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PHYLOGENY AND TAXONOMY OF THE *RANA PALMIPES* GROUP (SALIENTIA: RANIDAE)

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ABSTRACT: The *Rana palmipes* group consists of eight species of frogs distributed from southern México to Perú, Bolivia, and Brasil. The frogs currently recognized as *R. maculata* and *R. palmipes* are composites of two and three species, respectively. Frogs previously referred to *R. maculata* from the Maya Mountains of Belize are described as a new species, *R. juliani*. The three species previously included under the name *R. palmipes* comprise the *R. palmipes* complex: *R. palmipes* of eastern South America, *R. vaillanti* of Central America and western South America, and a newly described species, *R. bwana*, of the Pacific versant of the Huancabamba Depression in southwestern Ecuador and northwestern Perú.

Morphological variation in the *R. palmipes* group (*R. bwana, R. juliani, R. maculata, R. palmipes, R. sierramadrensis, R. vaillanti, R. vibicaria,* and *R. warszewitschii*) provides information on the phylogeny of the species. The group is easily defined on the basis of morphological and biochemical characters. Within the *R. palmipes* group, there is a primary dichotomy between the lowland species (*R. bwana, R. palmipes,* and *R. vaillanti*) and the montane species (*R. juliani, R. maculata, R. sierramadrensis, R. vibicaria,* and *R. warszewitschii*). Within this latter group, the southern Central American species (*R. vibicaria* and *R. warszewitschii*) form one clade and the northern Central American species (*R. sierramadrensis, R. juliani,* and *R. maculata*) form another clade. Within the northern Central American clade, *R. maculata* and *R. sierramadrensis*, which are separated by the Isthmus of Tehuantepec, are sister species. Diagnostic keys for both adults and tadpoles are provided for the species groups of Neotropical *Rana* as well as for the species of the *Rana palmipes* group.

Key words: Salientia; *Rana*; Phylogeny; Systematics; Taxonomy; Biogeography

> "I am not satisfied that the different names [in the synonymy of *Rana palmipes*] really refer to the same species. The difficulty is not likely to be solved soon—first, because the typical specimens are evidently in an indifferent state of preservation, and, secondly, because no collection contains sufficient material from the various localities of Tropical America to permit a satisfactory examination" [A. C. L. G. Günther, 1900].

THE *Rana palmipes* group has never been reviewed systematically, primarily because the problems noted by Günther in 1900 (see quote above) are still largely true today. The *R. palmipes* group is widely distributed from México to Perú, Bolivia, and Brasil, and few collections contain specimens from throughout this region. Although the montane Middle American species are relatively well known (Villa, 1979; Webb, 1978; Zweifel, 1964), the widespread *R. palmipes*, as currently conceived, has never been examined in a comparative sense from throughout its range.

As currently recognized, *R. palmipes* ranges from central México south through Central America, along the Pacific coast of South America to Perú, and east of the Andes through the Orinoco and Amazon basins to eastern Brasil. Although this one-taxon viewpoint has been dominant during this century, few if any systematists who have examined specimens of *R. palmipes* from throughout its range have accepted the validity of this concept without reservations (e.g., Cochran and Goin, 1970; Fowler, 1913; Günther, 1900). Although frogs of this nominal species are common, most museum collections contain specimens from a limited geographical area. Günther (1900), for example, was frustrated in attempts to understand the systematics of *R. palmipes* by the lack of comparative material. More recently, Cochran and Goin (1970) mentioned the possible composite nature of *R. palmipes*, but noted that an analysis of this species throughout its range was necessary in order to solve the problem.

Taxonomic problems in the *R. palmipes* group are not limited to *R. palmipes*. Lee

Representatives of the *Rana palmipes* species group. Clockwise from upper left: *Rana vibicaria* (not captured) from Monteverde, Puntarenas, Costa Rica, photographed by Michael and Patricia Fogden; *Rana sierramadrensis* (KU 195181) from Aqua del Obispo, Guerrero, México, photographed by William W. Lamar; *Rana warszewitschii* (not captured) from Corcovado National Park, Puntarenas, Costa Rica, photographed by Michael and Patricia Fogden; *Rana maculata* (KU 195106) from 10.7 km N Patulul, Suchitepéquez, Guatemala, photographed by William W. Lamar.

