

A SYSTEMATIC REVIEW OF THE MEXICAN FROG
RANA SIERRAMADRENSIS TAYLOR¹

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ABSTRACT: The variation of *Rana sierramadrensis* Taylor is discussed. A previously unreported secondary sexual characteristic is the presence of white spinous excrescences on the non-enlarged thumbs, chest and lower jaw of males. The tadpoles are described. *Rana sierramadrensis* is compared with *R. sinaloae* Zweifel. The former is retained in the *R. palmipes* species group, while the latter is transferred to the *R. tarahumarae* group, which is proposed for the inclusion of the Mexican species, *R. tarahumarae*, *R. pustulosa*, *R. sinaloae*, *R. pueblae*, and *R. johni*. *Rana sierramadrensis* is confined to the Sierra Madre del Sur in the Mexican states of Guerrero and Oaxaca, and seems to be most closely related to *Rana maculata*.

INTRODUCTION

Rana sierramadrensis is an upland tropical species in southern Mexico that is little known except for a few published locality records. My interest in *R. sierramadrensis* is a by-product of a study of frogs of the *R. pustulosa-tarahumarae* complex and *R. sinaloae* in western Mexico. Zweifel included both *R. sierramadrensis* and *R. sinaloae* in the *R. palmipes* species group (1954), and the two species *R. pustulosa* and *R. tarahumarae* in the *R. boylei* group (1955). In view of speculation that *R. sinaloae* is related to the *R. pustulosa-tarahumarae* complex, most available specimens of *R. sierramadrensis* were examined in order to determine its relationship to *R. sinaloae*.

The "Rana tarahumarae group" is proposed for the first time to accommodate the Mexican species *R. tarahumarae*, *R. pustulosa*, *R. sinaloae*, *R. pueblae* and *R. johni*. Biochemical data (Case 1976 and personal communication) suggest that *R. tarahumarae* (only Mexican species studied by Case) is not closely related to the two United States members of Zweifel's *R. boylei* group (1955), *R. boylei* and *R. muscosa*. Those two species also differ from *R. tarahumarae* and the other Mexican species in having two metatarsal tubercles (instead of one), and the larvae having four or more lower rows of teeth (instead of three), and in lacking marginal teeth.

Specimens examined are deposited in the following collections: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Natural History Museum of Los Angeles County (LACM); University of Kansas Museum of

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Rana sierramadrensis TAYLOR

Rana sierramadrensis has always been considered a distinct, monotypic species. There are no known synonyms of *R. sierramadrensis*. In the original description, Taylor (1939:397-398) listed six specimens (3963A, 3963B, 6565, 6566, 6567, and 6568), designating 3963B as the holotype and the remainder as paratypes; these numbers refer to the Edward H. Taylor-Hobart M. Smith private collection (EHT-HMS). Later, Taylor (1944:140) reiterated data about the types. Of the six specimens in the type series, four were subsequently sent to the FMNH and two were donated to the UIMNH. The type material is briefly discussed below.

The holotype (Fig. 1, formerly EHT-HMS 3963B) from "near Agua del Obispo, between Rincón and Cajones, Guerrero, July 1, 1932" is now FMNH 100038. It is a female 88.2 mm SVL and was described in some detail by Taylor (1939:398-399). The other large frog (formerly EHT-HMS 3963A) with the same data of collection as the holotype is UIMNH 27053 (Smith, Langebartel, and Williams 1964:32); a photograph of this paratype, 69.7 mm SVL, was published in the original description (Taylor 1939: Pl. XXIX, Fig. 1). Four small paratypes do not exceed 40 mm SVL.



FIGURE 1. Holotype of *Rana sierramadrensis*, FMNH 100038, from near Agua del Obispo, between Rincón and Cajones, Guerrero, Mexico.

One of them (formerly EHT-HMS 6565 and UIMNH 27054), 38.9 mm SVL from "about 9 km. southwest of Mazatlán, Guerrero (km. 337), July 21, 1936," is now USNM 139724 (Cochran, 1961:76). A small paratype (formerly EHT-HMS 6566), 33.5 mm SVL, from "near Agua del Obispo (km. 350-351), July 24, 1936," is now cataloged as FMNH 102202. The other two paratypes (formerly EHT-HMS 6567 and 6568), 37.0 and 28.8 mm SVL, both from "Agua del Obispo, August 1, 1936," are now cataloged, respectively, as FMNH 102201 and FMNH 103917. Museum locality data associated with some paratypes are slightly different from the localities quoted (above) by Taylor (1939).

