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FROGS OF THE RANA TARAHUMARAE GROUP IN EASTERN MEXICO

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Study of Mexican ranid frogs of the *Rana tarahumarae* group began in the 1960s. Despite ample material, taxonomic relationships remain perplexing and uncertain with regard to frogs from western and southern México. The purpose of this report is to up-date the extent of morphological variation of the two species of frogs of the *R. tarahumarae* group in eastern México, *R. pueblae* and *R. johni*. There has been little published data concerning either *R. pueblae* or *R. johni* since the original descriptions. Hillis *et al.* (1984) alluded to additional topotypic material of both species. Data are known only on 18 topotypic specimens of *R. pueblae* and on 59 specimens of *R. johni* (known from only three localities). *Rana pueblae* and *R. johni* are distinct from other populations of the *R. tarahumarae* group in western and southern México (*R. tarahumarae-pustulosa-zweifeli*). Hereafter the two species in eastern México are discussed as the *R. pueblae* complex, the other populations as the *R. tarahumarae* complex.

MATERIALS AND METHODS

Only external morphological features are utilized. Seven recorded measurements (made with dial calipers) include: snout to vent length from tip of snout to anterior edge of cloacal opening (SVL), tibiofibula length (leg length) from heel to fold of skin on knee (TL), head width at level of posterior margins of tympana (HW), head length from posterior margin of tympana to

tip of snout (HL), tympanum diameter (TD), eye diameter (ED), and distance between tympanum and eye (TE). Six ratios were derived from body measurements to evaluate differences in shape of head and leg length (HW/SVL, HL/SVL, HL/HW, TL/SVL, HL/TL, and HW/TL), and two ratios to determine relative size of tympanum and eye and distance between them (TD/ED and TE/TD). Scattergrams were made to ascertain ontogenetic variation (all eight ratios mentioned above plotted against SVL). Inspection of some scattergrams indicated ontogenetic variation, and a SVL of 60 millimeters as the demarcation of the two most divergent size-groups. In discussions of ontogenetic variation, "small" frogs are less than 60 millimeters SVL and "large" frogs 60 millimeters or larger. Institutional codes for museum specimens cited in text follow Leviton *et al.* (1985).

RANA PUEBLAE COMPLEX

Definition

Aspects of pattern, structure, and morphometric data are useful in characterizing different populations of the *Rana tarahumarae* group. The two species of the *R. pueblae* complex lack distinctive features of pattern. Features that distinguish the *R. pueblae* (from the *R. tarahumarae*) complex are discussed below.

Supralabial fold (Fig. 1).—This is a protuberant swollen fold extending posteriorly from below the eye to at least under the tympanum; this fold is absent on snout in front of the eye. The fold is usually most prominent under the tympanum where the upper margin often forms a distinct tuck or ridge. A postlabial segment may extend a short distance behind the tympanum and is either straight or slightly curved. Development of the fold is not ontogenetic. In the *R. tarahumarae* group, the supralabial fold is unique to the *R. pueblae* complex.

Tympanic fold.—This fold, above and behind the tympanum, is usually well developed, often coincident with dark pigment, in the *R. tarahumarae* complex in western México. However, the tympanic fold is usually absent or ill-defined in frogs of the *R. pueblae* complex. Blair (1947:3) noted the tympanic fold as "variable, ranging from absent to moderately well developed" in frogs of the type series of *R. moorei* (= *johni*).

Larvae.—Tadpoles of the *R. tarahumarae* complex characteristically have a few submarginal black denticles, usually forming one or two short rows, located on either side of the oral disc at angles between the upper and lower jaws (hereafter as "marginal



FIG. 1.—Left side of head showing supralabial fold (see description in text) characteristic of frogs of *Rana pueblae* complex. *Rana pueblae* above (SMBU 16702, SVL 100.7 mm.) and *R. johni* below (SMBU 16677, SVL 99.7 mm.). Note posterior extension of supralabial fold in *R. johni*.

teeth”) and usually have five upper rows of teeth (Webb and Korky, 1977). Examination of only two larvae of *R. johni* (larvae of *R. pueblae* unknown) indicates an absence of marginal teeth and the presence of only four upper rows of teeth (instead of five at comparable stage of development). Altig (1987:78) also noted four upper rows of teeth and failed to mention marginal teeth in *R. johni*.