(1976) reported a population of *Rana* from the Maya Mountains of Belize, based on a series of tadpoles and one metamorphosed juvenile, that he referred to *R. maculata*. Lee (1976) noted, however, that these tadpoles were distinctive in several respects from previously described tadpoles of *R. maculata*. Several other authors (Hillis, 1985; Villa, 1979; Webb and Korky, 1977) questioned the identification of these specimens, but until now no adults were available from this population for comparison to *R. maculata*.

A comparison of living and preserved specimens from throughout the ranges of the nominal species *R. palmipes* and *R. maculata* confirmed earlier authors' suspicions: there are three species to which the name *R. palmipes* is applied and two species to which the name *R. maculata* is applied. Names are available for two widespread members of the *R. palmipes* complex (*R. palmipes* and *R. vaillanti*). We describe herein two new species of *Rana*, provide a systematic review of the *R. palmipes* group, and discuss the phylogenetic history and biogeography of these frogs.

Keys to the Species Groups of Neotropical *Rana*

The following keys are applicable to all *Rana* that occur from México through South America. The *R. catesbeiana* group is distributed mostly north of this region; *R. catesbeiana* is the only member of this group that penetrates the Neotropics. This species occurs south to northern Veracruz, México, but is not sympatric with any member of the *R. palmipes* group. The *R. tarahumarae* group occurs from Arizona, USA, south through western México to northern Oaxaca, with two isolated species in eastern México (San Luís Potosí, Hidalgo, and Puebla). Only one species in this group (*R. zweifeli*) occurs sympatrically with a member of the *R. palmipes* group (*R. sierramadrensis*). The *R. pipiens* complex occurs from Canada to Panama, and several species in the *R. berlandieri* group of the *R. pipiens* complex are broadly sympatric with members of the *R. palmipes* group.

Key 1: Post-metamorphic Individuals

1. Distinct post-tympanic folds present .. 2
   No distinct post-tympanic folds 3
2. Tympana large (as large as eyes in females, larger than eyes in males); vocal slits and sacs present in males .... *R. catesbeiana*
   Tympana small (much smaller than eyes in both sexes), indistinct, or absent; vocal slits and sacs absent in males .... *R. tarahumarae* group
3. Skin smooth or rugose, but not denticulate; toe tips not expanded; sacral and presacral vertebrae not fused; usually with distinct dorsal blotches (may be obscure in large adults) .... *R. pipiens* complex
   Skin denticulate; toe tips expanded; sacral and presacral vertebrae fused; black borders along dorsolateral folds ..... *R. palmipes* group

Key 2: Tadpoles
[*Gosner (1960) Stage 25 and Later*]

1. Tooth formula 1–3(2–3)/2–3(1) (if upper rows 3, then lower rows 3); oral disk emarginate; marginal teeth absent .. 2
   Tooth formula 3–7(2–7)/3–4(1) (if upper rows 3, then lower rows 4); oral disk emarginate or not; marginal teeth present or absent 3
2. Tail and body olive-green with distinct black dots ..... *R. catesbeiana*
   Tail and body light tan to dark brown or black; body unicolored or vaguely blotched; tail weakly to strongly blotched ..... *R. pipiens* complex
3. Lower tooth rows 3; oral disk emarginate ..... *R. tarahumarae* group
   Lower tooth rows 3–5; if 3, oral disk not emarginate; otherwise, oral disk emarginate or not ..... *R. palmipes* group

Keys to the Species of the *Rana palmipes* Group

Key 3: Post-metamorphic Individuals

1. Tympanum large (greater than eye diameter); no distinct dark face mask; no distinct supralabial stripe 2
   Tympanum small (less than eye diameter); dark face mask present; light supralabial stripe present 4
2. Marked with numerous dark dorsal blotches (Fig. 1); no vocal sacs or slits in males; no distinct thigh or tibial crossbars; northwestern Perú and southwestern Ecuador ..... *R. bwana*

Dorsal blotches scattered or absent (Figs. 7, 9); vocal sacs and slits often present in males; thigh and/or tibial crossbars usually present 3

3. Ratio of tibial length/interorbital distance less than 6 (range 4.85–5.85; $\bar{x} \pm$ SD = 5.32 ± 0.27); South America east of Andes ..... *R. palmipes*

Ratio of tibial length/interorbital distance greater than 6 (range 6.31–7.81; $\bar{x} \pm$ SD = 7.01 ± 0.39); lowlands of Middle America and Pacific lowlands of Colombia and Ecuador .. *R. vaillanti*

