZ 76844, UNLV 2153, USNM 79686–90
Grand Canyon, North Rim at Big Saddle Hunting Camp USNM 71237
Grand Canyon, North Rim at Bright Angel Point MVZ 18044, 50976
Grand Canyon, North Rim at Point Sublime MVZ 18046, UMMZ 73409
Grand Canyon, North Rim at Robber's Roost LACM 4338
Grand Canyon, North Rim at Swamp Point LACM 4336–37
Grand Canyon, South Rim at Bright Angel Trail UMMZ 31755 (3)
Grand Canyon, South Rim at Desert View UAHC 66-219
Grand Canyon, South Rim at Grand View Point CU 7890, LACM 4335

Grand Canyon, South Rim at Red Butte LACM 4339
Grand Canyon, South Rim at Yaki Point FMNH 94949*
Heber, 34.7 km SW UAZ 36013
House Rock Spring USNM 44625
House Rock Valley UU 3004–5*
Jack Smith Tank, 9.6 km NE UMMZ 74028
Jacob Lake KU 49914
Jacob Lake, 13.6 km N IMNH (UI 169)*
Jacob Lake, 17.6 km E UMMZ 223401
Kachina Village, 0.8 km S UMMZ 218924
Kaibab National Forest UU 130–33*, 197*, 640*, 459–60*, 8017*
Kaibab Plateau BYU 8049, USNM 44629, 79954
Kaibab Plateau, Quaking Aspen Spring, 12.8 km E USNM 71238
Kehl Ridge, south of Long Valley (Photo voucher)
Parks, 8 km N UMMZ 223399
Rim Road and AZ 260, 5.9 km W UAZ 36005
San Francisco Peaks CAS-SU 6505, RRM 2269–72, 2274, 2305, UAZ 851, 856, 1974, 50858, UMMZ 74033, 79195, 214418, USNM 15799–813, 16198, 222978
Sitgreaves National Forest, Chevelon Butte, ca. 5.6 km S UNSM 15738*
Sitgreaves National Forest, Hart Canyon, SE of UNSM 15739–41*
Stoneman Lake USNM 59835
Vail Lake and Lake Mary, between CU 3168
Williams CU 3066, USNM 73748
Williams, 3.2 km N UAZ 1978
Williams, 4 km S BYU 49538*, 49540*
Williams, 9.6 km W TNHC 7439
Williams, 16 km W MVZ 8689

Arizona: Gila Co:
Globe, 16 km S UAZ 854*
Miami UMMZ 85014, 91968
Mount Ord (Photo voucher)
Payson UAZ 860, 37475*
Payson, 41.6 km NE KU 21934, 22230
Payson, 48 km NE UAZ 17947*, 20904–12*
Pinal Mountains, north slope UAZ 844*, 1982*
Pine BYU 2372–73, 2897, UMMZ 133976
Roosevelt UAZ 859*
Roosevelt, 12.8 km NW UAZ 848*
Roosevelt Reservoir USNM 104287–91*
Sierra Ancha CAS 80648
Sierra Ancha, Aztec Peak UAZ 849*
Sierra Ancha, Workman Creek MVZ 6307
Young, 36.8 km NW CAS 81523

Arizona: Graham Co:
Black River, at Whites Crossing UAZ 44756
Pinaleno Mountains, south slope on Shake Trail UAZ 4317*
San Carlos Indian Reservation, Ash Flat USNM 54589
San Carlos Indian Reservation, Chiricahua Ranch USNM 54590
San Carlos Indian Reservation, Point of Pines UAZ 39647
Santa Teresa Mountains, Mount Turnbull USNM 54610
Santa Teresa Mountains, Blue Ridge UAZ 35761–62
Stanley (historical) in Squaw Canyon MVZ 12885

Arizona: Greenlee Co:
AZ 75 and US 191, 52 km N UAZ 42659*
Bear Mountain MSB 20969, 20971
Bitter Creek, N of Duncan UAZ 42660–61*
Black Jack Canyon, on AZ 78 UAZ 36543*
Blue, 14.4 km S SIUC 12 (2)
Blue Mountains, Largo Creek MSB 20964
Blue Mountains, Telephone Ridge MSB 20966, 20968
Blue River, central segment UAZ 47435*
Clifton, 29 km N UAZ 35269*
Clifton, 64 km NNW UAZ 855*, 857*
Duncan, 9.6 km SE NMSU 4653
Granville, 3.2 km S UMMZ 121725 (2)
Hannagan Meadow, 4.8 km S UAZ 39648*
Morenci, 16 km N, 0.4 km W UAZ 4250*
Rose Peak UAZ 2100*, 2105*
Strayhorse Spring, 6.4 km NE Rose Peak UAZ 1985*

Arizona: Maricopa Co:
Alchesay Canyon UAZ 43169*
Cave Creek KU 11302

Arizona: Mohave Co:
Cerbat Mountains, 20 km NNW Kingman (Buus, 1983)
Chloride, 3.8 km N, 2.7 km E RWA 5026
Diamond Butte, 4.8 km S MPM 25476*
Hualapai Mountains USNM 60184–87*
Hualapai Mountains, Dean Peak BYU 49535–37*
Hualapai Mountains, east slope at Cedar (historical) UAZ 40623*
Hualapai Mountains, Flag Mine UTEP 13883
Hualapai Peak UAZ 20200, 20223, MVZ 16022
June Tank, 1.6 km W on Mount Trumball Loop UAZ 19119–20*
Kingman, 29.6 km E UMMZ 223403
Mount Trumbull USNM 44631, 44636
Mount Trumbull, 11.2 km N USNM 44630
Music Mountains, 67 km NNE Kingman (Buus, 1983)
Poverty Knoll, north of UAZ 20210*
Poverty Mountain, northwest of UAZ 20259*
Shivwits Plateau, Dome Sawmill UNLV 1330
Shivwits Plateau, Twin Point UNLV 1329
Snap Point, 5 km SE LACM 136194

Arizona: Navajo Co:
Cibeque, 16 km NW MCZ 101047–48*
Cibeque, 22.4 km NW MCZ 131037–38*
Fort Apache USNM 8255*, 8257*, 8575*, 293387*
Fort Apache Indian Reservation, 3.2 km N Chuck Box Lake UAZ 36007*
Gentry Lookout, 0.4 km E on Mogollon Rim Road UAZ 36006
Heber, 1.6 km E UMMZ 79196
Joe Tank Road and AZ 260 UAZ 36008
Lake of the Woods CU3552
Show Low, 4.8 km S UAZ 39651*
Show Low, 6.4 km N UAZ 1986
Show Low, 24 km E UCM 6504
Snowflake MPM 1637–38*
Snowflake, 10.7 km S UMMZ 124601 (2)
Whiteriver, 0.8 km N UAZ 1980, 1988

Arizona: Pima Co:
Davidson Canyon, east of Mount Fagan UAZ 42494*
Gardner Canyon Road, 9.6 km N on AZ 83 UAZ 50005*
Rincon Mountains AMNH 2557–58, CAS 33827–31, UAZ 1973*, 1977*, 11243*, 11245*, USNM 39311–12*, 48549*
Santa Catalina Mountains KU 126984, UAZ 872*, 2096*, 14947–49*, 31566–68*, 32289*, 33804*, 34563–64*, 40773*, 40794*, USNM 47937*
Santa Catalina Mountains, Bear Canyon Campground UAZ 30339*
Santa Catalina Mountains, General Hitchcock Campground UTEP 12156
Santa Catalina Mountains, General Hitchcock Tree UAZ 1975*
Santa Catalina Mountains, Mount Bigelow UAZ 46415*
Santa Catalina Mountains, Mount Bigelow Lookout Tower UAZ 25489*
Santa Catalina Mountains, Mount Lemmon CAS 34691–700, 34715–21, CAS-SU 10039–40, CU 7855 (8), KU 6965–66, RRM 2107, UAZ 852*, 1989*, 40796*, 40995*
Santa Catalina Mountains, 4 km N Palisade Ranger Station UAZ 49283–86*
Santa Catalina Mountains, Soldiers Camp UMMZ 72621
Santa Catalina Mountains, near Summerhaven UAZ 845*, 850*, 1987*, 14946*
Santa Catalina Mountains, Summerhaven, 0.4 km N FWM 6841
Santa Catalina Mountains, Summerhaven, 1.6 km E UAZ 25487*
Santa Catalina Mountains, Summerhaven, 2.2 km W RRM 2115, 2205, 2231
Santa Rita Mountains, Florida Canyon UAZ 2104*
Sonoita, ca. 9.6 km N on Empire Ranch Road UAZ 49996*
Tucson, 16 km E UF 78841
Whetstone Mountains, Bear Spring Canyon UAZ 51719*

Arizona: Pinal Co:
Galiuro Mountains, Oak Grove Canyon UAZ 43857*
Oracle UAZ 56628*
Oracle, 8–9.6 km SE (Gloyd, 1937)
Oracle, 12.8 km S UMMZ 69747
Superior, 9.6 km NE UAZ 46944–45*

Arizona: Santa Cruz Co:
Canelo, 5.1 km NW UAZ 50566–67*
Canelo Hills, 4.6 km S Canelo UAZ 48637*
Canelo Hills, 8.9 km S Sonoita UAZ 33174*
Canelo Hills, 17.9 km S Sonoita UAZ 11216*
Elgin, 8 km SE UCM 61034*
Elgin, 14.4 km S UTEP 12355
Fort Buchanan (historical) USNM 5272, 293317–21*
Pajarito Mountains, on Summit Motorway UAZ 873*
Pajarito Mountains, Sycamore Canyon UAZ 4232–33*, 4256*, 11239*
Patagonia, hill near Adobe Canyon UAZ 39641*
Patagonia, near Red Mountain UAZ 1979*
Patagonia, 20 km SE on FR 58 UTEP 12356
Patagonia Mountains, FR 61, 0.8 km SE FR 128 UAZ 52301*
Pena Blanca Lake, east side UAZ 47450*
Ruby UAZ 39640, UMMZ 91610
Santa Rita Mountains CAS 48849–50, 48852–58, 65890
Santa Rita Mountains, Florida Canyon UAZ 866*, 49282*
Santa Rita Mountains, Gardner Canyon UAZ 40787–88*, 49288*
Santa Rita Mountains, Josephine Saddle UAZ 33175*
Santa Rita Mountains, Madera Canyon LACM 4341, MVZ 80247, UAZ 853*, 1990*, 40789*, UMMZ 86065, USNM 61385–86*, 61454*
Santa Rita Mountains, Mount Wrightson Saddle AMNH 64334–35
Santa Rita Mountains, Mount Wrightson MCZ 32126*, UAZ 35059*
Sonoita, 4 km W, 1.9 km N UAZ 34672*

Sonoita, 8 km SW UAZ 2097*
Sycamore Canyon UMMZ 105658 (2)

Arizona: Yavapai Co:
Ash Fork ANSP 21219
Ash Fork, 16 km W UAZ 39652*
Bradshaw Mountains, Crown King UAZ 37477*
Bradshaw Mountains, south slope at Milk Creek UAZ 2099*
Camp Verde USNM 14816*, 24580–81*, 293447–49*,
Chino Valley, 4 km NW NMSU 2537–40
Cottonwood KU 61495
Fort Whipple USNM 11857–58*, 11862*, 293411–35*
Fort Whipple, 4.8 km N USNM 54584–86*
Mayer, Big Bug Creek UMMZ 105766
Mayer, Orme Ranch CAS-SU 22077
Mingus Mountain UAZ 31418–19*, UF 1211, USNM 59836–37*
Montezuma Well, 2.5 km SW on Beaver Creek Road UAZ 55988*
Mount Hope, 19.2 km N KU 20150–55
Oak Creek Canyon, Manzanita Camp MVZ 59443
Pine Flat, southwest of Mayer (Photo voucher)
Prescott FMNH 94950*, LACM 8558, USNM 15738*, 38555*, 56833–35*
Prescott, 4.8 km N KU 22799
Prescott, Buckman Spring Canyon UAZ 846*
Prescott, 14.4 km S UAZ 4674*
Seligman USNM 39048*
Seligman, 41.6 km S UMMZ 105737
Weaver Mountains USNM 252897–98*
Yarnell, 1.6 km S MVZ 66772

Colorado: Dolores Co:
Cahone, 46.9 km E UCM 19692

Colorado: Mesa Co:
Gateway, 22.4 km N DSC 1151
Piñon Mesa, Mud Spring UCM 21535–37
Piñon Mesa, 3.2 km S Mud Spring UCM 21538
Uncompahgre Plateau, Big Dominguez Creek USNM 40143
Uncompahgre Plateau, Spring Basin UCM 51309

New Mexico: Bernalillo Co:
Barton MSB 82954
Juan Tomas, 9.6 km S on NM 217 MSB 11384, 11417
Manzano Mountains MSB 4344
Manzano Mountains, Cedro Canyon MSB 5, 95–6, 98, 1250, 1346
Manzano Mountains, NE Miera MSB 4343
Pa-ako Ruins, ca. 4.8 km N San Antonito MSB 1239
San Antonito MSB 12901
San Antonito, 11.2 km E MSB 1355
Sandia Crest MSB 16482
Sandia Mountains MSB 1243, 11200
Sandia Mountains, SE slope MSB 1238
Sandia Mountains, Cienega Canyon MSB 2, 1344–45
Sandia Mountains, Sulfur Canyon MSB 124
Sandia Mountains, near Tree Spring MSB 8427
Sandia Park MSB 1268
Sandia Park, 8.2 km NW LACM 19703–04

Sandia Rim MSB 1247
South Sandia Peak MSB 1244, 1246
South Sandia Peak, trail to MSB 1245
Tijeras MSB 10970, 11014–15, 11386
Tijeras, 12.8 km S MSB 10560
West Mesa, South Volcano Cone NMSU 2050
Zamora Road, 3.2 km from US 66 MSB 11388–89

New Mexico: Catron Co:
Alma, 6.4 km ENE at Silver Creek Divide NMSU 5468
Arizona–New Mexico line, 10.9 km SE by US 60 UAZ 39406*
Black Range, at Wall Lake MSB 7160
Blue River at confluence with Dry Blue Creek MSB 20962
Datil MSB 82674
Datil, 1.6 km E MSB 10209
Datil, 3.2 km SW MSB 10210
Datil, 9.6 km SW MSB 4337, 6376
Datil, NW at Swingle Canyon CAS-SU 10840
Datil, at White House Canyon CAS-SU 10845
Deloche Trail, 0.3 km E on NM 78 MSB 26402
Elk Mountains USNM 47085*
Elk Mountains, SW USNM 47086*
Forest Cabin MSB 23133
Gila River, west fork FMNH 29448*, 29491–94*
Glenwood, 8 km NE MVZ 42575
Glenwood, 14.4 km S UMMZ 75700
Glenwood, NE on Deloche Trail MSB 26401
Glenwood, E at Whitewater Canyon MSB 6516
Glenwood, 49.6 km E at Willow Creek Campground SRSU 684
Howard Flat, near Datil CAS–SU 10841–42
Little Creek Trail MSB 41599–600
Luna, 4.8 km W MSB 38884
Luna, 11.2 km S MSB 32255
Luna, 11.7 km N, 2.2 km SE UAZ 35064*
Luna, 11.7 km N, 2.4 km SE UAZ 36066*
Luna, 16.3 km NE, 1.7 km N UAZ 36067–68*
Luna, 41.6 km N UMMZ 79198 (3)
McKenna Park airport NMSU 4615
McKenna Spring, 4.8 km SE MSB 41605
Mimbres Mountains, Big Rocky USNM 47089*
Mogollon, 5.7 km NE MSB 26395
Mogollon, 12.8 km N KU 6544
Mogollon, 16 km N KU 6546
Mogollon, 16 km E UTEP 6254
Mogollon, 56 km NE CU 3760
Negrito Creek USNM 47084*
Old Datil and Medley Tank, between CAS-SU 10844
Old Horse Springs MSB 6375, OSUS 1140
Old Horse Springs, 9.6 km WSW at Patterson Lake MSB 1257
Pine Park, near Datil CAS–SU 10843
Pueblo Park, 1.6 km NE MSB 1258
Quemado USNM 44701
Quemado, 17.6 km S on NM 32 MSB 44387
Red Hill, 4.2 km E ANSP 31250
Red Hill, 8 km N UTA 30810*
Reserve FMNH 38201–03*

Reserve, 4.8 km NE MSB 43402, 63061
Reserve, 8 km NE MSB 6122
Reserve, 16 km SW FMNH 51820*, 51823–30*
Reserve, 16 km WSW FMNH 51821–22*
San Francisco Mountains, 8 km N, 4.8 km W US 180 and NM 12 UAZ 39489*
Snow Lake NMSU 5586
Snow Park NMSU 4614
Trechado, S RWA 3249 (HERN?)
West Baldy Peak NMSU 4650
White Creek NMSU 4616, 4651
White Creek at confluence with Gila River MSB 41612
Willow Creek FMNH 29447*
Willow Creek Ranger Station, 1.9 km SW LACM 101545–47
Whitewater Baldy, at summit FMNH 29449*