Morphometrics.—Frogs of the *R. pueblae* complex differ from frogs of the *R. tarahumarae* complex in having ontogenetic variation in HW/SVL (HW increasing at a slightly faster rate than SVL in both species of *R. pueblae* complex); however, these values are not diagnostic in separating taxa of the two complexes. Also, frogs of the *R. pueblae* complex tend to have relatively short legs. Large frogs of *R. pueblae* have shorter legs (TL/SVL showing slight ontogenetic variation with TL about 41 to 42 percent SVL, $\bar{X} = 0.418$, see Table 1) than any population of the

TABLE 1.—Ratios of measurements (mm.) for *Rana pueblae* and *R. johni*. Data are mean \pm SE, with range and sample size below. Upper set of values is based on frogs less than 60 millimeters SVL, the lower set on frogs 60 millimeters SVL or larger.

Sample	HW/SVL	HL/SVL	HL/HW
<i>R. pueblae</i>	0.360 \pm 0.011	0.367 \pm 0.013	1.027 \pm 0.036
	0.34-0.39, 4	0.33-0.38, 4	0.96-1.10, 4
	0.390 \pm 0.003	0.357 \pm 0.003	0.920 \pm 0.007
	0.36-0.40, 14	0.34-0.38, 14	0.88-0.97, 14
<i>R. johni</i>	0.358 \pm 0.002	0.381 \pm 0.003	0.061 \pm 0.008
	0.34-0.38, 26	0.36-0.41, 26	0.99-1.15, 26
	0.376 \pm 0.003	0.364 \pm 0.003	0.970 \pm 0.008
	0.35-0.40, 29	0.34-0.39, 29	0.88-1.07, 29
Sample	TL/SVL	HL/TL	HW/TL
<i>R. pueblae</i>	0.432 \pm 0.009	0.845 \pm 0.017	0.825 \pm 0.017
	0.41-0.45, 4	0.80-0.87, 4	0.79-0.87, 4
	0.418 \pm 0.005	0.855 \pm 0.012	0.934 \pm 0.014
	0.38-0.44, 13	0.79-0.95, 13	0.85-1.01, 13
<i>R. johni</i>	0.425 \pm 0.005	0.903 \pm 0.015	0.848 \pm 0.010
	0.37-0.46, 25	0.79-1.06, 25	0.78-0.96, 25
	0.454 \pm 0.003	0.800 \pm 0.006	0.823 \pm 0.008
	0.41-0.48, 29	0.75-0.86, 29	0.76-0.90, 29

R. tarahumarae complex, as noted by Zweifel (1955); in the latter complex the shortest legs occur in the northern population of *R. tarahumarae* in Arizona, Sonora, and Chihuahua (TL/SVL lacking ontogenetic variation with TL about 46 to 47 percent SVL, \bar{X} = 0.466, 0.42 to 0.52, N = 99).

Preliminary data (only recently recorded for some specimens) regarding the relative size of the eye and the tympanum, and the distance between them, indicate possible differences between the *R. pueblae* and *R. tarahumarae* complexes, although data are available only for *R. johni* of the *R. pueblae* complex. Frogs of the *R. pueblae* complex have relatively small tympana (diameter usually about half or slightly less than half that of the eye) that are well separated from the eye (distance more than half the diameter of the tympanum); these dimensions are similar in frogs of the *R. tarahumarae* complex, and readily distinguish frogs of the *R. tarahumarae* group from *R. montezumae* and leopard frogs of the *R. pipiens* complex (large tympana near the eye). Data are known from 12 frogs of *R. johni*, 29.4 to 110.2 millimeters SVL (AMNH 57736-38, 59217-23, 84297-98); 15 *R. pustulosa*, 29.2 to 87.0 millimeters SVL, from Sinaloa and Nayarit (UTEP 6532, 6961-66, 7577-81, 7583-85); and 17 *R. tarahumarae*, 28.9 to 91.8

mm SVL, from Nayarit and Jalisco (UTEP 6972-82, 7491-93, 7573-75).