4. Two metatarsal tubercles on each foot; toe pads present; webbing on hindfeet reduced (I 1–2 II 1–2 or 1–3 III 1–2 or 1–3 IV 3–1 V) 5

One metatarsal tubercle on each foot; toe pads absent; webbing on hindfeet nearly full (I 0–0 or 0–1 II 0–1 III 0–0 or 0-1 IV 0–0 or 1–0 V) 6

5. Axilla, groin, and posterior surfaces of limbs red in life, uniform yellow-brown in alcohol; highlands of Costa Rica and western Panama ..... *R. vibicaria*

Concealed surfaces of thighs with 2–5 distinct light (cream to yellow) spots on a dark background; southern Honduras to eastern Panama .... *R. warszewitschii*

6. Tympana nearly as large as eyes; vocal sacs and slits absent in adult males; sides distinctly darker than dorsum; Maya Mountains of Belize ... *R. juliani*

Tympana approximately half the diameter of eyes or less 7

7. Continuous dark ventrolateral stripe present; femoral crossbars approximately one-half width of intervening spaces; vocal sacs and slits absent in adult males; breeding males with extensive denticles on anterior venter and forearms; Sierra Madre del Sur of Guerrero and Oaxaca, México .... *R. sierramadrensis*

Dark ventrolateral stripe broken or absent; femoral crossbars approximately as wide as intervening spaces; internal vocal sacs and slits present in adult males; montane and foothill regions east of the Isthmus of Tehuantepec, México, southeast to central Nicaragua ..... *R. maculata*

Key 4: Tadpoles
[*Gosner (1960) Stage 25 and Later*]

1. Tooth row formula 3–4(2–4)/4(1); marginal teeth absent 2

Tooth row formula 5–7(2–7)/3–6(1); marginal teeth present or absent 4

2. Upper tooth rows 3; oral disk not emarginate ..... *R. bwana*

Upper tooth rows 4; oral disk emarginate 3

3. Body length prior to metamorphosis 40–60 mm; tail fins usually with scattered, small dark spots, rarely heavily mottled ..... *R. palmipes*

Body length prior to metamorphosis 20–40 mm; tail fins usually heavily mottled ..... *R. vaillanti*

4. Marginal teeth absent; tooth row formula 5–6(2–6)/4(1) 5

Marginal teeth present; tooth row formula 5–7(2–7)/3–6(1) 6

5. Oral disk emarginate ..... *R. vibicaria*

Oral disk not emarginate .... *R. warszewitschii*

6. Lower tooth rows 3; oral disk not emarginate ..... *R. sierramadrensis*

Lower tooth rows 4–6; oral disk emarginate or not 7

7. Oral disk emarginate; lower tooth rows 5–6 ..... *R. juliani*

Oral disk not emarginate; lower tooth rows 4 ..... *R. maculata*

Species Accounts

In the following accounts, diagnostic characters are numbered and presented in a uniform fashion for each species. Descriptions of the holotypes and discussions of related species are provided for the new species. Specimens examined are listed in the Appendix. Tadpole tooth row formulae follow Altig (1970); webbing formulae follow Savage and Heyer (1967).

Rana ***bwana*** sp. nov.
(Figs. 1, 2)

Holotype.—Los Angeles County Museum of Natural History (LACM) 49205, an adult female from 1.5 km S Las Lomas, Río Chipillico, Piura Department, Perú, collected 7 December 1968 by James R. Dixon and John W. Wright.

Paratypes.—LACM 49190–204, 49206–12, 49213 (41 tadpoles), 49214, 49282; Texas Cooperative Wildlife Collection, Texas A&M University (TCWC) 28769–800, 28922, same data as holotype; TCWC 28801–02, 4.6 km ESE Las Lomas, Piura Department, Perú; TCWC 28801–02, 4.6