New Mexico: Eddy Co:
Klondike Gap UTA 35468

New Mexico: Grant Co:
Bayard NMSU 4634, 4640, 4644, 4646
Big Burro Mountains, 2.7 km SW FR 851 and Mangas Valley Road MSB 62808
Black Range, near McKnight Fire Cabin ANSP 21115
Cherry Creek Campground, 3.2 km S MSB 26403
Cherry Creek Campground, 4 km S MSB 26404
Cliff, 3.2 km S NMSU 4641
Fort Bayard, 3.2 km NE NMSU 4630
Gila Wilderness, 11 km N of NM 35 on NM 15 UAZ 34526*
Hanover, 3.2 km NE UTEP 1977
Mangas Springs, 3.2 km N MSB 14204
Mimbres, 19.2 km N MSB 1240
Mogollon Creek near Fall Canyon NMSU 4637
Mule Creek, 4.8 km W on NM 78 LACM 123341
Mule Creek, 7.2 km S, 0.8 km E MSB 38922
Pinos Altos NMSU 4618
Pinos Altos, 2.4 km W NMSU 4633
Pinos Altos, 8 km W NMSU 4632
Pinos Altos, 8 km N NMSU 4519
Pinos Altos, 14.4 km N UMMZ 78223 (2)
Pinos Altos Range, 9.6 km N, 4.8 km E MSB 42882
Rice Ranch, 1.6 km N, 0.8 km E NMSU 5307
San Lorenzo, 4.8 km E NMSU 4647
Santa Rita (= Santa Rita del Cobre, historical), 20.8 km NE NMSU 4628, 4638
Santa Rita del Cobre (32° 48' 13" N, 108° 03' 39" W) USNM 58389
Sawyer’s Rock, 20 km W NMSU 4972
Silver City ANSP 17486, KU 15516–18, MVZ 42567–70, NMSU 3802, 4617, 4619, 4621, 4624–27, 4636, 4645, 4648, USNM 48491*, UTEP 8992
Silver City, 1.6 km W MVZ 42572
Silver City, 3.2 km N NMSU 4629
Silver City, 4 km N NMSU 4518
Silver City, 6.4 km N NMSU 4642–43
Silver City, 3.2 km S, 8 km W MSB 42878
Silver City, 8 km N NMSU 4635
Silver City, 8 km NE NMSU 4620
Silver City, 9.6 km N NMSU 4631
Silver City, 11.2 km N MVZ 42573
Silver City, 11.2 km E, 3.2 km N MSB 42879

Silver City, 15.2 km NW NMSU 4622
Silver City, 16 km N NMSU 4639
Silver City, 16 km SW NMSU 3702
Silver City, 19.2 km NNW USNM 160406–08*
Silver City, 19.2 km WNW MVZ 42574
Silver City, 30.4 km SW NMSU 4623
Silver City, 38.4 km NE at Meadow Creek NMSU 4649
Silver City, 40 km N UTA 7736*
Tyrone, 3.2 km S, 9.6 km W MSB 42880

New Mexico: Hidalgo Co:
Animas, 36 km S NMSU 2052
Animas, 40 km S, 4.8 km E LACM 101539–41
Animas, 56.3 km S MSB 42881
Animas Peak, 3.6 km E, 9.2 km N MSB 36736
Animas Valley, west side at Clanton Draw MSB 6898
Animas Valley, Cowan Ranch MSB 32295
Animas Valley, Gray Ranch MSB 57523
Animas Valley, Indian Creek UTA 2163*
Animas Valley, McKinney Flats MSB 72845–46, 72890
Cloverdale, 3.2 km N LACM 4342
Cloverdale, 3 km NW MSB 43682
Cloverdale, 8 km NW NMSU 4652
Cloverdale, 11.2 km E NMSU 1502
Guadalupe Mountains, SW of Cloverdale MSB 4339
Indian Creek Canyon MSB 13626
Rodeo, 11.2 km SSE AMNH 84594
Rodeo, 1.6 km E, 6.4 km N MVZ 67183

New Mexico: Lincoln Co:
Alto TNHC 70978, 70980–81
Alto, 0.8 km W LACM 4346
Alto, W at Oak Grove Campground FWM 6383, UTEP 6475
Alto, 3.2 km W MSB 6726
Alto, 4.8 km W FWM 6401
Alto, 8 km W MSB 7495–96
Alto Mountain, Montgomery Reserve Station ASNHC 5764, 5804, 5806, 5879–80, NMSU 5515
Argentina Canyon MSB 57024
Bonito Creek UMMZ 67663
Bonito Creek–Eagle Creek Divide NMSU 0343–45
Bonito Lake UTEP 11137
Capitan RWA 2241
Capitan, 3.2 km E, 6.4 km N MSB 39679
Capitan, 12.3 km S MSB 49115
Capitan Mountains, Baca Campground MSB 22489
Lincoln, 6.4 km NW UMMZ 82022
Ramon, 16.8 km N MSB 30296
Ruidoso KU 28071, UMMZ 123545 (2), USNM 32992
Ruidoso, S of USNM 32991
Ruidoso, 3.2 km E MVZ 37005
Ruidoso, 3.2 km NW KU 61491
Ruidoso, 8 km ENE KU 61492–93
Ruidoso Junction TNHC 1174, 1176–77
Sacramento Mountains, White Mountain Park Trail MSB 6010, 6012
Sierra Blanca, Nogal Canyon, 7 mi. SSW UMMZ 121701

Sierra Blanca, Nogal Peak ANSP 21338
Sierra Blanca, north slope KU 77810
Sierra Blanca Peak, 3.2 km N MSB 7497
Sierra Blanca Peak, 3.2 km N, 4.8 km E NMSU 1507–09
Sierra Blanca, Rio Ruidoso CU 6086
Sierra Blanca, Ski Apache AMNH 109088

New Mexico: Los Alamos Co:
Bandelier National Monument, 8 km NW exit on NM 4 MSB 26393
Sandia Canyon, lower end MSB 36444

New Mexico: Luna Co:
Hermanas, 0.8 km W MSB 60799
Mimbres Valley near Cookes Peak ANSP 21118

New Mexico: Otero Co:
Cathey Peak, 0.4 km S, 4.8 km E MSB 41206
Cloudcroft AMNH 505, 60050, 63910, ANSP 15185–86, 15188–90, 15192–94, 17489–90, CU 5877, LACM 19700–01, MSB 1352, MVZ 49830, NMSU 342, TNHC 7255–61, 7433–34, 11839, UAHC 51-45, 51-46, UMMZ 64713 A–E, 64714 (2), 65184, UTEP 1723
Cloudcroft, at Wofford Lookout AMNH 84154, MES 372
Cloudcroft, 1.6 km E CU 5105
Cloudcroft, 1.6 km ESE LACM 19699, 101542–44
Cloudcroft, 1.6 km S MSB 6727–30
Cloudcroft, 2.4 km NE UMMZ 136024
Cloudcroft, 3.2 km N, 3.2 km E UTEP 1515
Cloudcroft, 3.2 km ESE TNHC 11824, 11834–38
Cloudcroft, 3.2 km NE UMMZ 121702
Cloudcroft, 4.8 km E CU 5104
Cloudcroft, 5.6 km S MSB 48985
Cloudcroft, 6.4 km NNW LACM 4343
Cloudcroft, 6.4 km N Fir Camp NMSU 05188
Cloudcroft, 8 km S UTEP 6996
Cloudcroft, 8 km NE MSB 48755
Cloudcroft, 9.6 km NNE NMSU 72
Cloudcroft, 9.9 km NE MSB 48742
Cloudcroft, 10.4 km S UTEP 6995
Cloudcroft, 10.9 km E LACM 19702
Cloudcroft, 11.2 km E MSB 4338
Cloudcroft, 12 km S MSB 48987
Cloudcroft, 16 km N MPM 25835*
Cloudcroft, 23.2 km S MSB 48988
Cloudcroft, 26.4 km S MSB 48986
Cloudcroft, 32 km SE USNM 32990
High Rolls ANSP 15175, 15191
High Rolls, 3.2 km NW TNHC 11842
High Rolls, 4 km S NMSU 3247
Hubbell Canyon TU 18649, 18830, UNSM 16788*
James Canyon, near Mayhill ANSP 15176
Lightning Lake, 5.6 km E TAIC 1711
Mescalero MCZ 15892*, USNM 25433–34
Mountain Park, 1.6 km E OSUS 1491
Peake Canyon MSB 489984
Sacramento ASNHC 4734
Sacramento Mountains NMSU 586
Sacramento Mountains, 3.2 km S FR 64 on FR 537

Sacramento Mountains, 26 km E, 13.6 km S Alamogordo ENMU 2674–76
Sacramento Mountains, 29 km E, 15.2 km S Alamogordo ENMU 2665–70, 2672–73
Sunspot, 12.8 km SE MSB 48743

New Mexico: Rio Arriba Co:
Abiquiu USNM 293374
Arroyo Jaspe MSB 32469
Broke Off Mountain, at summit MSB 15958–59
Burford Lake (= Stinking Lake) USNM 312997*
Canjilon Ranger Station MVZ 25219
Carson National Forest, near Jawbone Mountain UMMZ 121483
Carson National Forest, Lower Canjilon Lake MSB 56331
Cerro Pedernal, SE of summit (Photo voucher)
Cerro Pedernal, SW slope (Photo voucher)
Chama, 5 mi. N MSB 10953–54
Chama, 16.8 km E MSB 4197
Chama, 18.4 km NE MVZ 57675–76
Chama Canyon, 23.4 km N, 5.1 km W Abiquiu MSB 23091
Coyote, 3.2 km S, 3.2 km W KU 33642
El Rito, 6.4 km N KU 11300–01, 11303–04
Gallina, 4 km NW (Photo voucher)
Lagunitas Lakes ENMU 3692
Poso Spring, NNW (Photo voucher)
Truchas, 6 km N UTA 276

New Mexico: San Miguel Co:
Gallinas Canyon MSB 1348
Pecos USNM 32989*
Pecos, 5.7 km N LACM 19705–06
Sapello Canyon ANSP 14865–66, 15691

New Mexico: Sandoval Co:
Bandelier National Monument, Frijoles Mesa MSB 30660
Bland, 9.6 km NW MVZ 57681
Cochiti Canyon MSB 12089
Jemez Mountains, east slope at Pajarito Ruins LACM 19685
Jemez Mountains, 19 km NW Santo Domingo Pueblo UTEP 9615
La Cueva, SE MSB 33748
Placitas, 1.6 km W, 1.6 km S MSB 26231
Placitas, 6.4 km E, above Sandia Cave MSB 12695
San Antonio Creek, 1.6 km N NM 126 on FR 376 MSB 54821
Sandia Cave MSB 26139
Sandia Mountains, west slope (Juan Tabo–La Cueva) TU 20701

New Mexico: Santa Fe Co:
Cundiyo MSB 4334
Frijoles Canyon MSB 91
Glorieta FWM 5231, LSUS 5160, MSB 83–5, USNM 32988*
Glorieta, 0.8 km E MSB 7051
Golden, 1.6 km N MSB 32932
Otowi LACM 196684
Santa Fe KU 6967, 11305–07, MCZ 161078–79
Santa Fe, 8 km S MSB 1242

New Mexico: Sierra–Grant Co:
Mimbres Mountains, at Emory Pass AMNH 75555, ANSP 19683

New Mexico: Sierra Co:
Black Range UTEP 43
Black Range, Lookout Mountain MSB 4341
Black Range, 8.8 km N, 32 km W Winston USNM 311166*
Mimbres Mountains, 1.6 km SE Emory Pass MSB 8983
Hillsboro, 0.8 km S NMSU 6668
Hillsboro, 5.6 km E MSB 71726
Palomas Creek LACM 19682
Palomas Creek at confluence with Highland Creek LACM 19683
Truth or Consequences, 9.6 km N, 24 km W MSB 60140

New Mexico: Socorro Co:
Alamosa Creek, near Wildhorse Canyon MSB 51813
Magdalena Mountains, Kelly CAS–SU 3711–13, MCZ 62286
Magdalena Mountains, Water Canyon MSB 7050, 8618, 26082, 52149, USNM 320240*
Magdalena Mountains, north of Water Canyon MSB 4347
Monticello, 14.4 km N, 17.6 km E MSB 47358
No specific locality KU 17820–21
Rio Salado, 4 km W, 10 km S of Ladron Peak MSB 36735
San Mateo Mountains, Bear Trap Canyon LACM 4345–46, MSB 4346
San Mateo Mountains, 2.2 km NW Horse Mountain MSB 73300
San Mateo Mountains, Luna Park Campground USNM 320241–43*
San Mateo Mountains, San Mateo Peak USNM 44569–70
San Mateo Mountains, Springtime Canyon MES 373, MSB 11008
San Mateo Mountains, 1.5 km N, 2.6 km E Vicks Peak RRM 2360
Socorro, 16 km W BYU 40071
Socorro, 32 km SW CU 5690

New Mexico: Taos Co:
Taos OMNH 25215
Taos, 6.4 km S CU 5106

New Mexico: Torrance Co:
Edgewood, 4.8 km SW MSB 55906
Manzano Mountains, Capilla Peak AMNH 111149, MSB 165, UMMZ 123547
Manzano Mountains, 3.3 km S, 3.1 km W Manzano RRM 2315
Manzano Mountains, 3.3 km S, 3.8 km W Manzano RRM 2318
Manzano Mountains, 1.9 km S, 6.9 km W Manzano MSB 10248, 13925
Manzano Mountains, 8 km WNW Manzano MSB 6865, 6868, UMMZ 121698
Manzano Mountains, 9.6 km SSW Manzano TU 17107–08
Manzano Mountains, Fourth of July Canyon MSB 34223
Manzano Mountains, in Tajique Canyon, 4.8 km W Tajique MSB 50272

Texas: Culberson Co:
Guadalupe Mountains, rim between Dog Canyon and West Dog Canyon TNHC 70988
Guadalupe Mountains, east of Lost Peak TNHC 70987
Guadalupe Mountains, 0.3 km W Hunter Peak MSB 66895
Guadalupe Mountains, Pine Top TNHC 70985
Guadalupe Mountains, The Bowl SRSU 869, TNHC 16285, 20186, TNHC 70983–70984
Guadalupe Mountains, West Dog Canyon KU 61494, TNHC 70986, 70989

Texas: Jeff Davis Co:
Davis Mountains, Indian Hill, 1.9 km WSW of Mount Locke SRSU 722

Davis Mountains, west of Madera Canyon (Photo voucher)
Davis Mountains, Mount Locke MVZ 68220
Davis Mountains, 6.4 km ESE TX 118 on Madera Canyon Crossing, FWM 5533
Davis Mountains, 13.9 km S TX 118 & 166, on TX 118 TAIC 4668
Davis Mountains, between TX 17 an TX 166 MSB 61423–24
Davis Mountains State Park UTEP 3048
Davis Mountains State Park, near head of Limpia Creek SRSU 2447–48
Fort Davis CAS–SU 9840
L. E. Wood Picnic Area, 1.9 km E on TX 118 UTA 42524*

Utah: Garfield Co:
Bryce Canyon BYU 8055*, 11982*, 14782* DSC 484, 539, MVZ 44867, UU 1838
Escalante Mountains, 11.2 km E Widtsoe Junction MVZ 12879
Escalante Mountains, 2.1 km N Jct. FS 17 & 140 (Photo voucher)
Henry Mountains BYU 16668, UU 141, 302–05
Henry Mountains, 3.2 km SW Mount Ellen UU 3285
Mammoth Creek, southwest of Hatch CAS–SU 7773
Starr Springs BYU 12622
Starr Springs, 1.6 km W at Henry Mountains BYU 11738–39
Table Cliff Plateau BYU 201, 1101, 1104–07

Utah: Grand Co:
Pace Lake, 2 mi. N UCM 5192–93

Utah: Iron Co:
Bear Valley, west of Bear Valley Junction (= Orton) CAS–SU 7767, LACM 101551
Brian Head, south of Parowan USNM 45195–96*
Cedar Breaks National Monument INHS 8306
Cedar Mountain RJC 1–4, 6–8
Hurricane Cliffs, southwest end (Photo voucher)
Three Creeks, west of Bear Valley Junction AMNH 22868–70
Webster Flat BYU 49544
Webster Flat and Cedar Breaks National Monument, between BYU 4785*, 11311, 11323

Utah: Kane Co:
Alton, 6.4 km SE MVZ 49829
Dry Valley UMMZ 73402 (3)
Duck Creek BYU 49551*, UMMZ 73405 (2)
Duck Creek and Cedar Mountain, between UU 1700–05
Kanab UAZ 2012*
Mill Creek, 9.6 km N Skutumpah Road UAZ 26971*
Navajo Lake LACM 101553, UMMZ 122922
Orderville BYU 2185, 2821
Orderville, 22.4 km N BYU 8050
Paria, 8 km WNW BYU 11231
Sink Valley, south of Alton UU 1677

Utah: Millard Co:
Pavant Range, E of Fillmore UMMZ 70637

Utah: San Juan Co:
Abajo Mountains, Camp Jackson UU 2860
Blanding, 15.5 km N CAS 203875
Blanding, 56 km NW UU 2830
Elk Ridge, ca. 32 km WNW Blanding LACM 25386
Elk Ridge, on Round Mountain MSB 21943

La Sal BYU 11362
La Sal, 8 km NW UMMZ 68532
La Sal, 8–9.6 km NW UMMZ 68531
La Sal, 16 km NW UMMZ 68530
La Sal, east slope La Sal Mountains BYU 8015, 8017
Monticello AMNH 62112
Monticello, 24 km N UTA 30812
Monticello, 32 km N UTA 30811
Natural Bridges National Monument (Photo voucher)

Utah: Sanpete Co:
San Pitch Mountains, Maple Canyon UMMZ 64684 (6), UU 7983–84

Utah: Sevier Co:
Fish Lake BYU 11221
Willow Creek, E slope of Pavant Range UMMZ 101454

Utah: Washington Co:
Blue Spring, west of Anderson Junction AMNH 22862
Kolob Plateau AMNH 22865–67
Lower Kolob Plateau LACM 101556
Zion Canyon (Woodbury, 1928).