Differences in TD/ED between the three taxa are not marked; *R. johni* with TD about 44 to 45 percent ED (\bar{X} = 0.446, 0.38 to 0.52) shows slight ontogenetic variation (see species description), and has slightly smaller tympana than either *R. pustulosa* (0.504, 0.42 to 0.61) or *R. tarahumarae* (0.534, 0.46 to 0.61), which lack or have negligible ontogenetic variation. *Rana johni* also differs from the two species in western México in lacking obvious ontogenetic variation in distance between the eye and tympanum (TE/ED, \bar{X} = 0.779, 0.58 to 1.00). This distance increases with increasing size in *R. pustulosa* (0.595, 0.40 to 0.82, 10 small frogs; 0.806, 0.75 to 0.88, five large frogs) and *R. tarahumarae* (0.673, 0.48 to 0.82, 10 small frogs; 1.05, 0.90 to 1.26, seven large frogs). The data also suggest a marked difference in TE/TD between large frogs of *R. pustulosa* and *R. tarahumarae*.

Thus, the *Rana pueblae* complex of the *R. tarahumarae* group may be defined (distinguished from *R. tarahumarae* complex) as having a supralabial fold and a usually poorly developed (or absent) tympanic fold, in having ontogenetic variation in HW/SVL, and probably in larvae lacking marginal teeth and having only four upper rows of teeth at most stages of development.

Description

Frogs of the *Rana pueblae* complex occur along creeks and streams in hilly or mountainous areas on the eastern slopes of the Sierra Madre Oriental. The two species of the *R. pueblae* complex (*R. pueblae* and *R. johni*) are similar in having dark olive to brownish dorsal surfaces (indistinct darker markings may occur on the back), dark femoral bars usually wider than pale interspaces, mostly patternless ventrolateral areas on body, and gray suffusion on ventral surfaces in largest frogs. Tiny white pustules on the dorsal surfaces are most prominent in young frogs. Dorsolateral folds or coincident pale stripes, or both, and tiny white pustules on the tympana are absent. White supralabial stripes may be present. Supralabial folds are present. Tympanic folds are usually absent or moderately developed, but rarely prominent. Tarsal folds are absent. The one metatarsal tubercle is low and elongate throughout its length. Breeding males have dark, glandular excrescences on the thumbs. Females are larger than males. Tadpoles lack marginal teeth and have a maximum

of four upper rows of teeth (not known for *R. pueblae*—see description in account of *R. johni*).

Both species show slight ontogenetic variation in HW/SVL and HL/SVL, with HW increasing at a faster rate, and HL increasing at a slower rate, than SVL. The resultant HL/HW in both species indicates broader heads with increasing size, with small frogs having heads longer than broad, and large frogs having heads broader than long (Table 1). Other morphometric data are variable depending on species (see section on comparisons and Table 1). Tympana (data only for *R. johni*) are relatively small (diameter about half, or slightly less than half, that of the eye) and well separated from the eye (distance more than half the diameter of the tympanum).

Rana pueblae ZWEIFEL

Ra. pueblae Zweifel, 1955:253. Holotype, UMMZ 99474, adult female obtained by Herndon G. Dowling on 31 July 1948, from "2.8 miles northeast of Huauchinango, Río Texcapa, Puebla, México."

Description of holotype.—Measurements in millimeters include: SVL 111.7 (tip of snout to tip of urostyle as 110 millimeters fide Zweifel, 1955), TL 44.0, HL 38.2, and HW 43.4. Dorsolateral folds are absent, ventrolateral markings on the body are sparse, and roundish black bars on the femora are wider than the pale interspaces. However, all dorsal patterns are obscure owing to an overall dark gray-black background. The belly is dirty white with gray smudging.

Description.—Dorsal surfaces are dark brown (SMBU series) to gray-black (type series), mostly uniform with dark spots or blotching obscure or absent. Minute pearly white pustules are mostly absent on dorsal surfaces. The supralabial fold usually terminates under the tympanum (Fig. 1); a postlabial segment extending a short distance posterior to the tympanum is absent or not well developed (moderately so in AMNH 85299). Dorsolateral folds are lacking. The upper sides of the body are mostly smooth, not pustulose. White dorsolateral and supralabial stripes are lacking (smallest 35.2, 35.6, 40.8, and 58.1 millimeters SVL). Ventrolateral body pattern of small, dark, blotchlike markings is indistinct. Femoral bars are usually blotchlike or ovoid and wider than the pale interspaces (patterns obscure in type series). Large frogs acquire a dark grayish smudged and mottled pattern on most ventral surfaces (initially on the underside of the head and