DESCRIPTION

Color and pattern.—The dorsal ground color is brown or bronze-brown. The narrow, dorsolateral folds are usually slightly paler (usually buff, not white) than the ground color, have distinct, but narrow, black, lateral borders, and extend to the sacral region. A prominent white supralabial stripe extends from near the tip of the snout to above the insertion of the forelimb; this white stripe is widest posteriorly (above forelimb insertion) where it is often interrupted forming a posteriormost, white spot. There is a black canthal stripe, black diagonal posttympanic bar, black barlike mark on the anterior surface of the humerus at the insertion of the forelimb, and often a black blotch or barlike mark in the groin. A posttympanic fold is absent; however, the region is often somewhat swollen and a partial fold is discernable in AMNH 52624. Ventrolaterally the body has black markings that form an irregular-bordered, continuous or interrupted band extending from axilla to groin. The femora have narrow, dorsal, dark crossbars (pale interspaces usually three to five times wider), and a coarse pale-dark marbling (mostly dark) on the posterior surfaces. The ventral surface of the legs also has coarse dark marbling resulting mostly from lateral encroachment of pattern. The top of the head, back, and usually the sides of the body are devoid of pattern; occasionally, a few small black dots occur on the back. The ventral surface of the head-body may lack dark marks or smudging (LACM 35054; UIMNH 32444, 52783), but usually the chin-throat, chest and anterior part of the abdomen are dark-smudged and often uniformly dark. The features of color and pattern are most contrasting in young and subadults (Fig. 5) and tend to become obscured in the largest frogs (Fig. 1).

Sexual dimorphism.—There seems to be no marked discrepancy in the maximum size attained by males (100 mm SVL, KU 87284) and females (98 mm SVL, TCWC 8546). My examination of large males does not reveal vocal sacs or slits. A previously unreported, secondary sexual character in males is the occurrence of whitish, spinous, nuptial excrescences on the thumb that, at maximal development, extend onto the chest and edge of the lower jaw. All frogs having these spinous excrescences were determined by dissection to be males. There is no pronounced enlargement of the thumb in large males. A cluster of nuptial spines first appears on the joint between the penultimate and antepenultimate phalanges. The white, spinous patch then spreads over the inner, medial surface of the thumb. With further development small excrescences appear on the medial surfaces of the second and third fingers. At maximum

development spinous excrescences also occur on the dorsal surfaces of the first two fingers (and part of the third finger), and on the edge of lower jaw and part of the chest; the excrescences are more dense on the thumb joint than elsewhere (Fig. 2). Spinous patches are not evident until males attain a body length of about 70 mm; thereafter, however, the development and extent of the excrescences does not seem to be directly correlated with size. The smallest male with spinous patches (covering only proximalmost joint of thumb) is 74.2 mm SVL (KU 87280). Two other males, both dissected, of 74.0 (UMMZ 125901) and 84.4 (KU 87283) mm SVL lack excrescences. In contrast, a male of 85.8 mm SVL (UIMNH 52782) shows the most extensive development with white, spinous excrescences on digits, chest and lower jaw (Fig. 2). This non-correlation of size with development of excrescences would seem to reflect a seasonal change with maximum development during the breeding season. If so, the breeding season is prolonged since the two males showing the most extensive development of white excrescences, UIMNH 52782 and KU 87284 of 100.3 mm SVL, were collected on 25 December 1962 and 3 June 1964, respectively.

Body proportions.—Four morphometric characters were utilized. The following measurements (mm) were recorded with a dial calipers (abbreviations used in parentheses): snout to vent length (SVL); tibia (tibio-fibula) length from heel to fold of skin on knee (TL); head length from posterior margin of tympanum to tip of snout (HL); head width at widest point, generally at level of posterior margin of tympana (HW). Six proportions of body parts (HW/SVL, HL/SVL, HL/HW, TL/SVL, HL/TL, HW/TL) were plotted against SVL; the resultant data thus reflect relative differences in width of head and length of leg. Ontogenetic variation is variable depending on the ratios utilized. Sexual dimorphism is lacking and the sexes are combined in the analysis of variation. The data are presented in Table 1. The size-group demarcation (60 mm) was initially determined by the inspection of scattergrams that depicted the most pronounced ontogenetic variation in the ratios TL/SVL, HL/TL, and HW/TL.