Phrynosoma hernandesi ornatum

United States
Idaho: Cassia Co:
Trout Creek Mountain, NW slope (T. Jezkova, unpublished data)

Idaho: Owyhee Co:
Bruneau, 24 km S TCWC 57850
Jordan Valley Road, 53–63 km WSW ID 51 UTA 14249–53
Juniper Lake Basin and South Fork Owyhee River, between MVZ 24507
Nevada state line, 11.2 km N, near Little Owyhee River MVZ 24509–10
Nevada state line, 16 km N, near Little Owyhee River MVZ 24517
Nevada state line, 17.6 km N, near Little Owyhee River MVZ 24508
Riddle (T. Jezkova, unpublished data)
Squaw Creek, lower segment ca. 10.2 km SSE of Marsing UAZ 1992
Three Creek, 6.9 km NNW (T. Jezkova, unpublished data)

Nevada: Elko Co:
Bull Run Mountains USNM 44816*
Carlin UMMZ 43849–62, 43863–70, USNM 45291*
Cobb Creek BYU 5817*
Cobre BYU 5816*
Currie, 1.6 km S UMMZ 85017
Currie, 9.6 km SSW RRM 2414–15, 2472
Currie, 11.2 km S RRM 2419, 2438, 2471
Deeth CAS–SU 6300–04
Deeth, 35.2 km N MVZ 18447–49
Elko, 16 km S LACM 126909
Elko, 78 km N (T. Jezkova, unpubl. data)
Elko, 96 km N (Photo voucher)
Halleck USNM 44819–21*
Halleck, 4.8 km S USNM 71187*

Jackpot, 14.4 km W RRM 2417
Jackpot, 20.8 km S RRM 2421, 2473
Jackpot, 69 km SW RRM 2416
Jarbidge UNR 244
Jerry Creek, north end of Ruby Mountains MVZ 11979
Midas, 62.4 km W Tuscarora ANSP 26076
Mountain City USNM 44822–23*
Mountain City, 9.6 km SW MVZ 18450, BYU 5817*
Pequop Summit, 9.6 km NE UNR 7609
Shafter Siding, 4.3 km NE UMMZ 91837
Snow Water Lake (T. Jezkova unpubl. data)
Wells, 68.8 km S UAZ 32430*

Nevada: Eureka Co:
Austin, 56 km E FMNH 26043*
Eureka, 11.2 km W FMNH 26277*
Eureka, 59.2 km NW at Coils Creek MVZ 61809
Lone Mountain, east of UMMZ 85016

Nevada: Humboldt Co:
Disaster Peak USNM 53041
Humboldt River ANSP 8683
Jackson Mountains (T. Jezkova, unpublished data)
Owyhee Desert (T. Jezkova, unpublished data)
Paradise Valley, 24 km N UNR 3044, 3046, BYU 5814–15*
Paradise Valley, 27.2 km N MVZ 18451
Granite Peak, Santa Rosa Mountains MVZ 88525

Nevada: Lander Co:
Austin, 11.2 km NE UNR 7597
Austin, 48 km E FMNH 26042*

Nevada: Lincoln Co:
Cave Valley (T. Jezkova, unpublished data)
Lake Valley (T. Jezkova, unpublished data)
White Rock Mountains RJC 5

Nevada: Nye Co:
Monitor Range, Dobbin Basin MVZ 61810
Monitor Range, Long Canyon UNR 7612
Potts (historical), 17.5 km ENE BYU 5818*

Nevada: Washoe Co:
Wadsworth UU 175

Nevada: White Pine Co:
Ely BYU 18173–74, 18254
Ely, 12 km W MVZ 80248
Ely, 48 km N BYU 5820*
Hamilton (historical) CAS 139474
Hamlin Valley (T. Jezkova, unpublished data)
Harbecke Ranch, 1.6 km W (T. Jezkova, unpublished data)
Hobson (historical) BYU 5819*
Illipah Reservoir (T. Jezkova, unpublished data)
Lake Valley (T. Jezkova, unpublished data)
Lund, 12.8 km N MVZ 14232

Lusetti Canyon (T. Jezkova, unpublished data)
McGill, 4 km N UNLV 4004
Spring Valley (T. Jezkova, unpublished data)
Steptoe Valley BYU 5800*
Steptoe Valley, west side UMMZ 86121
Steptoe Valley and Cave Valley, between UMMZ 91838

Oregon: Malheur Co:
Blue Mountain Pass (Photo voucher)
Chicken Spring (Photo voucher)
Lookout Lake (Photo voucher)
Mud Spring PSM 10420–21
Mud Spring, 0.4 km S CAS 249834
Trout Creek Road, 5 km NW Turner Ranch Road (Photo voucher)
Upper Tenmile Reservoir (Photo voucher)

Utah: Beaver Co:
Beaver USNM 8652*, 293388*
Milford BYU 23581

Utah: Cache Co:
Dry Canyon, at mouth CAS 228879

Utah: Iron Co:
Cedar City, west at Dry Lake KU 20675
Kanarraville, 4.8 km S LACM 101552

Utah: Juab Co:
Eureka BYU 8874, 32064, 32070
Fish Springs BYU 11979

Utah: Millard Co:
Cove Creek, 8.8 km SSE Black Rock USNM 8088*
Cove Fort BYU 8034
Fillmore, 1.6–3.2 km E UMMZ 70635
Fillmore, 4.8 km SE UMMZ 70638 (2), 70639 (2)
Fillmore, 5.6 km E UMMZ 70636
Hinckley BYU 22158–59
Desert Range Experimental Station, west of Milford BYU 4331

Utah: Salt Lake Co:
Emigration Canyon LACM 111234 (xHERN?)
Emigration Canyon, at mouth UU 1351*, 2265*
Emigration Canyon, 1.6 km W UU 2846*
Fort Douglas BYU 2095, 2097, 2778, CAS 14153, 14155–58, 14493–94, 27156–58, 30930–32, 38764, UU 374*, 1356*, 1968–70*, 2306*, 3166*
Great Salt Lake, near shore UMMZ 59558–60
Midvale UMMZ 59554, 59557 (8), 59569–70
Saltair, near UMMZ 59553, 59555 (4), 59556 (3), 59567–68, 59571–72
Salt Lake City ANSP 21111, BYU 11973–76, OMNH 30207, USNM 42113, 60925–73, UU 125–29*, 3375*, 8012*, 8056*
Salt Lake City, west of UMMZ 59562–63
Salt Lake City, north of UMMZ 59565
Salt Lake City and Great Salt Lake, between UMMZ 59561, 59594
Salt Lake City and Saltair, between UMMZ 59564
Salt Lake City, 16 km SE UMMZ 75702–04

Salt Lake City, 22.4 km W LACM 113454
Sandy UMMZ 75701

Utah: Sanpete Co:
Ephraim UU 372*
Fairview BYU 2859
Indianola BYU 8032, 14788

Utah: Tooele Co:
Delle KU 56094
Dugway Proving Ground BYU 14841–42
Grantsville BYU 49545–50*
Grantsville, 3.2 km W LACM 111228, 113429–30, 113434–48
Grantsville, 6.4 km NW USNM 132009–10*
Ibapah, 9.6 km N UMMZ 91862
Orr's Ranch, 4 km S BYU 44330–31
Rush Valley BYU 12711
Skull Valley UMMZ 69470
Stansbury Mountains AMNH 69881–82
Stansbury Mountains, near BYU 11977–78
St. John Station LACM 111229–33, 113449–53
Tooele, 3.2 km S LACM 101554–55
Tooele Canyon (= Middle Canyon?) UU 205–06*
Tooele Valley UU 368*, 8011*

Utah: Utah Co:
Alpine Valley UU 369*
Cedar Fort BYU 32069, USNM 44762–63*
Chimney Rock Pass, NW of Elberta BYU 8063, 16688
Hobble Creek Canyon, east of Springville BYU 13132
Lehi, west of BYU 2786
Mount Timpanogos BYU 8051–53
Payson BYU 8031
Provo BYU 3356, 8062, 22822*, UU 371*
Provo, west of BYU 42364
Saratoga Springs, 8 km SW BYU 15091
Springville CAS 47903
Squaw Mountain, northeast of Provo BYU 3238–39
Utah Lake, east shore DSC 1147
Utah Lake, west shore BYU 37194, UU 2263*
West Mountain, north of Santaquin BYU 32044

Utah: Washington Co:
Beaver Dam Mountains BYU 37195
Enterprise DSC 1910
Enterprise, west of BYU 8056–57

Phrynosoma ornatissimum

United States
New Mexico: Bernalillo Co:
Albuquerque CAS–SU 5069, 5070–72, 5074–75, 5076, 5103–04, 5107, 6079, 6093, 6106, 6111, 7774, FMNH 1644, LACM 4349–50, MPM 238, MSB 50, 142, 1251, 1339, 1341–43, 1349–51, 5425, 7048–49, 8426, 10878, 11030, 11068, 11287, 11336, 11426, 11464, 12229, 12591, 12844, 12974, 13173, 16815–16, 16878–80, 17071, 17840, 19987, 22379, 23284, 26048, 38816,

41323, MVZ 5358–61, NMSU 4516, 4517, RRM 2206, 2209, 2211, 2212, 2232, 2304, 2306, 2339, 2359, UMMZ 133205, 173656–60, OMNH 30705, 30770, USNM 58420–21
Albuquerque, E of MSB 1249, 1338
Albuquerque, 4.8 km S US 66 and Volcano Road MSB 15109
Albuquerque, East Mesa MSB 192
Albuquerque, 4.8 km E, 6.4 km N MSB 4364
Albuquerque, 32 km E USNM 201
Albuquerque, 32 km NW at Rio Puerco Valley MSB 1241
Albuquerque, SW NMSU 2051
Carrizal, near Sandia Mountains CAS-SU 5049, 5051
Interstate 40 and 25, 6.4 km S, 6.2 km W RRM 2428
Manzano Mountains, west slope in Arroyo del Coyote MSB 11501
Rio Grande Valley, 5.7 km W, 7.7 km S of Interstate 40 and 25 RRM 2468
Sandia Peak Aerial Tramway, 0.8 km ESE MSB 10929
San Antonito, 11.2 km E MSB 1353, 1354, 1356, 1357
South Sandia Peak, west of MSB 1248
Tijeras Canyon MSB 13096
Tijeras Canyon Front Road and Four Hills Road, 1.6 km W MSB 26295
West Mesa MSB 19335–36
West Mesa, 1.6 km S, 1.6 km E South Volcano Cone CWU 252
West Mesa, at The Volcanoes MSB 19337

New Mexico: Catron Co:
Ake Ranch, southwest of Magdalena NMSU 1510
Magdalena, 64 km SW PAM 31

New Mexico: Chaves Co:
Tatum, 46.4 km W, 20 km N MSB 71945

New Mexico: Cibola Co:
Bernalillo County line, 16 km W on Interstate 40 RRM 2234

New Mexico: Guadalupe Co:
Vaughn MSB 1347
Vaughn, 0.8 km S NMSU 2049
Vaughn, 4.8 km S MSB 19985

New Mexico: Hidalgo Co:
Cotton City, 17.4 km N on NM 338 NMSU 5479
Lordsburg, 22.4 km W on salt flats OMNH 30746

New Mexico: Lincoln Co:
Carrizozo UMMZ 67852 A–H, 67854–57, UNLV 7235
Carrizozo, 1.6 km S UNLV 306
Carrizozo, 2 km N UNLV 305
Carrizozo, 6.4 km S MSB 30297
Carrizozo, 28.8 km N UTEP 3438
Carrizozo Malpais, N edge at R. M. Shafer Ranch RRM 2590
Corona LACM 4347
Lincoln–DeBaca County line, 0.3 km NW MSB 60681

New Mexico: Otero Co:
Cornudas Mountains, 9.6 km W Alamo Mountain UMMZ 71036
Hudspeth County line, 2.1 km N on Pinon Road UTEP 11138
Orogrande, 22.4 km ESE UTEP 4429
Orogrande, 32 km ENE UTEP 4420

Paxton Siding, 25 km E on NM 506 NMSU 6563
Wind Mountain A. H. Price (personal communication)

New Mexico: Rio Arriba Co:
Abiquiu USNM 8451

New Mexico: San Miguel Co:
San Miguel County line, 3.2 km N on NM 3 MSB 52869

New Mexico: Sandoval Co:
Jemez Canyon Dam, 3.2 km S MSB 19986

New Mexico: Santa Fe Co:
Interstate 25, 8 km S on NM 14 MSB 16598
La Bajada, 3.2 km E MSB 36448
Santa Fe, 12.8 km SW KU 11288–97
Santa Fe, 22.4 km SW MSB 175
Stanley MSB 17701–02, RRM 2338
Torrance County line, just west, near Interstate 40 MSB 23577
Torrance County line, 3.2 km N on NM 41 MSB 23578

New Mexico: Socorro Co:
Abeytas, 16 km W MSB 4853–54
Bernardo (Photo voucher)
Bingham, 10.4 km N LACM 62556
Bingham, 25.6 km E, 16 km S NMSU 5686
Blue Spring, 4.5 km NW on NM 47 UMMZ 133206
Carrizozo, 43.2 km NNW UMMZ 121699
Chupadera Mesa LACM 19690–91
Chupadera Mesa, 4.8 km N Cooper's Well LACM 19686
Sevilleta National Wildlife Refuge MSB 50778, 55256, 61393
Sevilleta National Wildlife Refuge, Five Points Grassland MSB 55800, 58740, 58826
Sevilleta National Wildlife Refuge, Nunn Flat MSB 61063
Socorro, ca. 25.6 km S at White Sands Missile Range MSB 60919, 60931–32
White Store, 0.5 km NW on US 380 LACM 19687

New Mexico: Torrance Co:
Cedarvale MSB 1254–56
Encino, 3.2 km from FMNH 98394*, 106458–59*
Encino, 6.4 km E ENMU 138–40
Estancia, 16 km E MSB 26325
Interstate 40, 3.7 km E US 285 RRM 2262
Lobo Hill MSB 32086
Lucy, 6.4 km N LACM 4351–53
Lucy, 8 km E LACM 19697
Lucy, 15 km E LACM 19696
Moriarty RRM 2317
Moriarty, 12.8 km E LSU 86008
Mountainair, 3.2 km N UMMZ 121700
Mountainair, 8 km N, 5.6 km W ENMU 1727
Pedernal, 14.4 km WSW Encino UMMZ 67851 (4)
Pedernal, 3.2 km W LACM 19698
Torrance USNM 65832
Vaughn, 9.6 km W RWA 3248
Willard, 3.2 km W, 3.2 km N MSB 4342
Willard, 11.2 km E KU 189229

New Mexico: Valencia Co:
Belen, 13 km E of NM 47 MSB 61458
Belen, SE MSB 73125–26
Belen, 16 km SE RWA 1584
Belen, 20.8 km E, 3.2 km N MSB 32913
Los Lunas, 3.7 km W on NM 6 MSB 17144
Los Lunas, 8 km W on NM 6 MSB 19334
Los Lunas, 9.6 km W on NM 6 MSB 15369, 19333

Texas: El Paso Co:
Fort Bliss AMNH 28662, FMNH 383

Texas: Hudspeth Co:
El Paso, 59.2 km E on US 62 & 180 OMNH 30795
Hueco Mountains, east slope, ca. 11.2 to 14.4 km N US 62 & 180 RRM 2474, 2448–49, UTEP 11191, 17303