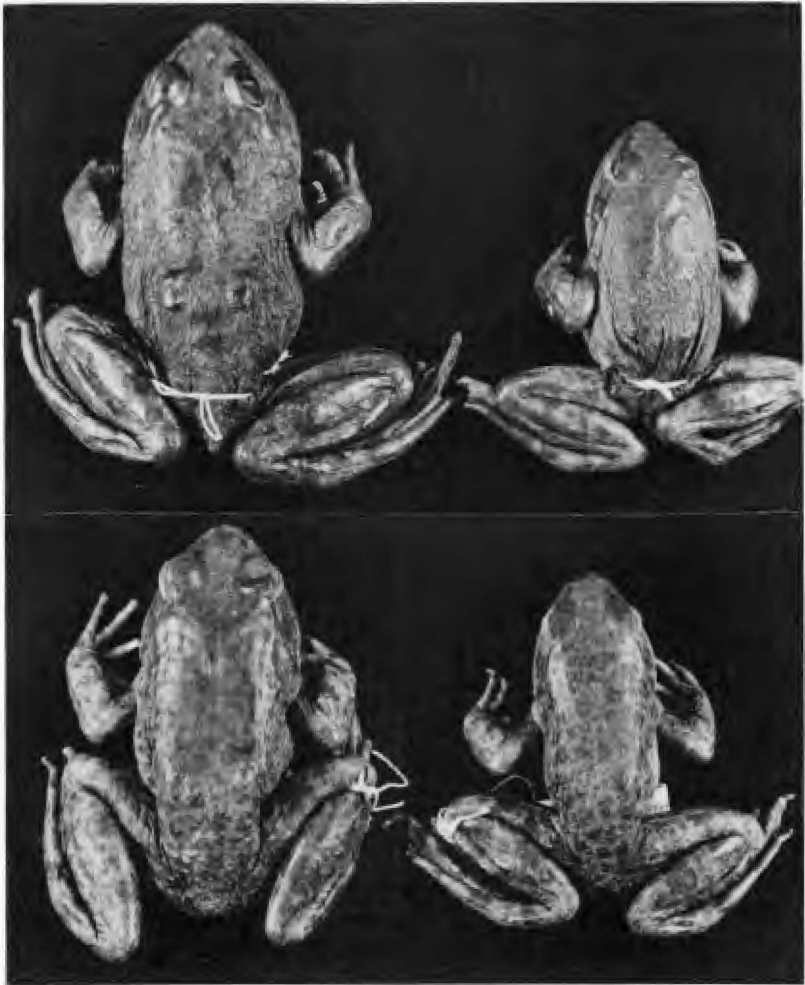


FIG. 2.—*Rana pueblae* above (left, SMBU 16701, female, SVL 108 mm.; right, SMBU 16705, male, SVL 80.5 mm.) and *R. johni* below (left, SMBU 16674, female, SVL 96.8 mm.; right, SMBU 16671, male, SVL 78.1 mm.).

on the chest). Dorsal views of a male and female are shown in Figure 2.

The largest female (holotype) is 111.7, the largest male 88.1 millimeters SVL (UMMZ 99468). Some ratios of measurements vary ontogenetically (data for all six body ratios in Table 1). Slight ontogenetic variation occurs in HW/SVL and HL/SVL, with HW increasing at a faster rate, and HL increasing at a

slower rate than SVL. Heads thus become broader with increasing size, with small frogs having heads longer than broad (HL/HW, $\bar{X} = 1.027$) and large frogs having heads broader than long ($\bar{X} = 0.92$). Slight ontogenetic variation occurs in TL/SVL with TL increasing at a slower rate than SVL ($\bar{X} = 0.432$ in small frogs, 0.418 in large frogs), but variation is lacking in HL/TL. Decided ontogenetic variation occurs in HW/TL ($\bar{X} = 0.825$ in small frogs, 0.934 in large frogs). See section on comparisons and Table 1.

Distribution.—The 18 specimens are known only from the vicinity of the type locality, 2.8 miles NE Huauchinango, via Mexican Hwy. 130, along the Río Texcapa (= Río Necaxa) in the state of Puebla. Of 12 specimens in the type series, UMMZ 99468-71, 99472 (four specimens), and 99473-76, three have been exchanged to other institutions (UMMZ 99469, 99473 = MVZ 60241, 60240, respectively; UMMZ 99476 = UIMNH 39844). Other specimens are AMNH 85299, 2.8 miles NE Huauchinango, Río Texcapa, and SMBU (Bryce C. Brown) 16701-05, 2 miles NE Huauchinango, edge of muddy river.