In the ratio HW/SVL, ontogenetic variation seems to be negligible or the HW increases at a slightly slower rate than the SVL. Ontogenetic variation is somewhat more pronounced in HL/SVL with the HL increasing at a slightly slower rate than the SVL. Heads are usually longer than broad (HL/HW exceeding 1.00). Although the data suggest much variation in small frogs, the heads tend to become relatively more broad with increasing size with some of the largest frogs having heads broader than long (two males). The ontogenetic variation in HL/HW thus seems to be reflected in the relatively slow rate of increase of HL (HW increasing at about same rate as SVL). There is more pronounced ontogenetic variation in TL/SVL with the TL increasing at a faster rate than the SVL; large frogs have on the average relatively longer legs than juveniles, with their TL averaging slightly more than half the body length. Ontogenetic variation is also expressed when the ratios HW/TL and HL/TL are plotted against SVL, with the variation most pronounced in HL/TL (owing to slow rate of increase of HL and fast rate of increase of TL relative to that of SVL).

In comparing ratios derived from body measurements in different kinds of frogs, it is necessary to determine the presence (if any) and degree of ontogenetic variation in each. The comparison of ratios may be taxonomically useful only when utilizing



FIGURE 2. Adult male of *Rana sierramadrensis* (UIMNH 52782, 85.8 mm SVL) showing white, spinous, excrescences on chest and lower jaw (above), and on dorsal surfaces of inner three digits of right forelimb (below).

TABLE 1

Ontogenetic variation in six body proportions of *Rana sierramadrensis*. The upper set of values is for frogs less than 60 mm SVL, the lower set for frogs 60 mm SVL or larger. The data for each proportion are mean \pm its standard error, one standard deviation, and range (in parentheses).

Ratio	N	Variation
HW/SVL	14	0.357 \pm 0.005, 0.018 (0.33-0.39)
	36	0.346 \pm 0.002, 0.013 (0.31-0.37)
HL/SVL	14	0.383 \pm 0.004, 0.016 (0.36-0.41)
	36	0.363 \pm 0.003, 0.016 (0.33-0.41)
HL/HW	14	1.072 \pm 0.001, 0.054 (0.97-1.15)
	36	1.043 \pm 0.006, 0.035 (0.94-1.12)
TL/SVL	14	0.506 \pm 0.008, 0.031 (0.44-0.54)
	36	0.568 \pm 0.004, 0.025 (0.53-0.63)
HW/TL	14	0.708 \pm 0.002, 0.057 (0.63-0.81)
	36	0.610 \pm 0.004, 0.026 (0.56-0.66)
HL/TL	13	0.746 \pm 0.001, 0.053 (0.67-0.84)
	36	0.638 \pm 0.005, 0.030 (0.58-0.68)

restricted size groups. An on-going study of the *R. pustulosa-tarahumarae* complex, for example, indicates differences in ontogenetic variation between taxa in some ratios. The foregoing data for *Rana sierramadrensis* may be useful to future investigators in subsequent comparisons with related species.

Larvae.—The larvae or tadpoles of *Rana sierramadrensis*, not previously described, are discussed below and compared with larvae of sympatric and related ranid species in Mexico. Three tadpoles (KU 87660, N = 4) from 3.3 km north San Vicente, Guerrero, 920 m, collected on 8 June 1964 are assigned to *R. sierramadrensis* (see below). Another tadpole included in this lot of four tadpoles is smaller (24 mm total length) than the other three; the upper tooth rows are lacking (three lower rows present), the lateral margin of the oral disc is emarginate, and the dark-blotched tail fin has numerous filamentous melanophores. This small tadpole does not seem to be representative of *Rana sierramadrensis*. The description is based on the three larger larvae that exhibit the ranid features of sinistral spiracle, dextral anus, eyes more dorsal than lateral, and a papillate fringe along the lower lip; however, the lateral margins of the oral disc are not emarginate.