Phrynosoma ornatissimum brachycercum

Mexico
Chihuahua:
Chuhuichupa BYU 14502–03
Ciudad Chihuahua, 36 km SW MSB 32625
Ciudad Cuauhtémoc, near KU 188430–31
Ciudad Cuauhtémoc, east of BYU 14484
Ciudad Cuauhtémoc, 11.2 km WSW MVZ 67383
Ciudad Cuauhtémoc, 20.8 km E BYU 14484*, 15203, 15691
Ciudad Cuauhtémoc, 24 km E KU 188428–29
Colonia Juárez BYU 13508, 14333*, 15193–201, 15202*, 15750, 16966, 17110
El Gavilán, near UAZ 30978
General Trías MSB 33200, UAZ 34845
General Trías, 41 km WNW TCWC 35202
Gómez Farías, 25.1 km N UAZ 35021
Hidalgo del Parral, 30 km W MCZ 78546
La Junta, 3 km SW RRM 2103
Miñaca MCZ 16055
Ramos (= Rancho Ramos) MCZ 36888
San Buenaventura, 8 km S UAZ 34041
San Buenaventura, 16.8 km SW UAZ 35022
San Diego AMNH 558–59
San José de Babícora, 3.2 km SW KU 47414–25
Santa Bárbara AMNH 68229, 68271–74, 68964–68
Santo Tomas, 6.4 km S, 1.6 km W KU 45312–17
Sierra del Nido UTEP 2520–21
Sierra del Nido, west slope UTA 4544–45*
Sierra Mojina MVZ 89679
Temósachic UAZ 34846
Yepómera UAZ 33692, 33929–31, 34039, 34166–67, 34173–78, 34190, 34204–05, 34307–12, 34847–53, 35020
Yepómera, 3 km NW UAZ 34565

Durango:
Atotonilco UTEP 3641–42
Atotonilco, 2 km N MSU 10415
Boquilla, 6.4 km NNE MSU 732–33, 3153

Ciudad Durango UMMZ 46632
Ciudad Durango, 8 km N KU 28068
Ciudad Durango, 28 km S UTEP 9369
Hacienda El Chorro, 1.6 km N KU 39922–23
La Resolana, 1.6 km N LACM 101557
Mezquital, 24 km N MSU 4345–46

Zacatecas:
Fresnillo, 68.8 km W UMMZ 118569
La Ordeña (Smith & Flores–Villela, 1994)

Colorado Plateau (*Phrynosoma hernandesi* x *Phrynosoma ornatissimum*) hybrid zone

Arizona: Apache Co:
Adamana MVZ 9014–15, RRM 3298–99, USNM 82309
Chinle MCZ 9147, UF 23054–60
Chinle, 8 km SE USNM 44626
Chinle, 16 km NE USNM 60172
Chinle, 83.2 km S UF 23053
Chuska Mountains, 3.2 km NW of Indian Reservation Route 13 UAZ 25324
Chuska Mountains, 3.2 km N, 3.7 km E Tsaile Peak UAZ 33478
Concho, 16.6 km E UAZ 36012
Ganado FMNH 51831
Ganado, 6.4 km NW USNM 44627
Holbrook ANSP 19869
Holbrook, ca. 38.4 km SE on US 180 UAZ 51929
Holbrook, 41.4 km SE on US 180 UAZ 51930
Liittle Colorado River UMMZ 85018
Petrified Forest National Park, 16 km SSE UAHC 66-220
Sanders, 16 km S UCM 24268
Sanders, 19.2 km S UCM 24269
St. Johns MVZ 9018–27
St. Johns, 1.6 km W TNHC 7437
St. Johns, 6.4 km N UAZ 36011
St. Johns, 6.4 km S UCM 40852*
St. Johns, 9.6-12.8 km S MVZ 9016–17
St. Johns, 19.2 km S LACM 126931
St. Johns, 24 km S UCM 24270
St. Johns, 27.2 km N UCM 24271
Tsaile Lake Dam, 0.5 km SW UAZ 33632
Zuni River USNM 3219, 293248–49

Arizona: Coconino Co:
Black Tank Lava Beds MVZ 16023–24
Black Lava Beds USNM 15814
Deadman Flat MVZ 8668–70, UAZ 1976, 2101, UMMZ 74029–30
Deadman Flat, 20.8 km N MVZ 8671–72, 8688
Flagstaff, 40 km NE UMMZ 223395–96
Gray Mountain, 6.9 km S RRM 2106, 2147, 2268, 2326
Gray Mountain, 9.9 km S RRM 2122, 2167
Gray Mountain, 12.8 km S RRM 2263
Little Colorado River USNM 4580, 4599
Lockett Tank, 8 km W Tappan Spring USNM 60188–89, 60191–92
Meteor Crater LACM 101536, RRM 3297, UAZ 44548*
Meteor Crater, 5.1 km N, 1.7 km W LACM 121576

Painted Desert USNM 15815–19
Sunset Crater CU 5708, TNHC 11604
Sunset Crater, 0.9 km N RRM 2247
Sunset Crater, 8.3 km NW RRM 2265
The Gap, 8 km N MVZ 65809–10
Tuba City BYU 807, MVZ 17866–67, UAZ 871
Tuba City, 1.6 km S UU 1500, 2317
Winona, 0.8 km E UMMZ 74027 (3)
Winona, 1.6 km N USNM 60179
Winona, 4.3 km N, 7.2 km W RWA 4861
Winona, 4.8 km NW USNM 60177–78
Winslow, 14.4 km W RRM 2233
Winslow, 16 km W UNLV 2152
Wupatki National Monument UAZ 1984, UMMZ 223402

Arizona: Navajo Co:
Bidahochi MPM 1633–35
Black Mesa, at summit FMNH 23046
Hotevilla UAZ 1991
Joseph City BYU 12817
Kayenta MVZ 17868–69
Kayenta, 19.2 km SW at Marsh Pass FMNH 23044, 23047, UU 2170, 2362
Kayenta, 24 km SE UAZ 40038–39
Keams Canyon UAZ 39650
Kykotsmovi (= New Oraibi), 27.2 km ESE UAZ 862
Oraibi FMNH 51832–33, LACM 19672, MVZ 16025, UAZ 867–68, USNM 73749–51
Oraibi, south of RRM 3306
Polacca UAZ 28245
Seba Dalkai, 4.5 km E, 7.7 km S UTEP 12354
Shonto Canyon UU 2174
Skeleton Mesa, at summit FMNH 23557–58
Snowflake MPM 1637–38*
Snowflake, 10.7 km S UMMZ 124601 (2)
Toreva MPM 1630–32
Winslow FMNH 932, 218755, UAZ 39649
Winslow, 1.6 km W UMMZ 223404–05
Winslow, 1.6 km N UMMZ 74031
Winslow, 16 km SE UMMZ 223406
Winslow, 32 km NE MVZ 8932
Zilnez Mesa UU 2363

Colorado: Archuleta Co:
Chimney Rock summit, 4.1 km NW UTEP 2160
Chromo, 3.2 km N UCM 7271*
Pagosa Springs USNM 8443, 11964, 293351
Pagosa Springs, 32 km E MVZ 105115

Colorado: La Plata Co:
Durango UCM 51263
Durango, 6.4 km S RRM 3294
Durango, 6.4 km W UCM 51262
Durango, 19.2 km W LACM 101538
Florida USNM 35469
Perins Peak RRM 3293

Colorado: Montezuma Co:
Ackmen (historical), 4.8 km SW Pleasant View FMNH 29364–67
Ashbaugh's Ranch USNM 40138
Cortez UCM 51264–67
Cortez, 32 km S UCONN 2240
Mancos AMNH 13603, TNHC 11927
McElmo (Cary, 1911)
McPhee Reservoir, east of UCM 67317
Mesa Verde National Park UCM 7458
Mesa Verde National Park, at campground LACM 109550
Mesa Verde National Park, East Canyon UCM 32240–58
Mesa Verde National Park, near headquarters KU 105936
Mesa Verde National Park, 0.4 km NNW Middle Well KU 51491
Mesa Verde National Park, Moccasin Mesa, 6.4 km S north rim KU 105937
Mesa Verde National Park, Prater Canyon UCM 5591
Yellow Jacket UCM 10057

Colorado: San Miguel Co:
Big Gypsum Creek UCM 447 (2)

New Mexico: Cibola Co:
Blue Water Canyon MSB 11514
Blue Water Lake State Park MSB 47263, 61064
Casa Blanca, 0.8 km S Interstate 40 MSB 23285–86
Cerro Venada, 1.3 km ENE MSB 73121
El Morro National Monument (Inscription Rock) KU 11298–99, MSB 1237
Grants USNM 44805
Grants, 1.6 km SE NMSU 1511
Grants, 16 km S CU 5601A,B,C
Grants, south at lava beds USNM 44702
Grants, 48 km S, 9.6 km W at "Point of Malpais" MSB 4335
La Mosca Lookout on Mount Taylor CU 5453A, 5453B
McCarty's USNM 16000–01
Milan, 0.8 km W MSB 23096
Mount Sedgwick USNM 44566
Mount Taylor KU 28062
Ojo Redondo Canyon, SSW of Blue Water Lake CU 5707
Quemado, 41.6 km N MSB 15533
San Fidel Lake MSB 19984
San Mateo CAS-SU 5061, 5063
Schuman's Ranch, W of Cebollita Peak (34° 43' 5.9" N, 107° 55' 52.5" W) UMMZ 86617 (2)

New Mexico: McKinley Co:
Continental Divide AMNH 62853–54
Crownpoint, 8 km W MSB 32239
Fort Wingate MSB 52941, USNM 14396, 14408, 293444–45
Gallup CU 5841
Gallup, 16 km N TNHC 11654–55
Mexican Springs, 12.8 km E, 6.4 km S MSB 3238–39
Prewitt, 3.2 km S KU 28063
Seven Lakes CU 5620A–C
Thoreau, 3.2 km S MSB 13722
Thoreau, 9.6 km S CU 5103(2), 5119, 5233, 5447A–B, 5632, 5709, MSB 47197, 47238–39, 47258–59, UMMZ 121704
Thoreau, 12.8 km S KU 28061

New Mexico: Rio Arriba Co:
San Juan River, 6 km SE Allison MSB 2969
San Pedro Mountains USNM 58419
Southwest corner of Rio Arriba County UMMZ 97496 (2)

New Mexico: San Juan Co:
Aztec AMNH 9683, MSB 1340
Blanco MCZ 96057–59
Chaco Culture National Historic Park MCZ 161080–81, MSB 2972, 3390, 21715–18, 33349, UAZ 45830*
Chaco River, west of Burnham MSB 3195
Cottonwood Canyon near Navajo Lake MSB 2965
Farmington, 56 km S UMMZ 127847
Four Corners, 9.6 km E, 9.6 km S MSB 3240
Nageezi, 3.2 km NW MSB 4150
Navajo Lake, north shore, 4.8 km SE Allison MSB 2967
Pine River Road, SSW of Burnt Mesa MSB 2966
San Juan River, 7.4 km ESE Allison MSB 7386
San Juan River, at confluence with Los Pinos River MSB 7544–45
Sheep Springs, 22.7 km E MSB 60936

New Mexico: Sandoval Co:
Counselors, 4 km S, 1.6 km E MSB 60294
Cuba MPM 19987, 19992–94
Jemez Springs, 3.2 km N NMSU 4885
Porter, 1.6 km E FR 534 and 539 MSB 32470
Sierra Nacimiento UMMZ 97497

Utah: San Juan Co:
Navajo Mountain, 3.2 km SE at Dunn Trading Post MVZ 17870

Mountains–plains hybrid (*Phrynosoma hernandesi* x *Phrynosoma ornatissimum*) zones

New Mexico: Bernalillo Co:
Albuquerque KU 11308, USNM 58422
Albuquerque, NE on mesa RRM 2340
Manzano Mountains, Cedro Canyon MSB 97
Sandia Mountains, west foothills at "U" hill MSB 1259, 14435

New Mexico: Eddy Co:
Guadalupe Mountains USNM 32983
Guadalupe Mountains, Dark Canyon MSB 4340

New Mexico: Grant Co:
Santa Rita del Cobre (historical; 32° 48' 13" N, 108° 03' 39" W) UMMZ 55740

New Mexico: Lincoln Co:
Alto TNHC 70977, 70979
Capitan, 9.1 km NW MSB 22490
Capitan, 3.2 km E, 6.4 km N MSB 39680
Carrizozo UMMZ 67852 (2), 67857
Carrizozo UMMZ 67852 (3)
Carrizozo, 7.4 km E MSB 30294
Gallinas Peak (Photo voucher)

New Mexico: Otero Co:
Cloudcroft ANSP 15210

New Mexico: Santa Fe Co:
Santa Fe AMNH 112194, RRM 2343

New Mexico: Sandoval Co:
Placitas MSB 22139
Placitas, 6.4 km E MSB 12694
Sandoval County, SE corner on NM 14 MSB 26362

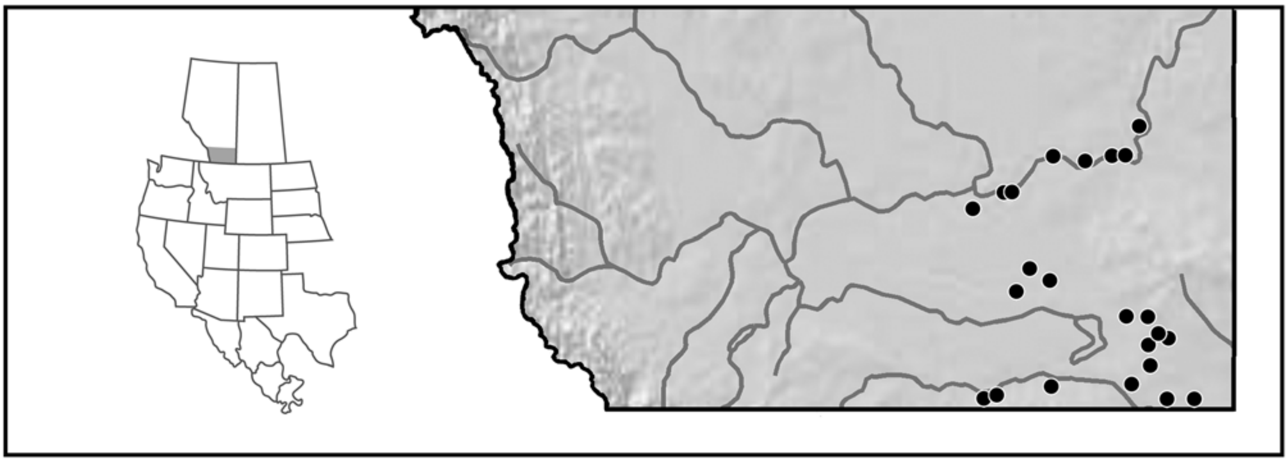
New Mexico: Sierra Co:
San Andres Mountains, Bear Den Canyon MSB 60489

New Mexico: Socorro Co:
Adobe Ranch, 0.4 km N LACM 19688
Augustine (historical; 34° 06' 48" N, 107° 40' 12" W) MSB 4348
Chicken Spring, 2.4 km E LACM 19689

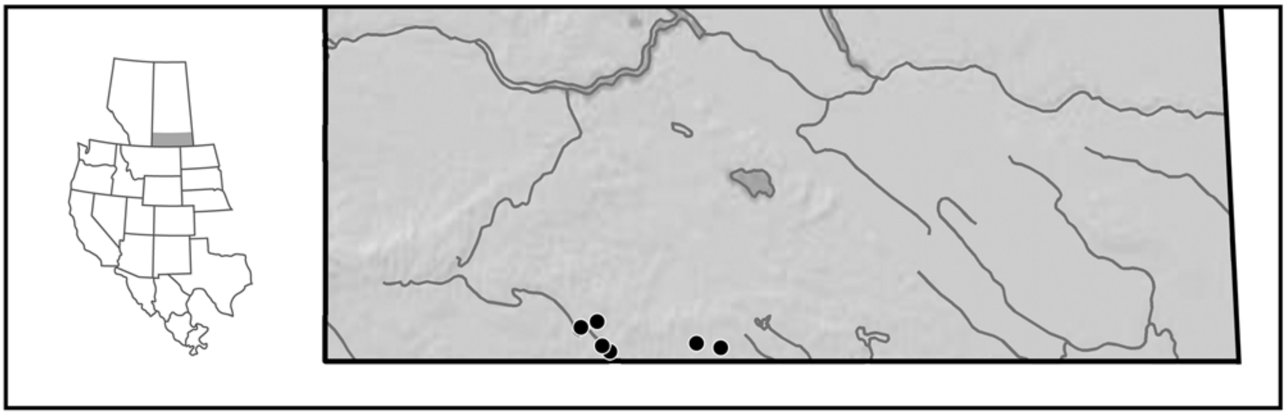
Texas: Culberson Co:
Guadalupe Mountains USNM 32984