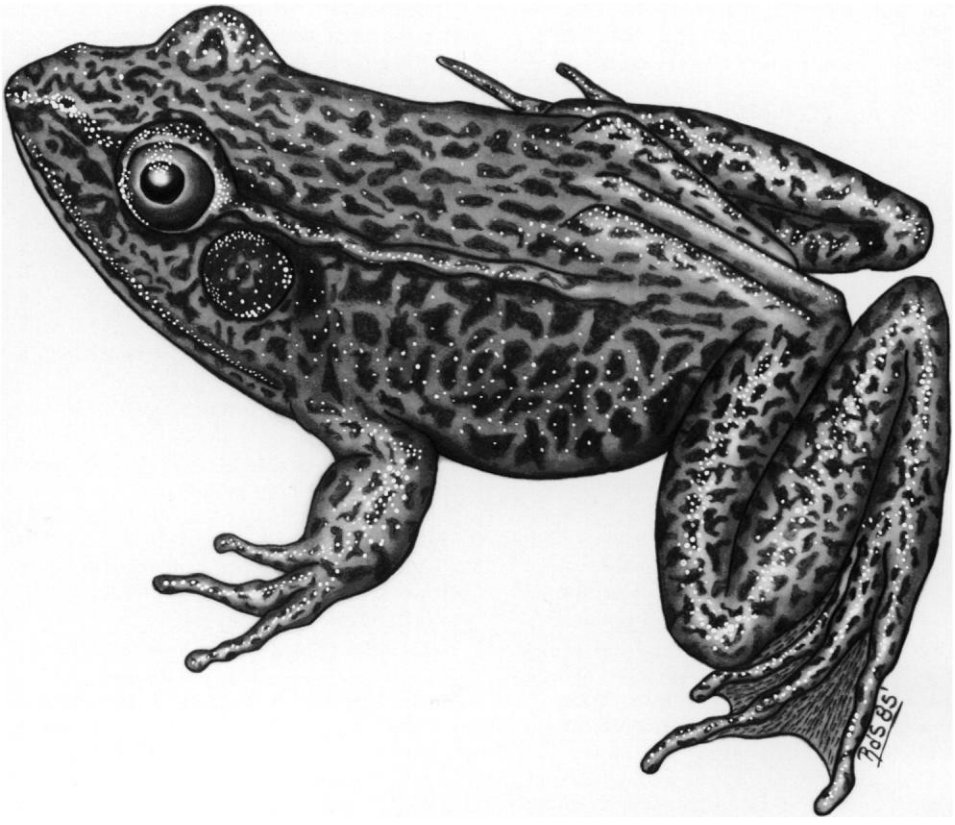

FIG. 1.—Holotype of *Rana bwana* (LACM 49205).

km W Suyo, Piura Department, Perú; Texas Natural History Collection, University of Texas (TNHC) 37414–15, 24 km N Macará, Loja Province, Ecuador.

Definition.—1) Larval tooth formula: 3(2–3)/4(1); 2) larval marginal teeth absent; 3) larval oral disk not emarginate; 4) toe tips slightly expanded; 5) vocal slits absent; 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused; 8) tympanum large, equaling or slightly exceeding diameter of eye; 9) one metatarsal

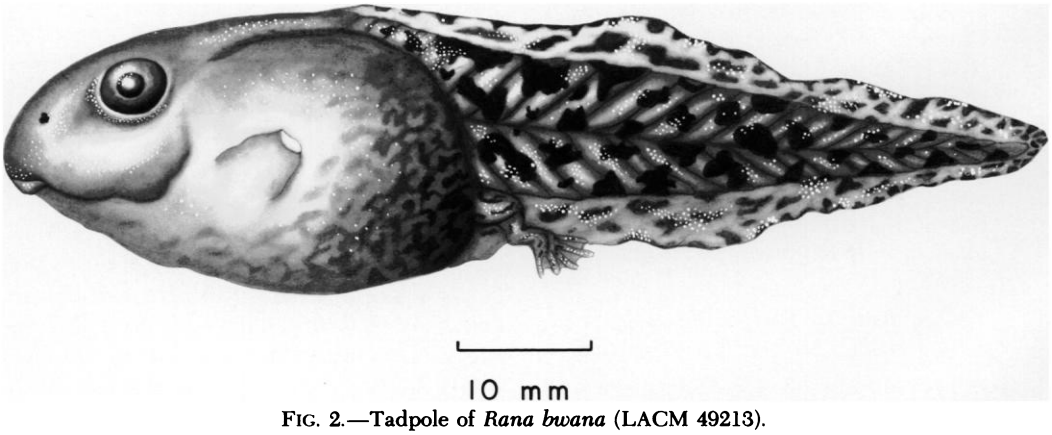

FIG. 2.—Tadpole of *Rana bwana* (LACM 49213).