The three larvae measure 38, 41, and 50 mm in total length and correspond to limb bud stages I and V, and paddle stage X, respectively, according to the ranid staging system of Taylor and Kollros (in Rugh, 1962:70-71); corresponding stages of Gosner (1960) are 25, 30, and 35. The bodies of all three larvae have obscurely margined, broad pale dorsolateral areas. All three larvae either lack or have only sparse pigmentation on the tail and fins. The ventral tail fin is completely devoid of melanophores. The mostly clear dorsal fin has only a few small scattered dark pigment

patches (dendritic melanophores) and in some places the otherwise clear parts of the fin contain some scattered punctate (not filamentous) melanophores. The tail musculature is lightly and mostly uniformly pigmented, most dense on the dorsal half, and lacks definitive spots-blotching. The relatively streamlined tail with the reduced and not highly arched dorsal fin is illustrated (smallest larva of 38 mm) in figure 3D; however, the dorsal fin seems to be slightly more arched in the two larger larvae. The lateral margins of the oral disc are not infolded between the upper and lower tooth rows. There are submarginal papillae along the sides of the upper and lower lips. The fleshy flaplike lower lip with a papillate fringe seems unusually broad (especially larva of 38 mm) and may be folded down (Fig. 3C) or up against the lower tooth rows. The oral disc is large; the relative sizes of the oral discs of *R. sierramadrensis* and the sympatric *R. pustulosa* (stages X (35) and II (26), respectively; stages of Gosner, 1960, in parentheses) are compared in similar-sized larvae in figure 3A and 3B. The tooth row formula, modified from Altig's terminology (1970), is 7(2-7)/1-4/3(1); the numbers between diagonal lines indicate rows of marginal teeth. The edges of the horny beaks are pigmented and serrated. One of the larvae (41 mm) has irregular alignment of some upper tooth row segments that number eight when counted on the left side. Careful manipulation is required to discern the short seventh upper row of teeth on the right side of the largest larva. The first upper tooth row is continuous, all other upper tooth rows are separated, most by the upper beak. Larvae may have six upper tooth rows (and perhaps eight) owing to ontogenetic and/or individual vari-

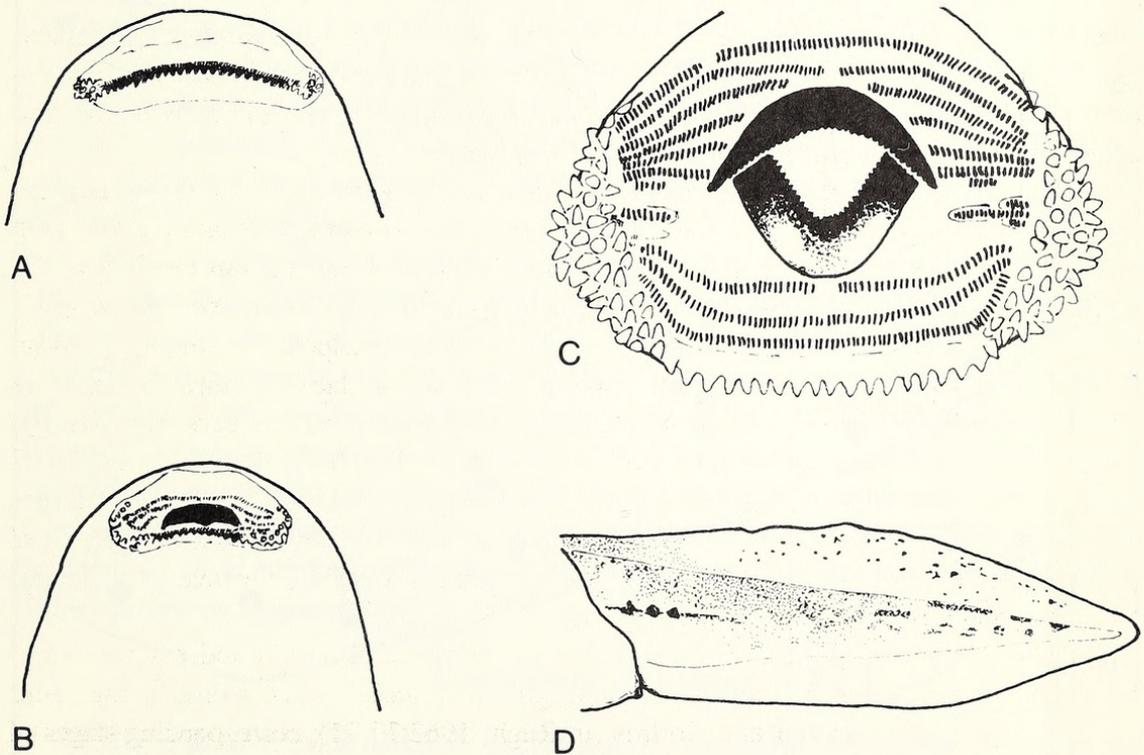


FIGURE 3. A, large oral disc of larva (50 mm total length) of *Rana sierramadrensis* (KU 87660, N = 3); B, small oral disc of larva (52 mm total length) of *Rana pustulosa*, compare with A; C, mouthparts of larva (38 mm) of *R. sierramadrensis*; D, shape and melanophore pattern of tail of larva (38 mm) of *R. sierramadrensis*.