Appendix II

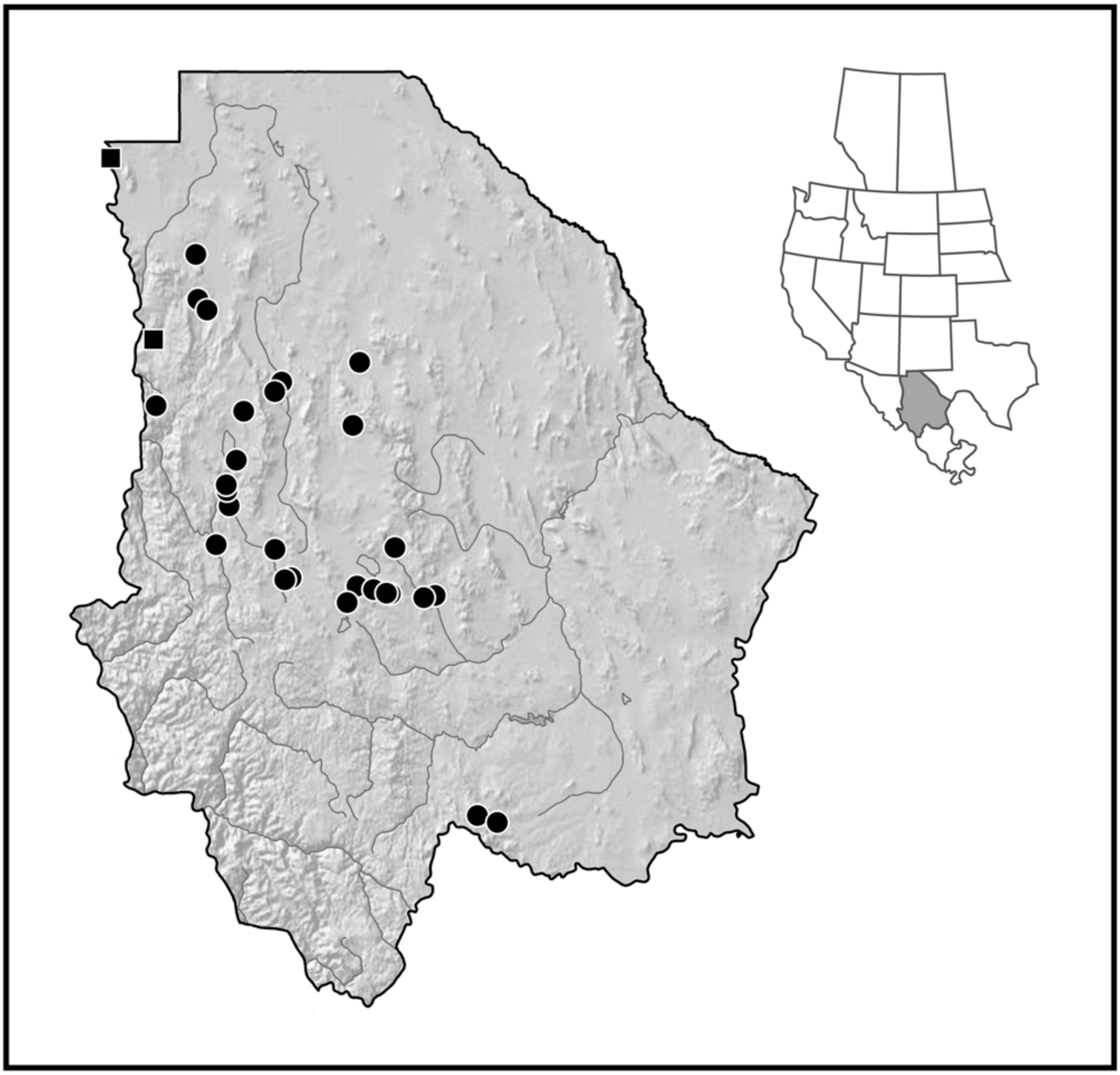
The distribution maps of the taxa belonging to the *Phrynosoma douglasii* (species complex) are presented for Canada, Mexico, and the United States in alphabetical sequence by country and state or province.



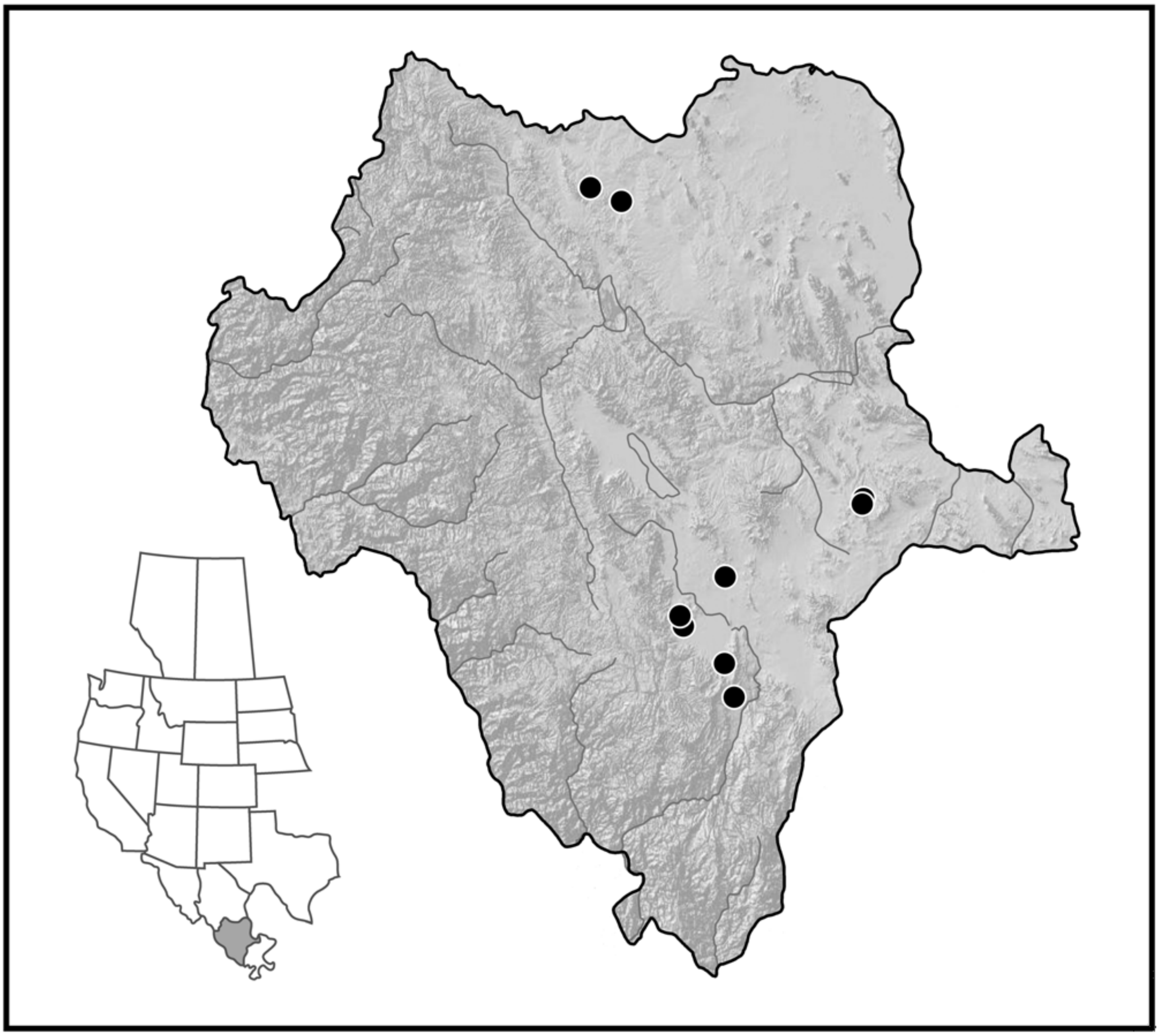
MAP 1. Locality records for *Phrynosoma brevirostris* in Alberta, Canada. Symbols represent multiple adjacent localities. See Powell & Russell (1998) for additional records on a micro-geographical scale.



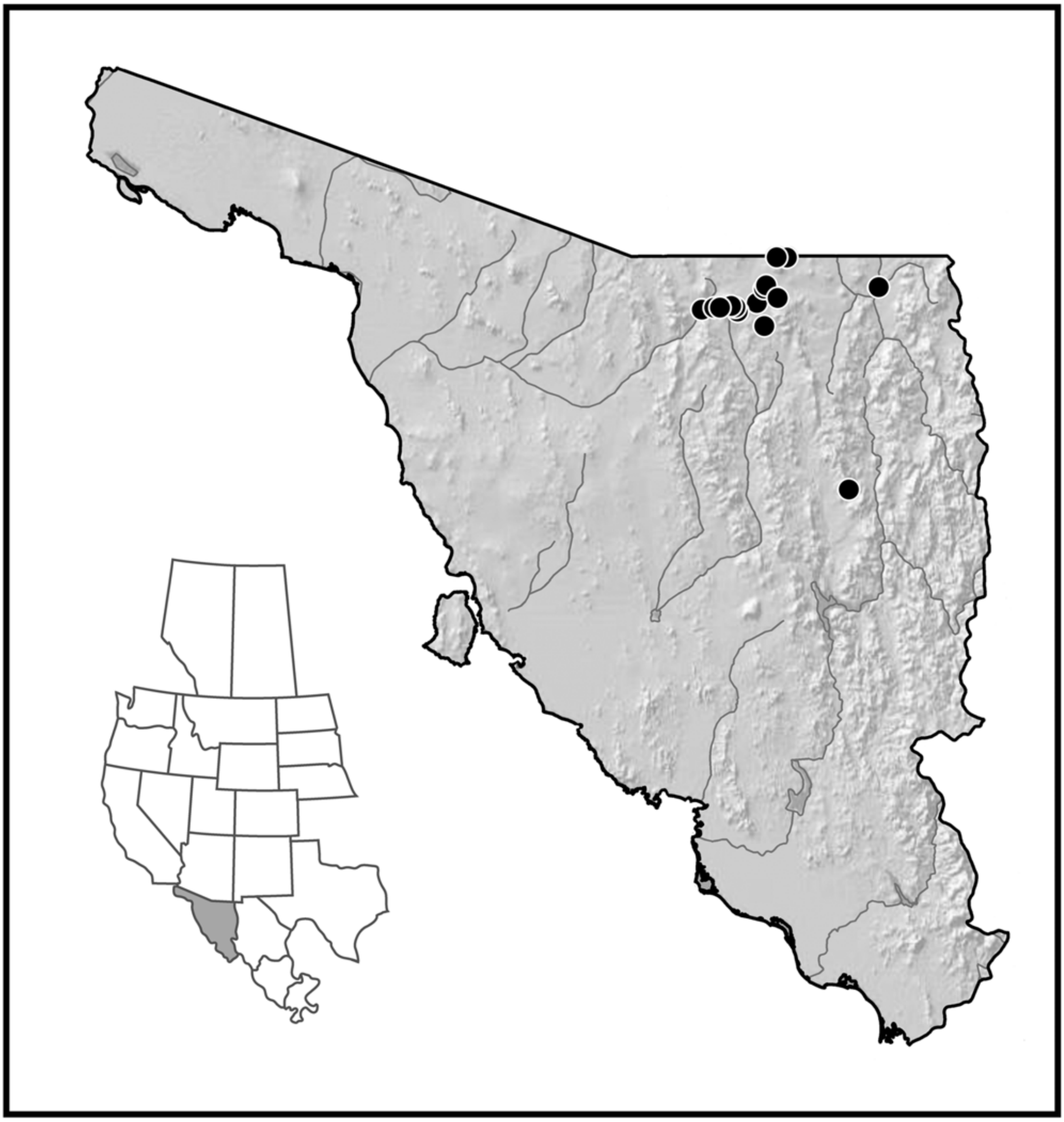
MAP 2. Locality records for *Phrynosoma brevirostris* in Saskatchewan, Canada. Symbols represent multiple adjacent localities. See Powell *et al.* (1998) for the micro-geographical distribution along Frenchman River and Butte Creek and Rock Creek coulees.



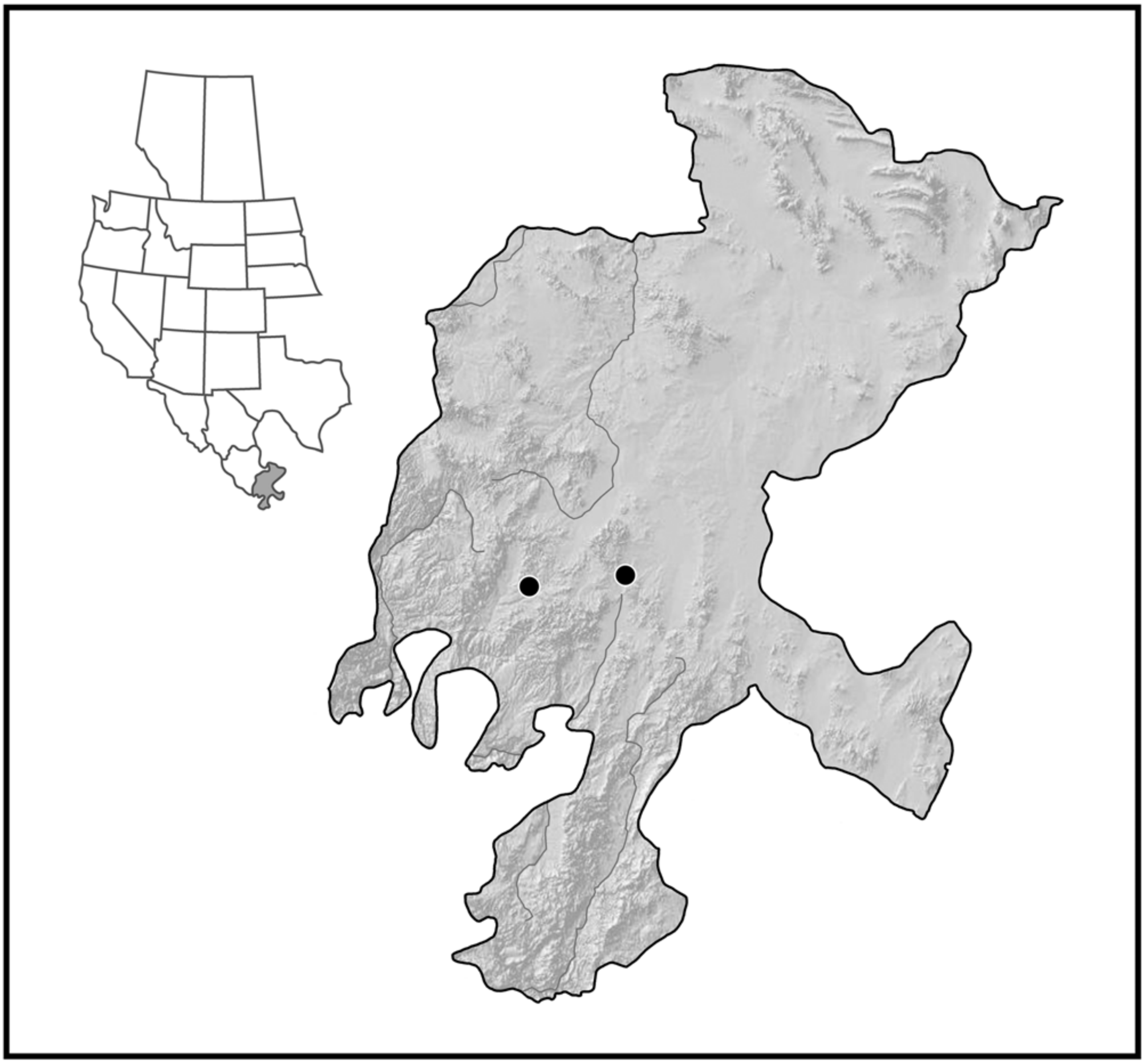
MAP 3. Locality records for *Phrynosoma hernandesi* (squares) and *P. o. brachycercum* (circles) in the state of Chihuahua, Mexico.