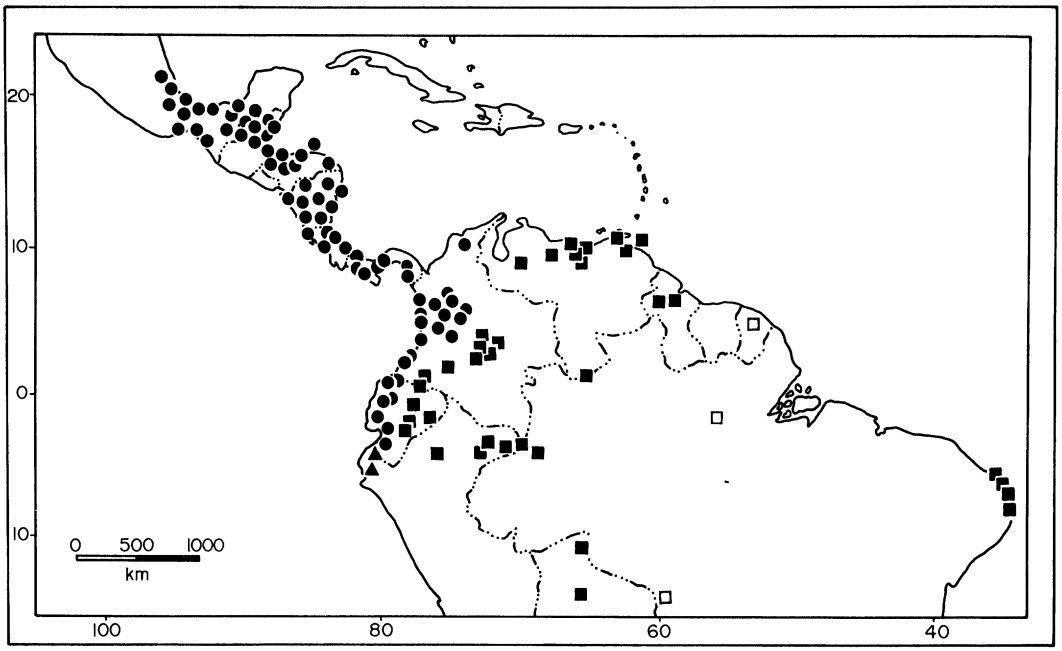

FIG. 3.—Distribution of members of the *Rana palmipes* complex. Circles represent locality records for *Rana vaillanti*; squares represent records for *Rana palmipes* (specimens represented by open squares were not examined; see Appendix and Miranda-Ribeiro, 1923); triangles represent records for *Rana bwana*. Multiple localities in close proximity are represented by a single symbol.

tubercle; 10) webbing of hindfeet: I 0–1 II 0–1 III 0–0 IV 0–0 V; 11) no supralabial stripe; 12) black border along dorsolateral folds; 13) no black face mask; 14) color in alcohol—dorsum covered with numerous dark blotches; tympanum darkly pigmented; no cross bars on tibia or thighs (also see description of holotype); 15) adult snout–vent length (SVL) 65–95 mm females, 53–63 mm males.

Description of holotype.—Snout–vent length: 92.4 mm; tibial length: 48.1 mm; head width: 38.2 mm; head length: 36.3 mm; foot length: 46.5 mm; tarsus length: 26.7 mm; eye–naris distance: 9.2 mm; interorbital distance: 7.1 mm; internarial distance: 8.6 mm; tympanum diameter: 8.6 mm; eye–tympanum distance: 3.1 mm. Webbing of hindfeet extends from tip of first toe to penultimate phalanx of second, from tip of second to the penultimate subarticular tubercle of third, and from tip to tip between the third and fourth and between the fourth and fifth toes. Dorsal and lateral coloration (in alcohol) grayish brown with numerous dark brown to black blotches that cover the dorsal portions of the body, head, eyelids, and limbs. The throat and venter are nearly uniform cream with slightly dusky coloration posteriorly. The dorsolateral folds and tympana are bordered with dark black pigment.

Distribution.—Pacific versant of the Huancabamba Depression, in tributaries of the Río Chira in the Department of Piura, Perú, and the Province of Loja, Ecuador. Recorded from the Río Chipillico and Río Quiroz in Perú and the Río Catamayo in Ecuador, at elevations of 300–700 m (Fig. 3).