ation. The A-2 gap is narrow (about equal to the width of five or six individual teeth) or the two lateral segments are nearly juxtaposed medially. The marginal teeth (corners of oral disc) may be scattered or arranged in rows; there are four small rows on the right side in the largest larva. The first lower tooth row is narrowly interrupted medially, the gap about equal in length to the medial gap in row A-2; the other two lower tooth rows are continuous. The oral disc and mouthparts are illustrated in figure 3C.

The three tadpoles assigned to *R. sierramadrensis* are not positively identified through direct association with metamorphosed individuals, although some such frogs (KU 87276-80) were collected at the same locality as the larvae. The three larvae are presumed to be of this species based on marked differences when compared with numerous larvae of the *R. pipiens* and *R. tarahumarae* groups from western Mexico. See subsequent section for comparison of larvae.

DISTRIBUTION

Rana sierramadrensis occurs along tropical-subtropical, foothill-montane, swift-flowing, often cascading, streams of the Sierra Madre del Sur in the Mexican states of Guerrero and Oaxaca (Fig. 4). A total of 70 specimens was examined (some of these are late-transforming frogs or are damaged and were not included in the data

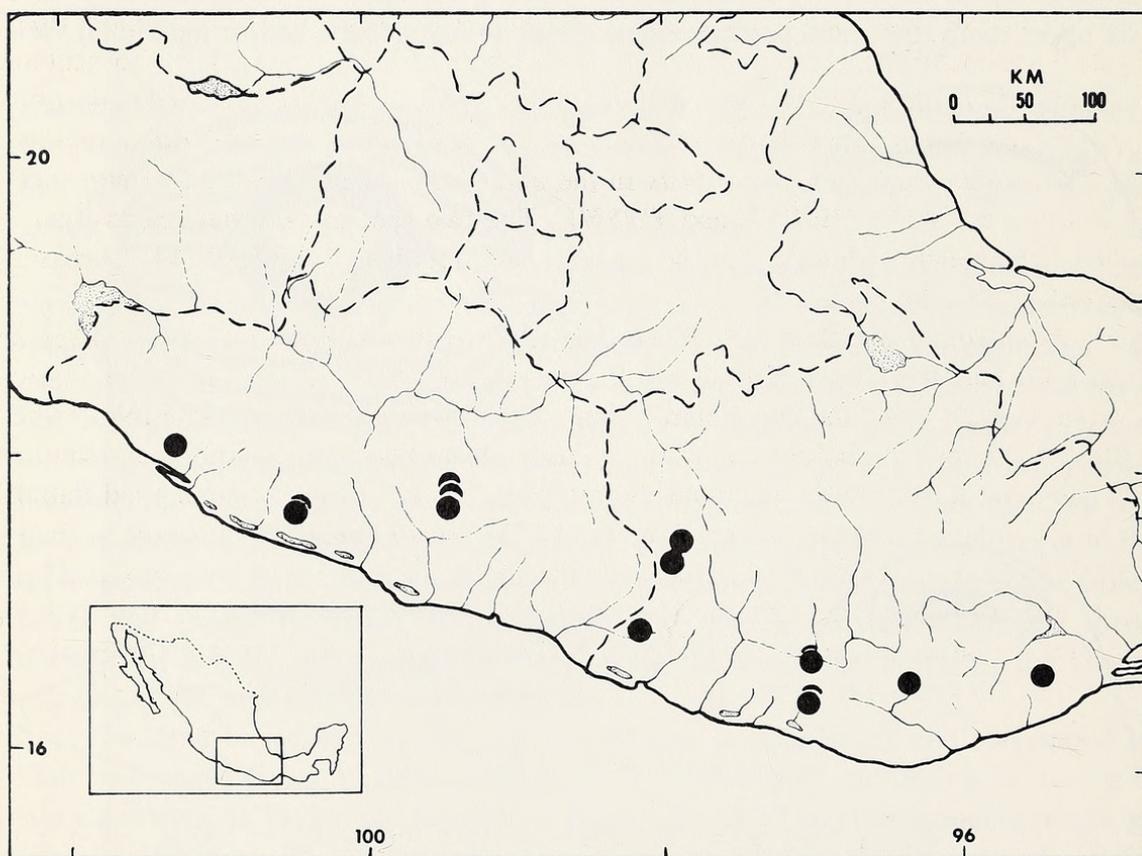


FIGURE 4. Map of southern Mexico showing localities (solid circles) for *Rana sierramadrensis* in the states of Guerrero and Oaxaca. Some localities a short distance apart share the same symbol.

analysis). The type-locality (Agua del Obispo) and other place-names in the Chilpancingo area of Guerrero were mapped by Davis and Dixon (1959).