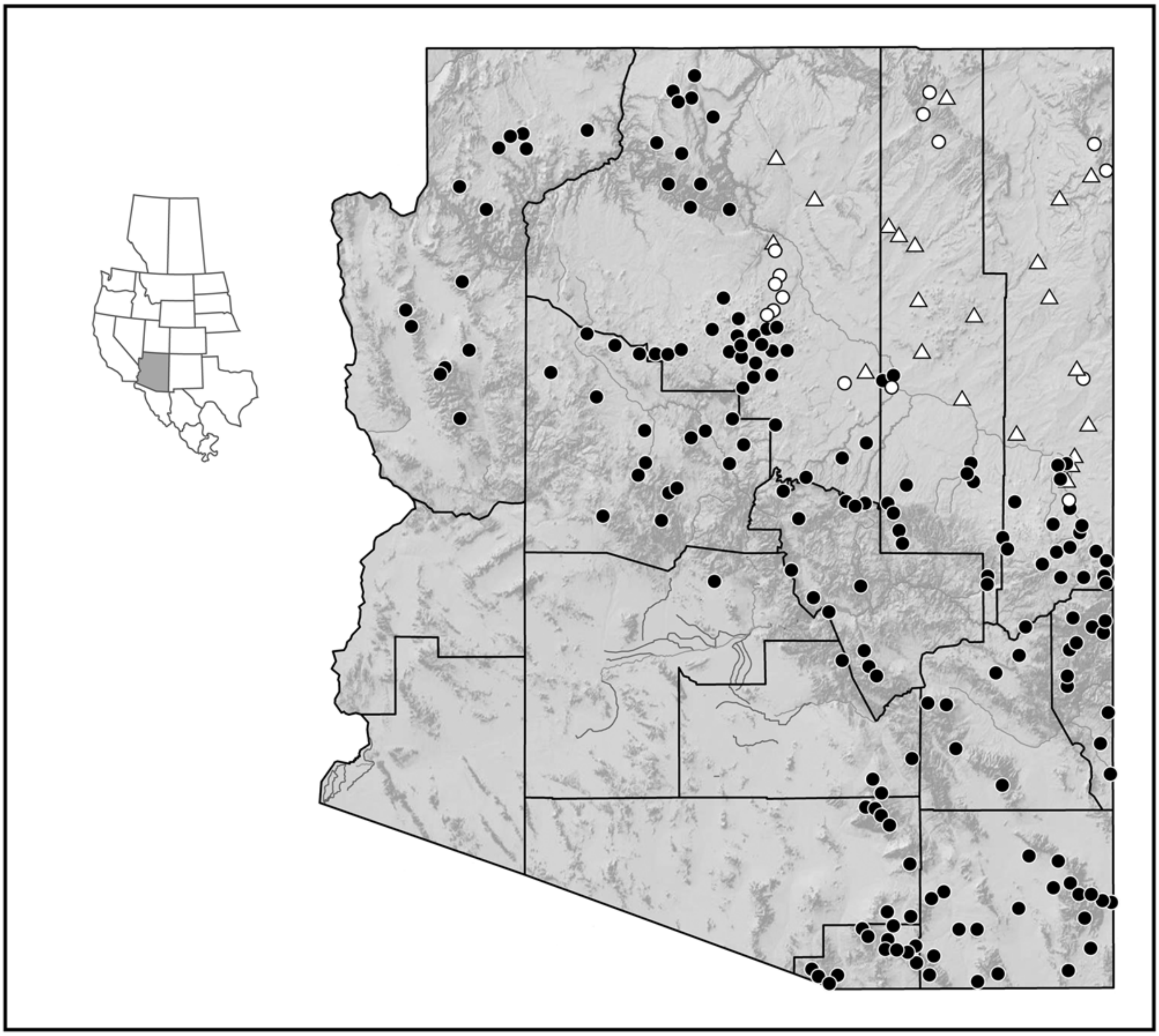
MAP 4. The distribution of *Phrynosoma ornatissimum brachycercum* in the state of Durango, Mexico.



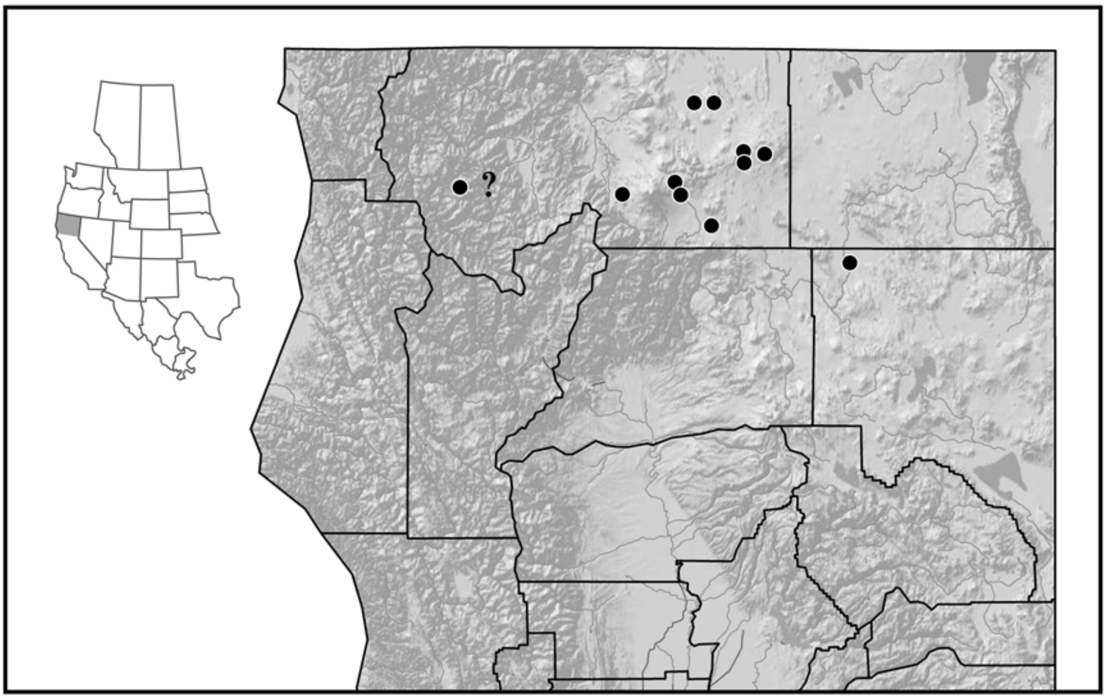
MAP 5. The distribution of *Phrynosoma hernandesi* in the state of Sonora, Mexico.



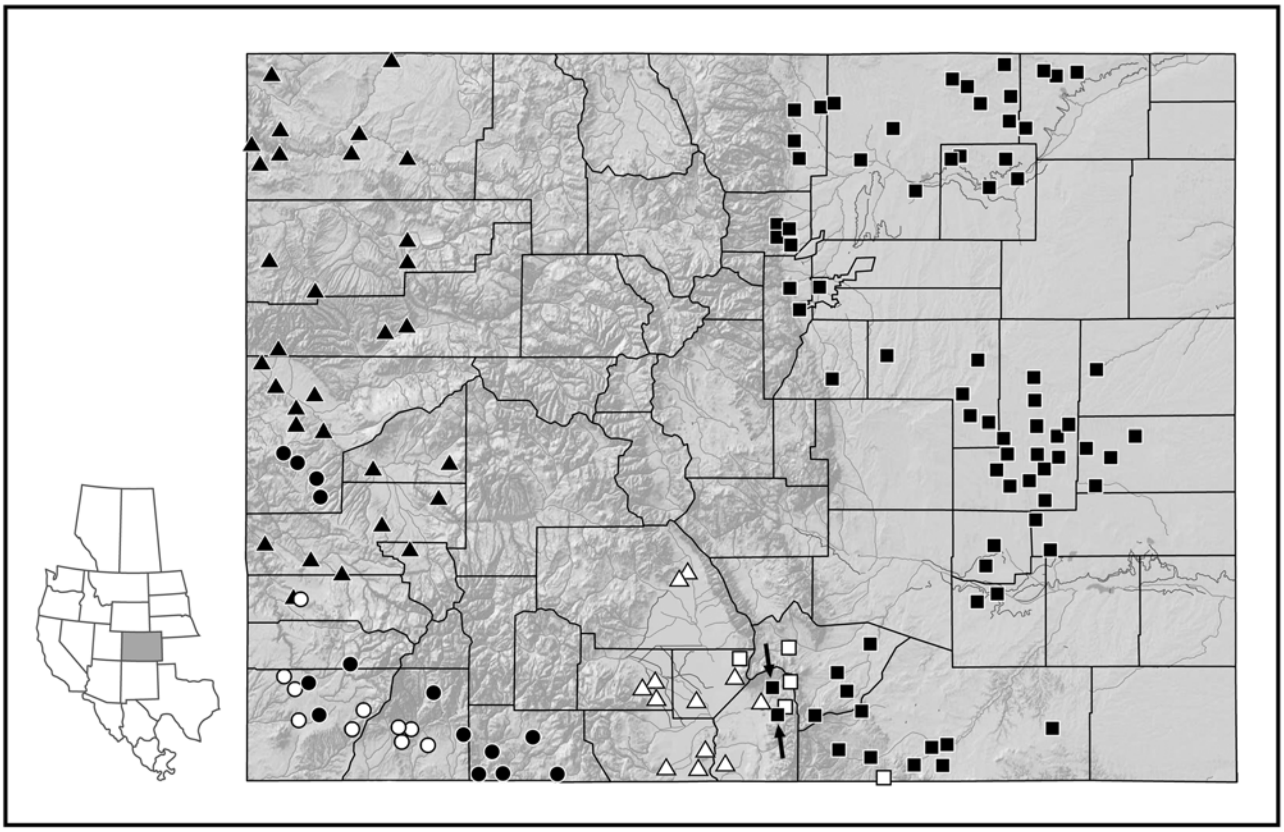
MAP 6. Locality records for *Phrynosoma ornatissimum brachycercum* in the state of Zacatecas, Mexico.



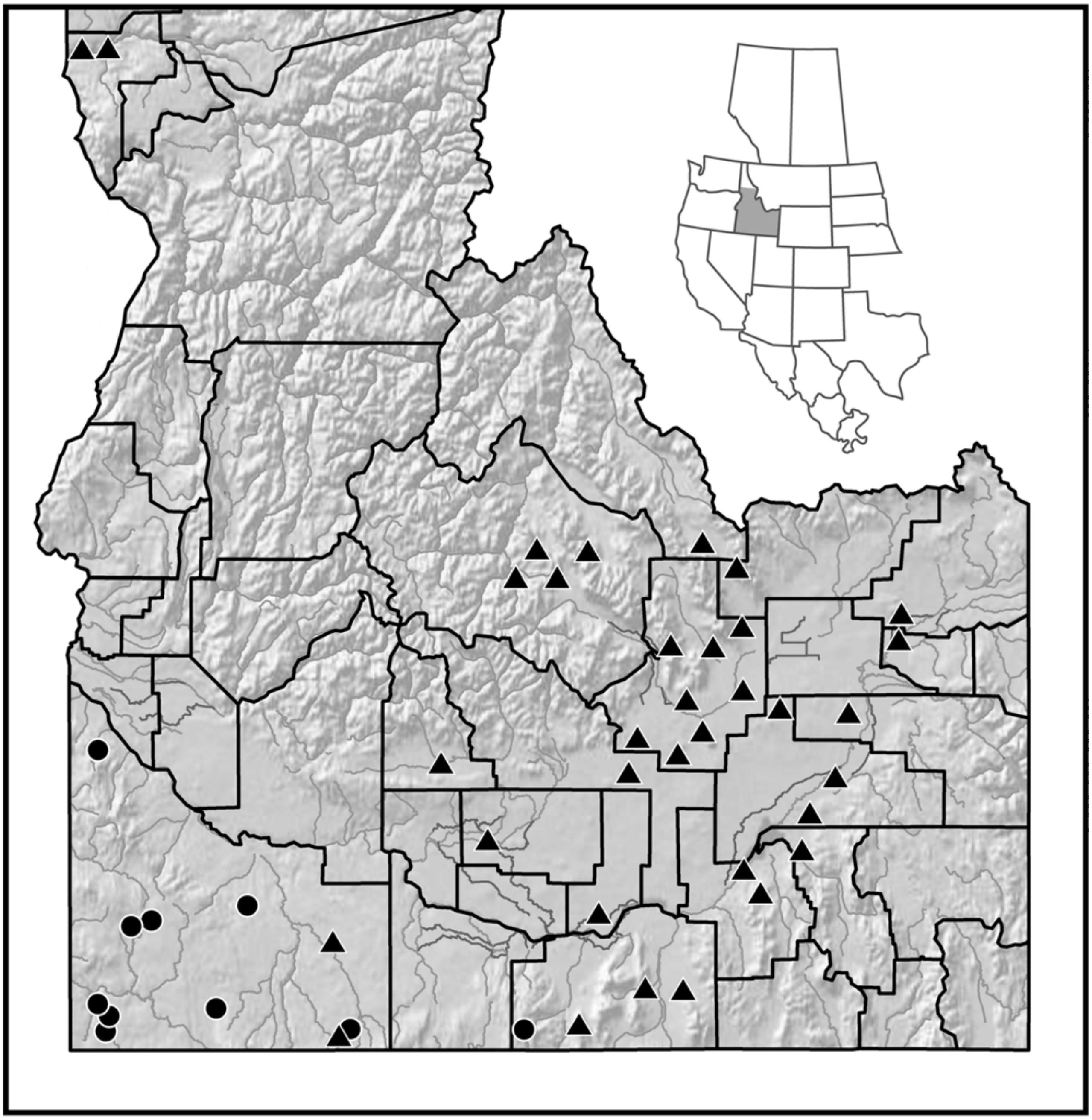
MAP 7. The distributions of short-horned lizards in Arizona, showing localities for *Phrynosoma hernandesi* (solid circles), hybrids (*P. hernandesi* x *P. ornatissimum*) morphologically similar to *P. hernandesi* (open circles), and intermediate hybrids and hybrids morphologically similar to *P. ornatissimum* (open triangles).



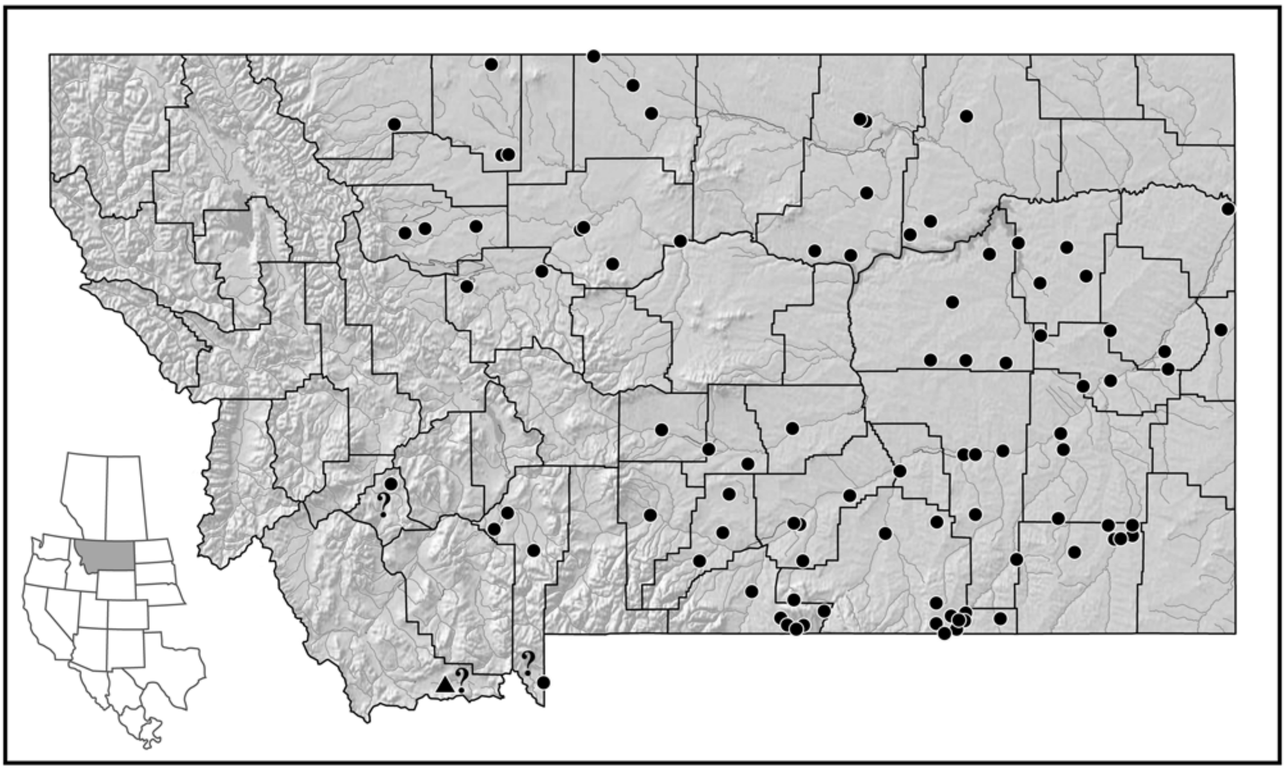
MAP 8. The distribution of *Phrynosoma douglasii* in northern California. The correct location of Clear Lake in the Klamath Mountains is indicated by a solid circle with a question mark.