Rana johni BLAIR

Rana moorei Blair, 1947:5. Preoccupied by *Anchylorana moorei* Taylor, 1942 = *Rana moorei* fide Holman, 1963. Holotype, AMNH 52908, male obtained by A. P. Blair and J. A. Moore on 9 September 1946, from "Arroyo Sacahuite at Palictla, 6 miles (by highway) north of Tamazunchale, San Luis Potosi, Mexico."

Rana johni Blair, 1965:517. Replacement name for *Rana moorei*, 1947.

Description of holotype (Fig. 3).—Measurements in millimeters are SVL 60.3 (Blair, 1947:5, recorded 62), TL 27.0, HL 21.9, and HW 22.1. Dorsolateral folds are absent, but minute pale tubercles are aligned to form indistinct whitish lines anteriorly. Ventrolateral areas on the body are almost patternless (some small dark marks on the right side), and femoral dark bars are wider than pale interspaces (one bar on each femora faded). A pale (whitish) supralabial fold extends posteriorly from under the eye to above the insertion of the forelimb (postlabial segment interrupted). Folds above and behind the tympanum are absent (dark coincident line suggests fold). The back and sides are minutely pustulose (pale-tipped). Dorsal surfaces are dark, with indistinct darker markings on back. Dark bars occur on each tibiofibula (two), on the tarsometatarsus and foot, and two small dark



FIG. 3.—Holotype of *Rana johni* (AMNH 52908, male, SVL 60.3 mm.).

blotches occur on each forearm. Undersurfaces are pale and patternless.

Description.—Dorsal surfaces are dark gray to brown in preservative (dark olive green fide Blair, 1947:5, or brownish olive inscribed on SMBU field tags, in life), slightly paler in larger specimens. Indistinct dark spots and markings may occur on the

back and top of the head. Small white-tipped tubercles on the dorsal surfaces are mostly absent on head and back in large frogs (few on eyelid edges). Dorsolateral folds are lacking, but minute tubercles may be aligned to form semblance of lines (AMNH 52917, right side of AMNH 52913). Upper sides of the body (mostly lateral) may be noticeably pustulose. Ventrolateral body areas are usually patternless, or have small dark markings (TTU 5674, right side AMNH 52905). A tympanic fold is usually absent, or weakly developed (AMNH 52910), or occasionally well developed (TTU 5654; AMNH 52912; AMNH 52907 left side, absent on right side). Presence of a tympanic fold often is emphasized by a coincident black line, which may be flanked dorsally by a short pale stripe. Young frogs may have a broad pale area in front of the tympanum. The tympanum lacks tiny pearly white tubercles (counts of 1/0 occurred in three of 32 frogs). Femoral bars (the pattern may be irregular) are usually as wide as or wider than the pale interspaces (bars are narrower than interspaces in AMNH 52914); the bars may be subcircular or blotchlike (TTU 5661-62). Small dark markings may occur in interspaces between femoral bars (SMBU series). Usually two dark bars occur on the tibiofibulae, one on the tarsometatarsus, and two blotches on each forearm. Frogs smaller than 60 millimeters SVL lack ventral dark smudging, whereas larger frogs acquire a dark gray suffusion over most ventral surfaces. Dorsal views of a male and female are shown in Figure 2.

The supralabial fold extends posterior to the tympanum as a prominent, short postlabial fold that may be separated from the rest of the fold and oriented diagonally (Fig. 1). The supralabial fold is coincident with a white stripe in at least some small frogs (fold-stripe absent anterior to the eye). Blair (1947:3) noted that all but one of the frogs comprising the type series of *R. johni* (largest about 60 to 62 millimeters SVL) have a prominent white supralabial stripe, and he provided a photograph of a living frog of 49 millimeters SVL (AMNH 52924) with such a stripe (same photograph in Zweifel, 1955:279, pl. 4c). A large topotypic male (MCZ 24836) of 76.0 millimeters SVL lacks white supralabial stripes. In 17 specimens (TTU, 52 to 104 millimeters SVL), the pale supralabial striping is best developed in TTU 5672 (56.8 millimeters SVL) but is almost absent in all other frogs (smallest SVL in millimeters: 51.9, TTU 5673; 53.6, TTU 5657; 53.8, TTU 5670; 59.1, TTU 5663). Thus white supralabial stripes in small frogs (near 50 to 60 millimeters SVL) seem to be lost with

increasing size. Presence of whitish supralabial stripes may be variable or altered by preservative in small individuals as seven small frogs (AMNH 59217-23, 27.0 to 47.5 millimeters SVL) lack noticeable white stripes.