Guerrero: near Agua del Obispo, between Rincón and Cajones (FMNH 100038, 102201-02, 103917; KU 87282; TCWC 10992; UIMNH 27053, 32442, 32444; UMMZ 115419, 125902-N = 5, 125903; USNM 114009-12; 9 km. SW Mazatlán, km. 337 (USNM 139724); 5.8 mi. S Mazatlán (UMMZ 115420); 3.7 mi. S Mazatlán (UMMZ 115421); 1 mi. SE San Andres de la Cruz (UMMZ 125901, N = 4); 3.3 km. N San Vicente (KU 87276-80); 37 km. S Chilpancingo (KU 87281); Acahuizotla (TCWC 8533-37, 8540-41, 10220-28, 26380; LACM 35054-55); 6 mi. NW San Jeronimito (UMMZ 125902, N = 5).

Oaxaca: 6 mi. N San Gabriel Mixtepec (MSU 10464); 6 km. NNW San Gabriel Mixtepec (KU 87283); 12 km. NNW San Gabriel Mixtepec (KU 87284); 14.8 km. N San Gabriel Mixtepec (KU 137539-40); Río Jalatengo, 0.8 km. S Jalatengo (KU 137538); 5.1 km. S Jalatengo (KU 137537); 13.1 km. N Juchatengo (KU 137541); 11 km. S Chicahuaxtla (MSU 12660); 3 mi. S Putla (UIMNH 52783-84); Cacahuatpec, at river (UIMNH 52782); Santa Lucía, near Tehuantepec (AMNH 52624).

COMPARISON WITH *RANA SINALOAE*

Rana sinaloae shares some features of color and pattern with *R. sierramadrensis*—evidence of dark face mask bordered below by distinct white supralabial stripes; pale dorsolateral stripes; top of head, back and sides of body mostly devoid of pattern; narrow, dark, dorsal crossbars on femora; and black, irregular-bordered, and often interrupted, ventrolateral bands on body (see comparison in Fig. 5). *Rana sinaloae* is also similar to *R. sierramadrensis* in the body proportions affected by ontogenetic variation, especially HL/SVL and TL/SVL. The two species both have heads that in most specimens are longer than broad, and have relatively long legs (TL increasing at faster rate than SVL).

Rana sinaloae differs from *R. sierramadrensis* in having folds above and behind the tympana, in lacking distinct black posttympanic bars, in lacking distinct black lateral borders along the dorsolateral folds, and in having the dorsolateral folds (when present) terminating before the groin. Perhaps most important, the breeding males of *R. sinaloae* have swollen glandular thumb pads, instead of the non-enlarged thumbs and white, spinous excrescences of males of *R. sierramadrensis*. *Rana sinaloae* shares all these features with the other included species of the *R. tarahumarae* group. There are also corresponding differences in the larvae (see below). *Rana sinaloae* is considered to be a member of the *Rana tarahumarae* group and not a member of the *Rana palmipes* species group

COMPARISON OF LARVAE

Since *R. sierramadrensis* is geographically sympatric with frogs of the *R. tarahumarae* group (currently referred to *R. pustulosa*) and *R. pipiens* group (hereafter referred to as *R. pipiens*), larvae of any one, or two, or all three, species could be expected to occur in a random sample. The larvae of *R. pipiens* are easily distinguished from those of *R. sierramadrensis* in having a maximum of three upper tooth rows