Related species.—*Rana bwana* is related to *R. palmipes* and *R. vaillanti*; these three species compose the *R. palmipes* complex. *Rana bwana* can be readily distinguished from the other two species (Figs. 7–10) by its distinctive pattern of numerous dorsal blotches, the lack of thigh or tibial crossbars, and by consistent morphometric differences and distinct tadpoles (see below). Males of *R. bwana* also consistently lack vocal sacs and slits, whereas these structures are present in most

TABLE 1.—Morphometric variables included in discriminant function analysis. Values presented are means ± 1 standard deviation; ranges are in parentheses. All values are in millimeters. Variables preceded by an asterisk were selected by the program for inclusion in the discriminant functions.

Variable	*R. bwana* $n = 10$	*R. palmipes* $n = 60$	*R. vaillanti* $n = 60$
*Snout–vent length	83.1 ± 8.70 (66.0–94.6)	92.0 ± 12.50 (55.4–116.4)	91.3 ± 10.80 (66.9–108.1)
*Tibial length	42.8 ± 4.12 (34.4–48.1)	47.3 ± 6.07 (29.5–59.7)	49.8 ± 6.04 (35.3–61.6)
*Head width	32.9 ± 3.90 (26.3–38.2)	35.8 ± 4.90 (20.8–45.1)	34.0 ± 4.18 (24.4–41.2)
*Head length	31.7 ± 3.57 (26.0–36.6)	35.7 ± 4.77 (20.6–44.1)	35.1 ± 4.03 (27.1–42.6)
*Eye–naris distance	7.7 ± 0.89 (6.3–9.2)	8.8 ± 1.10 (5.4–11.5)	9.1 ± 1.15 (6.5–11.5)
*Interorbital distance	6.3 ± 0.55 (5.4–7.1)	8.9 ± 1.16 (5.9–12.2)	7.1 ± 0.87 (4.7–8.6)
*Internarial distance	7.2 ± 0.68 (6.2–8.6)	8.1 ± 0.99 (5.4–10.5)	7.7 ± 0.85 (5.8–9.1)
Foot length	42.8 ± 4.13 (34.4–47.9)	49.2 ± 6.07 (30.3–60.6)	49.2 ± 5.68 (36.1–60.7)
Tarsus length	23.2 ± 2.47 (18.2–26.7)	25.4 ± 3.35 (15.4–32.6)	26.8 ± 3.37 (19.2–33.7)
Tympanum diameter	7.4 ± 0.73 (6.3–8.6)	8.3 ± 1.07 (4.8–10.5)	8.0 ± 0.80 (6.1–10.0)
Eye–tympanum distance	2.8 ± 0.50 (2.1–3.8)	3.4 ± 0.67 (1.9–4.9)	3.5 ± 0.80 (1.4–6.1)

sexually mature male *R. vaillanti* (88.7%) and many male *R. palmipes* (42.8%).

Morphometric analysis.—Samples from throughout the ranges of *R. bwana, R. palmipes,* and *R. vaillanti* were measured for the purposes of a discriminant function analysis (BMDP7M; Dixon et al., 1981). Specimens of *R. palmipes* from Bolivia, eastern Colombia, Guyana, eastern Ecuador, eastern Perú, and Venezuela; of *R. vaillanti* from western Colombia, western Ecuador, Guatemala, México, Nicaragua, and Panama; and of *R. bwana* from northwestern Perú were used in the analysis (see Appendix). The following measurements were taken: snout–vent length, tibial length, head width, head length, hindfoot length, tarsus length, eye–naris distance, interorbital distance, internarial distance, tympanum diameter, and eye–tympanum distance. Means, ranges, and standard deviations of these variables for the three species are presented in Table 1. The program was stopped when *F*'s-to-remove of all variables in the model were above the $\alpha = 0.05$ level of significance ($F_{2,127} = 3.06$) and none of the *F*'s-to-enter of variables not in the equation were above this level.