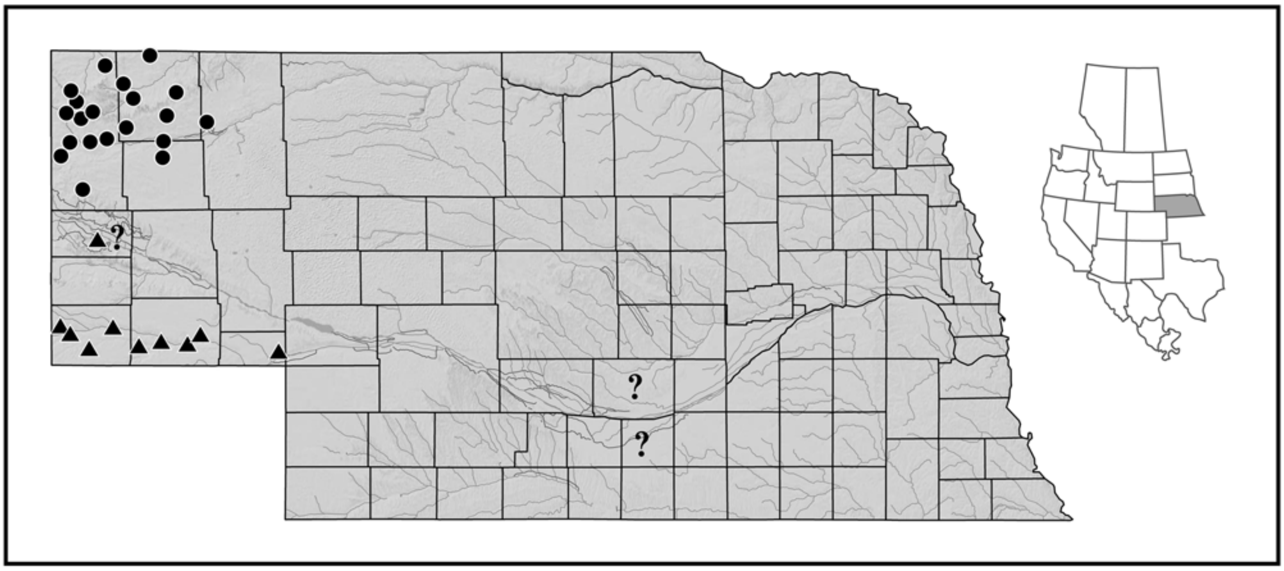
MAP 9. The distributions of short-horned lizards in Colorado, showing localities for *Phrynosoma brevirostris* (solid triangles), *P. bauri* **sp. nov.** (solid squares), *P. diminutum* **sp. nov.** (open triangles), *P. bauri* **sp. nov.** x *P. hernandesi* hybrids (open squares), *P. hernandesi* (solid circles), and hybrids (*P. hernandesi* x *P. ornatissimum*) morphologically similar to *P. hernandesi* (open circles). Arrows indicate records for *P. bauri* **sp. nov.** on the western slope of the Sangre de Cristo Range. After Hammerson (1999) with modifications.



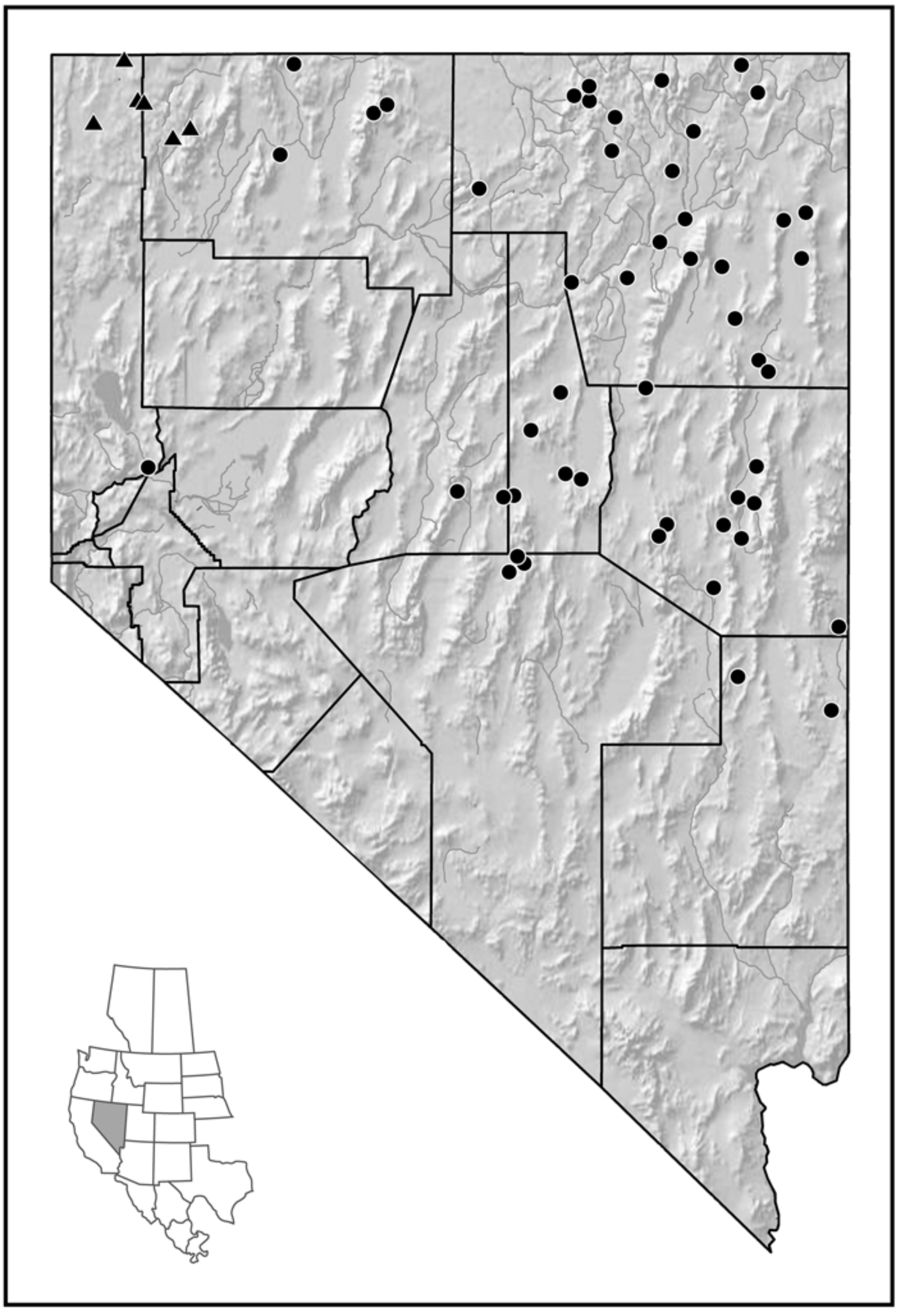
MAP 10. The distribution of *Phrynosoma douglasii* (triangles) and *P. hernandesi ornatum* (circles) in Idaho. Specimen vouchers for the four records in central Custer County (*fide* Nussbaum *et al*. 1983), have not been located. Museum voucher records for Boise and Glenns Ferry have not been plotted because they are erroneous.



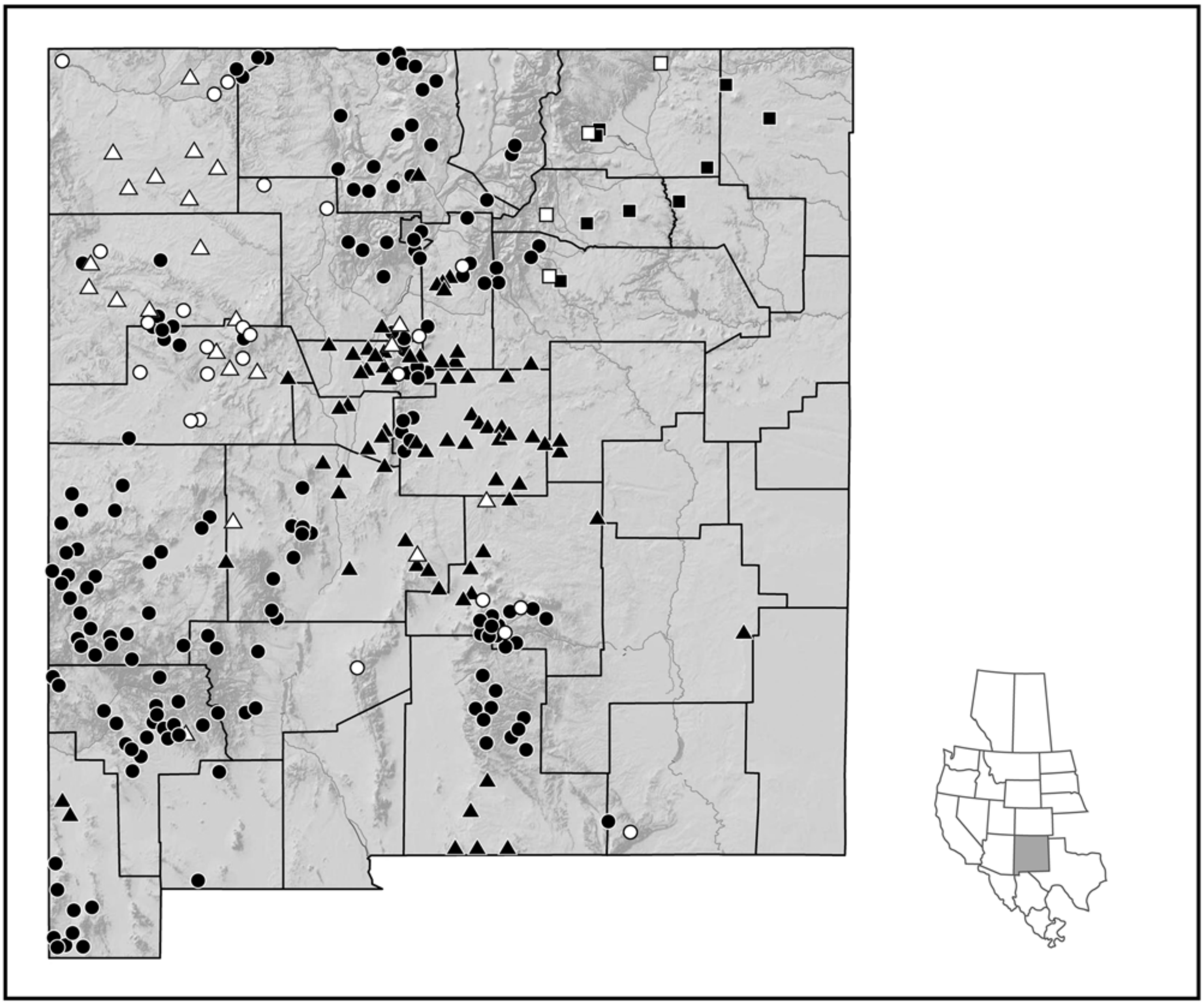
MAP 11. Locality records for *Phrynosoma brevirostris* (circles) in Montana. Symbol with question mark in Silver Bow County denotes possible introduced population near Butte. A second questionable record is near West Entrance to Yellowstone National Park in southern Gallatin County. The possible occurrence of *P. douglasii* (triangle) is indicated for the Centennial Valley. After Maxell *et al*. (2003) with modifications.



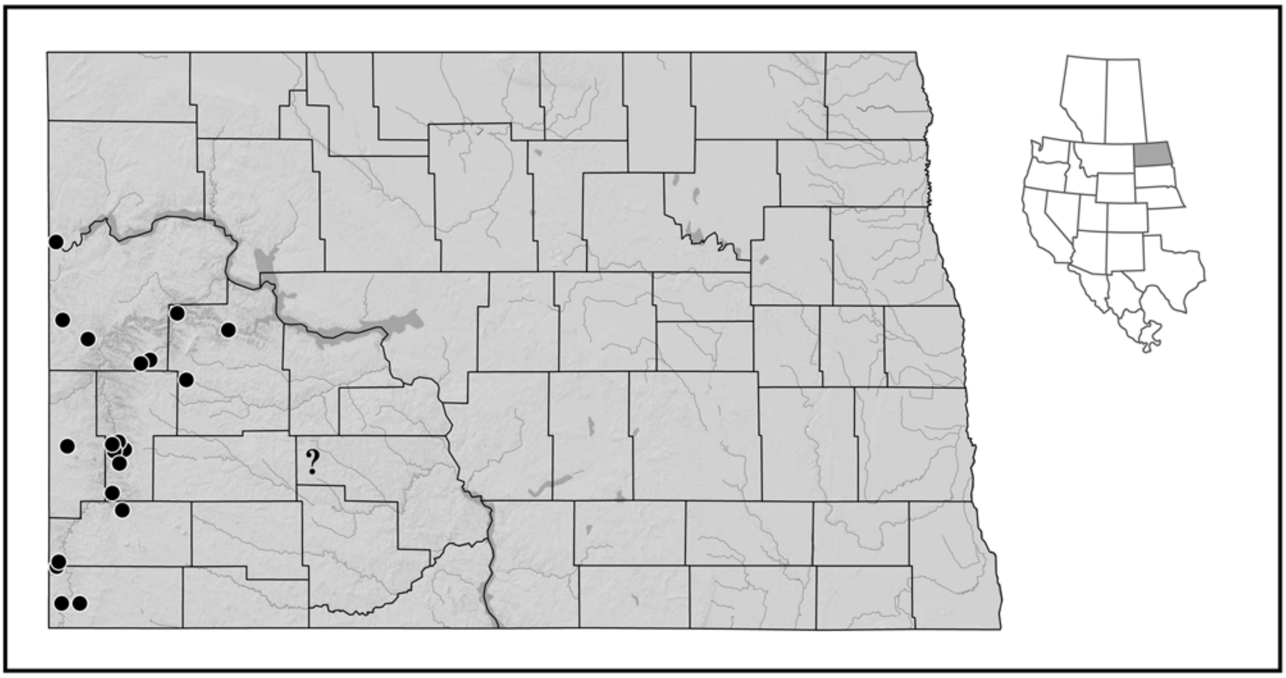
MAP 12. The distribution of *Phrynosoma brevirostris* (circles) and *P. bauri* **sp. nov.** (triangles) in Nebraska. Extralimital records in Buffalo and Kearney counties are indicated by question marks. Symbol with question mark at Gering, Scotts Bluff County, indicates taxonomic uncertainty (see text). After Ballinger *et al*. (2010) with modifications.



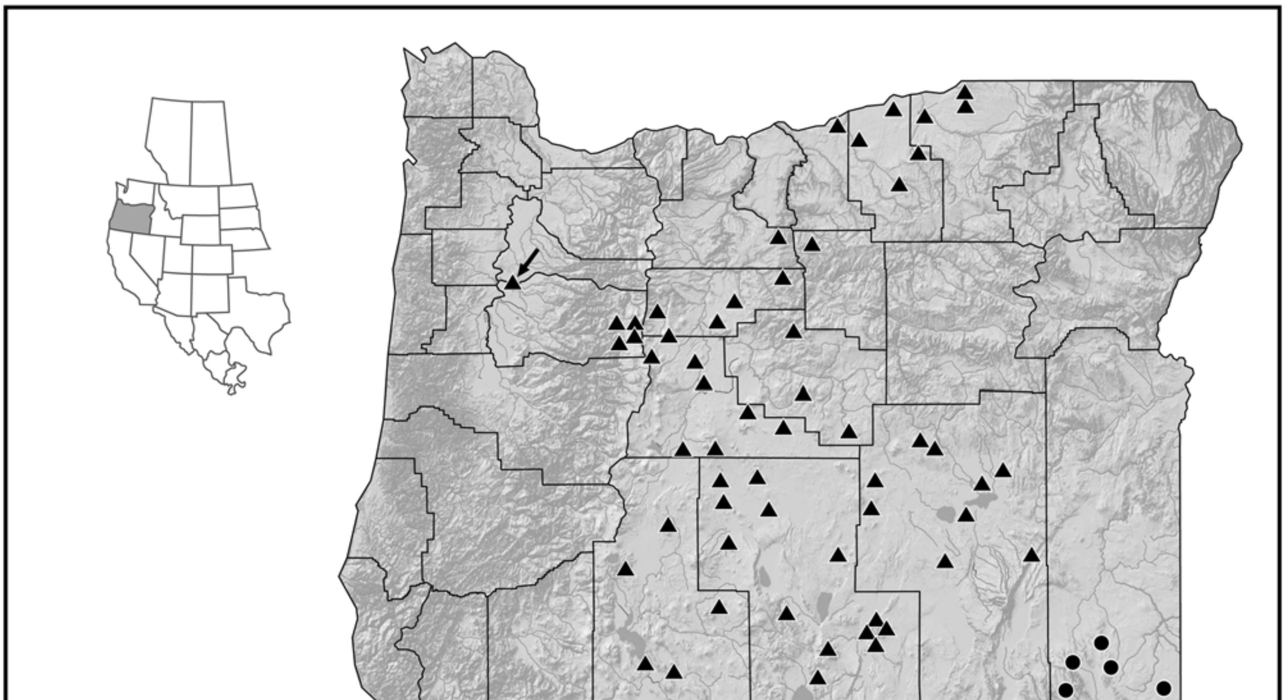
MAP 13. The distribution of *Phrynosoma douglasii* (triangles) and *P. hernandesi ornatum* (circles) in Nevada.