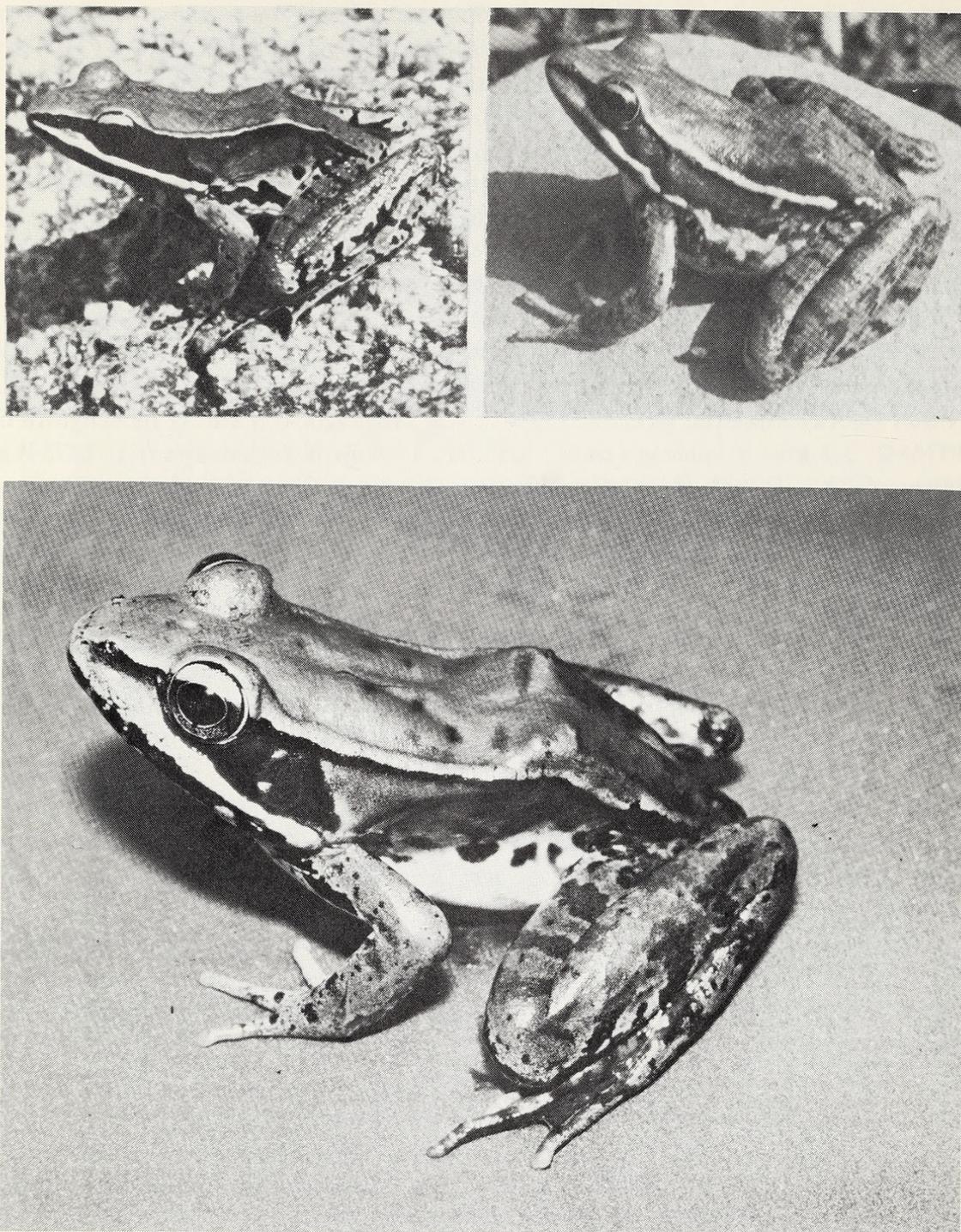


FIGURE 5. *Rana sierramadrensis* (upper left, MSU 12660, 51.3 mm SVL, 11 km. S Chicahuaxtla, Oaxaca), *Rana sinaloae* (upper right, MSU 12661, 75.8 mm SVL, 22 km. WSW Ameca, Jalisco), and *Rana maculata* (bottom, AMNH, 88 mm SVL, Finca El Rosario Vista Hermosa, ca. 7 km N Escuintla Guatemala, from kodachrome by Richard G. Zweifel), for comparison in pattern.