Some morphometric data of specimens of the type series are in Blair (1947:16). The largest female is 110.2 (AMNH 84297), the largest male 89.4 millimeters SVL (AMNH 84298). Scattergrams suggest ontogenetic variation in some ratios of measurements (data for all six body ratios are in Table 1). Slight variation occurs in HW/SVL and HL/SVL, with the HW increasing at a faster rate, and the HL increasing at a slower rate, than the SVL. Heads thus become broader with increasing size, with small frogs having heads longer than broad (HL/HW, $\bar{X} = 1.061$) and large frogs having heads broader than long ($\bar{X} = 0.970$). Slight ontogenetic variation occurs in TL/SVL with TL increasing at a faster rate than SVL ($\bar{X} = 0.425$ in small frogs, 0.454 in large frogs); variation is more marked in HT/TL ($\bar{X} = 0.903$ in small frogs, 0.800 in large frogs). Ontogenetic variation is negligible or lacking in HW/TL. See comparisons and Table 1.

The diameter of the tympanum is usually slightly less than half that of the eye (TD/ED, $\bar{X} = 0.466$, 0.38 to 0.52, N = 12), but shows slight ontogenetic variation (0.421, 0.38 to 0.47, seven small frogs; 0.482, 0.43 to 0.52, five large frogs). The distance between the eye and the tympanum is more than half the diameter of the tympanum (TE/TD, $\bar{X} = 0.779$, 0.58 to 1.00, N = 12).

Larvae.—I have examined three ranid tadpoles (AMNH 83936-38) from the type locality of *Rana johni*. Two of them (83936-37), both near stage 40 (Gosner, 1960), are 59 and 75 millimeters in total length (bodies, 25 and 33 millimeters, respectively). The bodies are pale brown with fine dark brown marbling on the dorsum, and the tail fins and musculature are smudged with brown blotches. The largest larva, near metamorphosis, shows three upper and three lower rows of "teeth," but has lost the entire first upper row and middle part of the third lower row; the smallest larva has four upper and three lower rows of teeth. Both larvae have a wide A-2 gap, a short P-1 gap, and lack marginal teeth. The expanded toe-tips of the well-developed hind limbs readily identify these two tadpoles as *R. johni* (not as members of the *R. pipiens* complex).

The third and smallest larva (AMNH 83938), 56 millimeters total length (body, 24 millimeters) in stage 29 (small hind limb

buds), has three upper and three lower rows of teeth and no marginal teeth, and otherwise generally resembles the two tadpoles of *R. johni* mentioned above. However, the dorsal tail fin is deeper (by about one millimeter, compared to the larva of comparable size—59 millimeters, AMNH 83937). The two larvae of *R. johni* have dark pigmentation (stippling in small, irregular pattern in both large larvae) across the chin-throat (lacking in AMNH 83938). The smallest larva (AMNH 83938), for the moment, is considered to be representative of the *R. pipiens* complex.

The limited material suggests that larvae of *R. johni* (and probably *R. pueblae*) have at least four upper tooththrows and lack marginal teeth. Altig (1987:78) characterized tadpoles of *R. johni* as having a maximum tooththrow formula of $4/3$ and tail and body that is gray with dark reticulations.