Seven of the variables were found to be significantly different in combination among the groups and were selected by the program to enter into the discriminant functions. These variables, in order of entry, were interorbital distance (X_1), tibial length (X_2), head width (X_3), head length (X_4), eye–naris distance (X_5), internarial distance (X_6), and snout–vent length (X_7). These measures were combined into the following canonical variables:

$$\begin{aligned} \text{CVI} = &-2.60X_1 + 0.18X_2 - 0.65X_3 \\ &+ 0.33X_4 + 0.79X_5 + 0.65X_6 \\ &+ 0.13X_7 + 1.05 \\ \text{CVII} = &-1.28X_1 - 0.06X_2 + 1.51X_3 \\ &- 1.38X_4 - 0.70X_5 + 0.86X_6 \\ &+ 0.05X_7 + 3.96 \end{aligned}$$

These two canonical variables can be used to discriminate completely among the three species (Fig. 4). *Rana palmipes* is separated from the other two species primarily along canonical axis I. Therefore,

R. palmipes can be distinguished from *R. bwana* and *R. vaillanti* by its wider interorbital distance, shorter legs, wider but shorter head, and shorter eye–naris and internarial distances. *Rana bwana* is similar to *R. vaillanti* on canonical axis I, but is differentiated from both *R. vaillanti* and *R. palmipes* on canonical axis II. Therefore, *R. bwana* is distinct in its combination of small interorbital distance, intermediate limb length, broad but short head, and large internarial distance.

Larvae.—The tadpoles of *R. bwana* are known from a single lot of 41 specimens (LACM 49213). These tadpoles have relatively short, muscular tails; large, rounded bodies; low tail fins; and large, dark body and tail blotches (Fig. 2). They are also unique among species in the *R. palmipes* group in tooth formula [3(2–3)/4(1)]; all other species in this group have at least four upper rows (one specimen examined has a highly abbreviated fourth row on one side). The tadpoles of *R. bwana* are also distinct from those of *R. palmipes* and *R. vaillanti* in that the oral disk is not emarginate.

Vocalizations.—None known.

Etymology.—This species is named in honor of one of the collectors of the holotype, James R. Dixon, affectionately known to his students and colleagues as "Bwana Jim." The specific epithet *bwana* is a noun in apposition.

Rana juliani sp. nov.
(Fig. 5)

Rana maculata (in part): Henderson and Hoevers (1975), Lee (1976), Webb and Korky (1977), Villa (1979).

Holotype.—University of Texas at Arlington (UTA) 9068, an adult male from SW end of Little Quartz Ridge, Maya Mountains, Toledo District, Belize, 16°24′ N, 89°6′ W, elevation 915 m, collected 21 June 1983 by W. F. Pyburn, P. B. Medley, and C. W. Truitt.

Paratypes.—UTA 9067 (adult male), 9069–79 (tadpoles), same data as holotype; University of Kansas, Museum of Natural History (KU) 157161 (juvenile), 157162 (12 tadpoles), 23.2 km S Georgeville, Little Vaquero Creek, Cayo District, Belize, collected 30 August 1974 by Julian C. Lee.

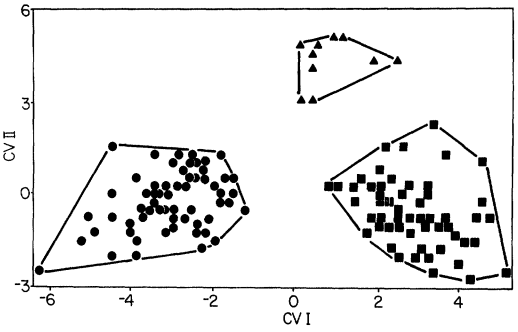

FIG. 4.—Scattergram of specimens of *Rana bwana* (triangles), *Rana palmipes* (circles), and *Rana vaillanti* (squares) for canonical variables I and II as determined in the discriminant function analysis.

Definition.—1) Larval tooth formula: 5–7(2–7)/5–6(1); 2) larval marginal teeth present; 3) larval oral disk emarginate; 4) toe tips expanded; 5) vocal sacs and slits absent; 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused; 8) tympanum large, subequal to eye diameter; 9) one metatarsal tubercle; 10) webbing of hindfeet: I 0–1 II 0–1 III 0–1 IV 1–0 V; 11) supralabial stripe present; 12) black border along dorsolateral folds; 13) black face mask present; 14) color in life—dusky blotches ventrally, uniform dark brown laterally, and medium brown dorsally with scattered dark blotches; 15) adult SVL 69–70 mm (2 males).