(but usually only two), no marginal teeth, more extensively pigmented dorsal tail fins, and in having the lateral margins of the oral disc emarginate. The larvae of *R. pustulosa* usually have some dark marks and blotches on the dorsal tail fins and musculature (mostly clear in *R. sierramadrensis*) and at least distally on the ventral fins (virtually lacking in *R. sierramadrensis*); in some larvae of *R. pustulosa* with relatively clear dorsal fins small punctate melanophores are more extensive than in *R. sierramadrensis*. The oral disc is relatively smaller in *R. pustulosa* (about two-thirds) than in *R. sierramadrensis*, and the lateral margins are infolded in larvae of *R. pustulosa* (see comparison in figure 3A, B). Less reliable is the number of upper tooth rows in distinguishing the two species, which is usually five (maximal at six) in larvae of *R. pustulosa*, and which is probably six but certainly seven in larvae of *R. sierramadrensis*. The larvae of *R. sinaloae* resemble those of *R. sierramadrensis* only in having a mostly clear dorsal tail fin; the larvae of *R. sinaloae* otherwise are not different from those of *R. pustulosa* and are distinguished from larvae of *R. sierramadrensis* by the same features that differentiate those two species.

The larvae of *R. sierramadrensis* are easily distinguished from larvae of both *R. maculata* (*macroglossa*) and *R. palmipes* (comparative data in Volpe and Harvey, 1958) in having only three lower tooth rows, and in the mostly clear tail fins. The larvae of *R. sierramadrensis* may have more highly arched dorsal fins than larvae of *R. maculata*. The larvae of *R. sierramadrensis* and *R. maculata* otherwise share several features that distinguish them from larvae of *R. palmipes*. The larvae of both species have a maximum of six or seven upper tooth rows (four or maximum of five in *R. palmipes*), have a narrow medial A-2 gap (wider in *R. palmipes*), have marginal teeth (lacking in *R. palmipes*), and have a suctorial oral disc that lacks infolded lateral margins (infolded in *R. palmipes*).

RELATIONSHIPS

Rana sierramadrensis is currently placed in the *Rana palmipes* species group (Zweifel 1954). So far as known the white, spinous excrescences in males of *R. sierramadrensis* are unique. One seemingly trenchant feature is shared with the member species of the *R. tarahumarae* group—three lower rows of teeth in larvae (the number may be variable in *R. sierramadrensis*, but is invariably three in *R. tarahumarae* group). All other member species of the *R. palmipes* group have larvae with four lower tooth rows (*R. palmipes*, *R. maculata*, *R. vibicaria*, *R. warschewitschii*); Lee (1976) referred some peculiar tadpoles from Belize with five lower tooth rows to *R. maculata*.

Variation in the two species *R. palmipes* and *R. maculata* (nearest geographically to *R. sierramadrensis*) has not been investigated in detail. In addition to other features distinguishing the two species, *R. palmipes* is especially distinctive from *R. sierramadrensis* in males having enlarged, glandular thumb pads; males of *R. palmipes* based on statements by Boulenger (1920:417), Taylor (1952:908), and Zweifel (1967:54) seem to have internal slits but lack external vocal sacs. *Rana maculata* differs from *R. sierramadrensis* in having well-developed vocal sac slits, but resembles *R. sierramadrensis* in having the thumbs "not larger than in females" (Smith 1959:216); presumably males of *R. maculata* lack the white, spinous excrescences of

R. sierramadrensis. *Rana sierramadrensis* seems to be most closely allied to, and the trans-isthmian counterpart of, *R. maculata*. Aside from the above-mentioned difference and those that readily distinguish the larvae (tail pigmentation and number of lower tooth rows), both species share general features of pattern (Fig. 5), occupy upland habitats, and have larvae with stream-adapted modifications. In pattern, *R. maculata* differs from *R. sierramadrensis* in having wider dark bars on the femora, in usually lacking a continuous black, ventrolateral band, and (at least in some specimens) in having a green dorsum (Kodachrome slide of R. G. Zweifel, Fig. 5).

RESUMEN

La variación de *Rana sierramadrensis* se discute. Los renacuajos son descritos por primera vez. Una característica secundaria sexual no conocida es la presencia de tuberculos espinosos blancos en los no engrandecidos pulgares, pecho, y mandíbulas inferiores de los machos. *Rana sierramadrensis* se retiene en el grupo *R. palmipes*. *Rana sinaloae* se traslada al grupo *R. tarahumararum*, qual se propone para inclusión de las especies *R. tarahumararum*, *R. pustulosa*, *R. sinaloae*, *R. pueblae*, y *R. johni*. *Rana sierramadrensis* ocurre solamente en la Sierra Madre del Sur en los estados Mexicanos de Guerrero y Oaxaca, y parece ser relacionada a *R. maculata*.

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