Distribution.—The geographic range of *Rana johni* is rather restricted with frogs known only from streams of the Río Moctezuma (Río Panuco) drainage in extreme southeastern San Luis Potosí and adjacent northern Hidalgo, México. Specimens examined (59): HIDALGO: 3/4 km. ENE Tehuetlán (TTU 5654, 5656-57, 5667, 5674); 4 km. E San Felipe Orizatlán (TTU 5655, 5661-64, 5666, 5670-73, 5675-76). SAN LUIS POTOSÍ: Palictla, 6 road mi. N Tamazunchale (AMNH 52903-15, 52917-20; specimens AMNH 52916, 52921, and 52922-24 not examined, exchanged to MCZ, UIMNH, and UMMZ, respectively; TTU 6519); Palictla (AMNH 57736-39); 6 mi. N Tamazunchale (AMNH 59217-23); 6.4 mi. N Tamazunchale (AMNH 84297-98); Palitla, 5 mi. N Tamazunchale (MCZ 24836); 6 mi. NW Tamazunchale (SMBU 16668-77 = Bryce C. Brown 6668-77). The place-name "Palitla" (= "Palictla") is so designated by a signpost on Mexican Hwy. 85 and is 5.4 road mi. N Río Moctezuma bridge in Tamazunchale.

COMPARISONS

Rana johni differs from *R. pueblae* in having a postlabial segment of supralabial fold (Fig. 1), and in having this fold whitish in (at least some) young frogs. The gray smudging on the ventral surfaces seems to be darker, more extensive, and acquired at smaller sizes in *R. pueblae* than in *R. johni*.

Morphometric data for both species are compared in Table 1. Both species acquire broader heads with increasing size. However, large frogs of *R. johni* have longer heads (HL/HW, $\bar{X} = 0.970$) than those of *R. pueblae* ($\bar{X} = 0.920$). Both species also show

slight ontogenetic variation in TL/SVL; however, TL increases at a slower rate in *R. pueblae* and at a faster rate in *R. johni*, than the SVL, which is reflected in large frogs having slightly shorter legs in *R. pueblae* (TL/SVL, $\bar{X} = 0.418$) than in *R. johni* ($\bar{X} = 0.454$). The HL/TL shows negligible ontogenetic variation in *R. pueblae* because HL and TL both increase at a slightly slower rate than SVL; however, HL/TL shows ontogenetic variation in *R. johni* ($\bar{X} = 0.903$ in small frogs, 0.800 in large frogs) because HL increases at a slower rate and TL increases at a faster rate, than SVL. The HW/TL shows negligible ontogenetic variation in *R. johni* because HW and TL both increase at a faster rate than SVL; however, HW/TL shows marked ontogenetic variation in *R. pueblae* ($\bar{X} = 0.825$ in small frogs, 0.934 in large frogs) because HW increases at a faster rate and TL increases at a slower rate, than SVL. These morphometric data indicate that with increasing size, *R. pueblae* acquires a broader head and shorter legs than *R. johni*, which are differential features also noted by Hillis *et al.* (1984:402). The body proportion that best distinguishes the two species is HW/TL in frogs 60 millimeters SVL or larger. Key characters that distinguish the two species of the *Rana pueblae* complex are given below.

Rana johni.—Postlabial segment of supralabial fold (extending posterior to tympanum) present; white supralabial stripes (behind the eye and coincident with the fold) present in small frogs (less than 50 to 60 millimeters SVL); HW about 82 percent TL in frogs 60 millimeters SVL or larger (HW/TL, $\bar{X} = 0.82$, 0.76 to 0.90).

Rana pueblae.—Postlabial segment of supralabial fold absent; white supralabial stripes absent in small frogs; HW about 93 percent TL in frogs 60 millimeters SVL or larger (HW/TL, $\bar{X} = 0.93$, 0.85 to 1.01).

EPILOGUE

The two species of the *Rana pueblae* complex most closely resemble *Rana tarahumarae* of the *R. tarahumarae* complex in pattern and morphometrics. It has been established that *R. johni* has a longer head and legs than *R. pueblae*, and that *R. johni* also differs from *R. pueblae* in that young frogs have whitish supralabial stripes. Correlation of these traits also occurs in different populations of *R. tarahumarae* in western México. Frogs of the southern population of *R. tarahumarae* (mostly Nayarit

and Jalisco) have slightly longer heads and legs than frogs of the northern population (Arizona, Sonora, Chihuahua) and (at least some) young frogs have white supralabial stripes (lacking in northern population).

This character-correlation (long heads and legs with white dorsolateral and supralabial stripes—broad heads and short legs and lack of white stripes) is characteristic of the *R. tarahumarae* group, but expression of these characters varies in different populations. In western México, these character extremes occur in the northern population of *R. tarahumarae* (shortest legs and broadest heads, and no pale stripes) and in *R. pustulosa* (longest legs and narrowest heads and prominent white dorsolateral and supralabial stripes).

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