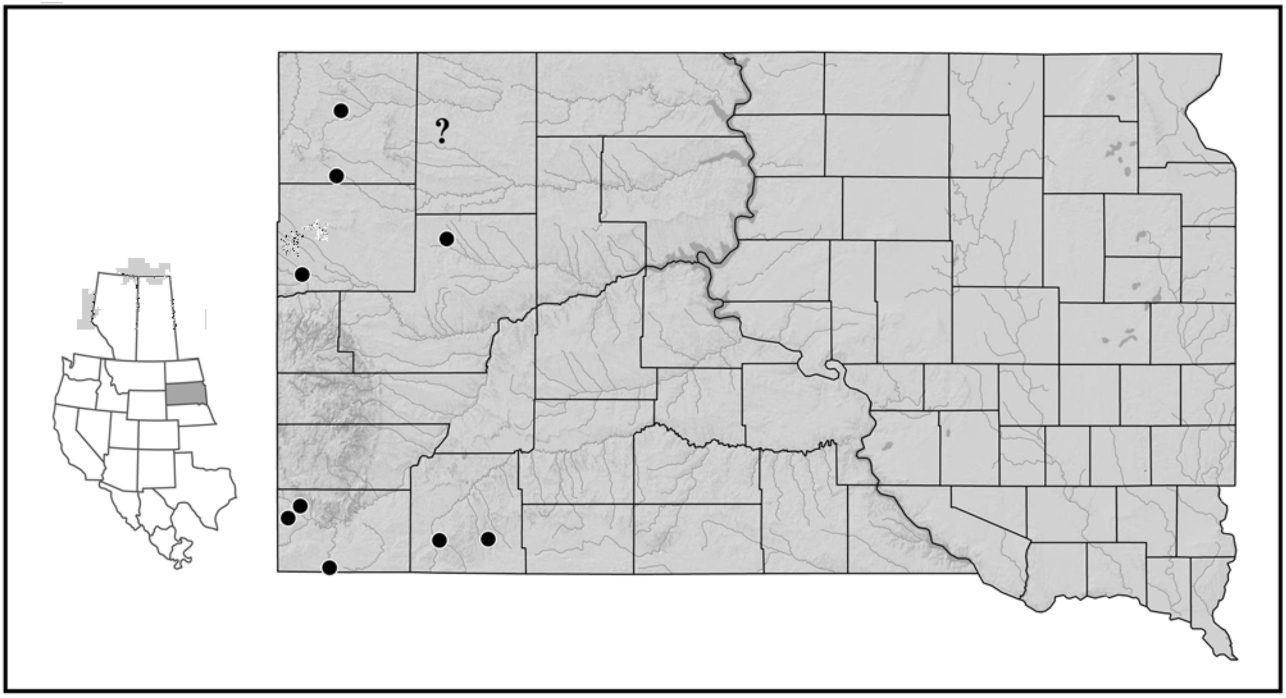
MAP 14. The distributions of short-horned lizards in New Mexico, showing locality records for *Phrynosoma bauri* **sp. nov.** (solid squares) *P. hernandesi* (solid circles), *P. ornatissimum* (solid triangles), *P. bauri* **sp. nov.** x *P. hernandesi* hybrids (open squares), hybrids (*P. hernandesi* x *P. ornatissimum*) morphologically similar to *P. hernandesi* (open circles), and intermediate hybrids and hybrids morphologically similar to *P. ornatissimum* (open triangles).



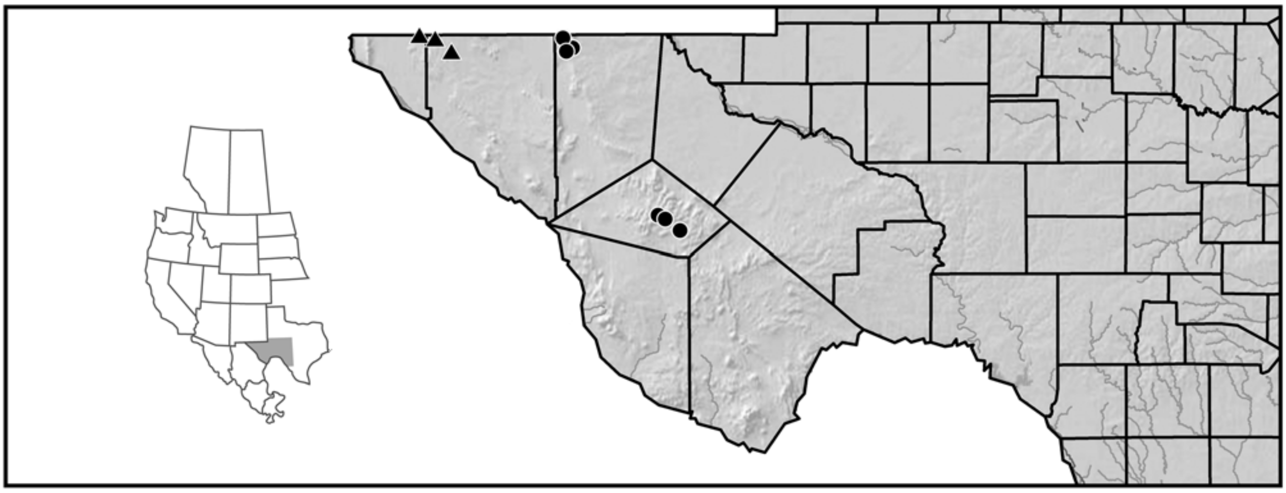
MAP 15. The distribution of *Phrynosoma brevirostris* in North Dakota. Question mark denotes unspecified record for Morton County. After Jundt (2000), with modifications.



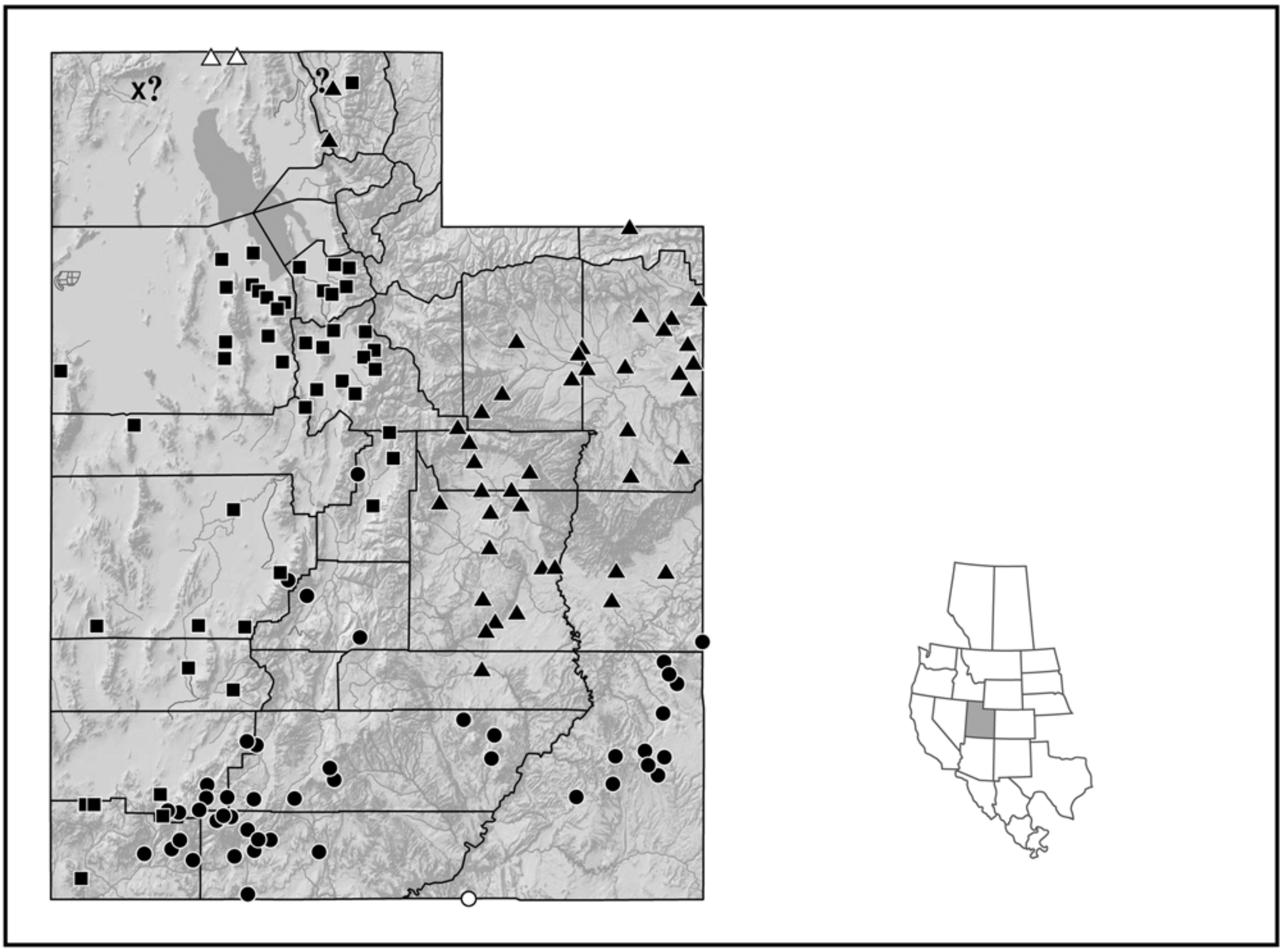
MAP 16. The distribution of *Phrynosoma douglasii* (triangles) and *P. hernandesi ornatum* (circles) in Oregon. Arrow denotes recent sight record near Jefferson, Marion County, in the Willamette Valley.



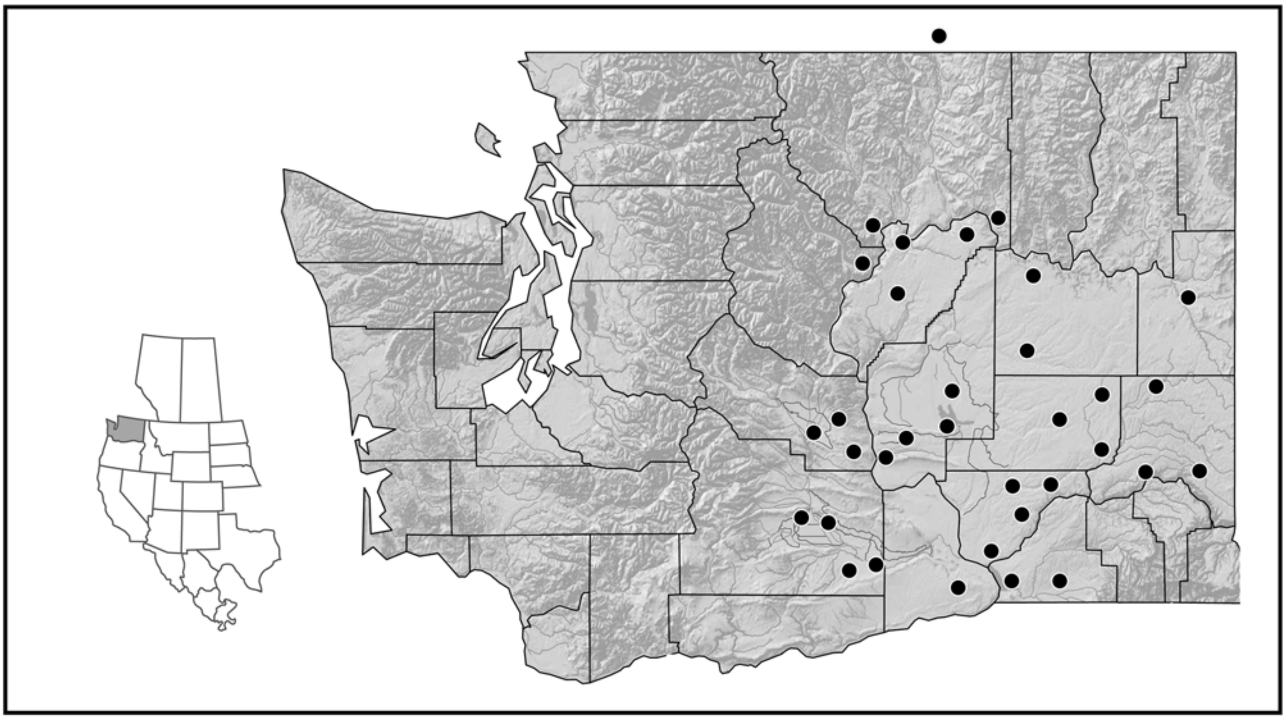
MAP 17. Locality records for *Phrynosoma brevirostris* in South Dakota. Question mark denotes unspecified record for Perkins County.



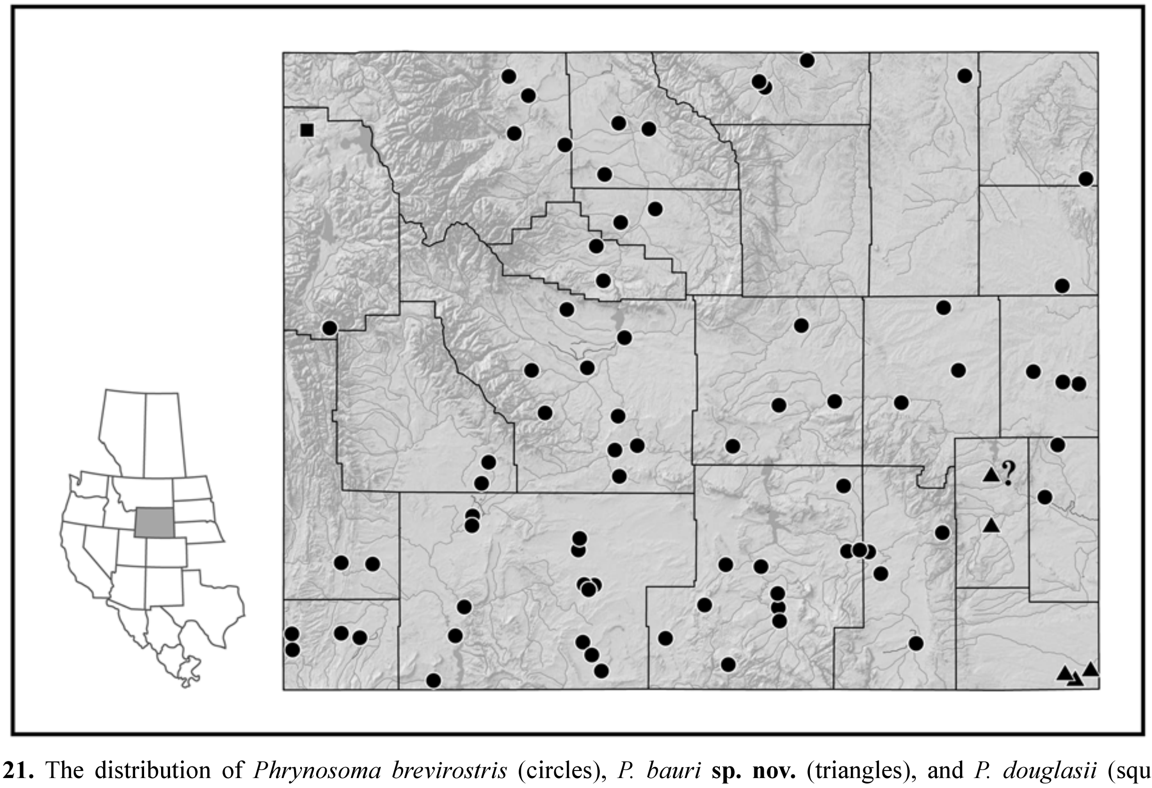
MAP 18. Locality records for *Phrynosoma hernandesi* (circles) and *P. ornatissimum* (triangles) in west Texas.



MAP 19. The distributions of short-horned lizards in Utah, showing locality records for *Phrynosoma brevirostris* (solid triangles), *P. douglasii* (open triangles), *P. hernandesi* (solid circles), hybrid (*P. hernandesi* x *P. ornatissimum*) morphologically similar to *P. hernandesi* (open circle), and *P. h. ornatum* (squares). Question mark with x indicates possible record for *P. douglasii* or *P. h. ornatum* SW of Rosette, Box Elder County. Symbols with question marks indicate uncertain taxonomic assignment.



MAP 20. The distribution of *P. douglasii* in Washington and the locality record for Osoyoos, British Columbia.



MAP 21. The distribution of *Phrynosoma brevirostris* (circles), *P. bauri* **sp. nov.** (triangles), and *P. douglasii* (square) in Wyoming. Question mark near symbol indicates taxonomic uncertainty. After Baxter & Stone (1985) with modifications.