Description of holotype.—Snout–vent length: 69.8 mm; tibial length: 40.8 mm; head width: 23.7 mm; head length: 26.7 mm; foot length: 35.3 mm; tarsus length: 21.0 mm; eye–naris distance: 7.0 mm; interorbital distance: 5.3 mm; internarial distance: 6.1 mm; tympanum diameter: 7.0 mm; eye–tympanum distance: 1.9 mm. Nearly uniform medium brown dorsally (in alcohol) with a few scattered dark brown markings; dark brown laterally (below dorsolateral fold), except for a lighter brown tympanum and a cream supralabial stripe; thin crossbars on dorsal surfaces of hindlimbs; dark cream ventrally with dark brown mottling concentrated on undersurfaces of limbs and throat. Tympanum large, extending from dorsolateral fold to supralabial stripe. Toe tips expanded. Side

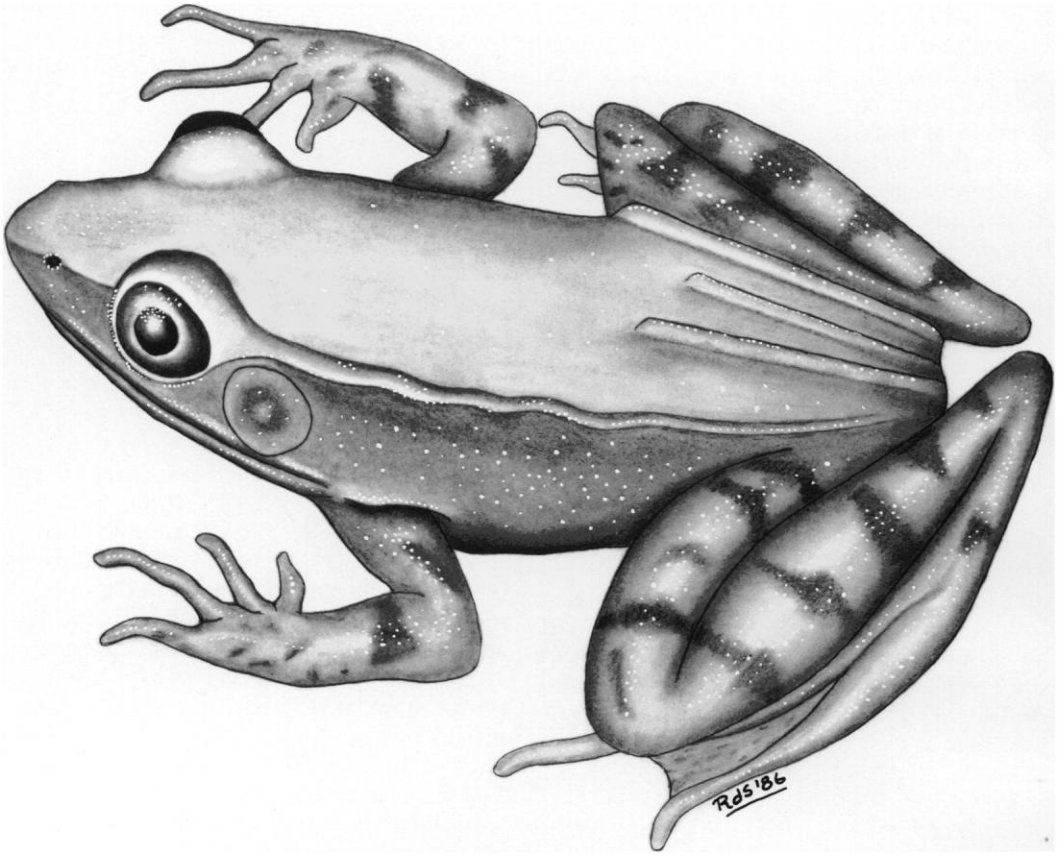

FIG. 5.—Holotype of *Rana juliani* (UTA 9068).

of body covered with raised striations; dorsal surfaces denticulate. Dorsolateral folds thin, distinct, and bordered by dark pigment.

Distribution.—*Rana juliani* is known from two localities (450 and 915 m elevation) in the Maya Mountains of Belize, on Little Quartz Ridge and Mountain Pine Ridge (Fig. 6).

Related species.—As noted by Lee (1976), this species is phenotypically similar to *R. maculata*. The two species are easily distinguished, however, by the following characteristics. The tympana of *R. maculata* are much smaller (approximately half the diameter of the eyes) than those of *R. juliani* (slightly subequal to diameter of eyes). Vocal sacs and slits are absent in *R. juliani* and present in *R. maculata*. Lateral coloration in *R. juliani* is uniform dark brown, whereas in *R. maculata* it is blotched. Femoral crossbars are much narrower than the intervening spaces in *R. maculata*. The tadpoles of *R. maculata* possess four lower tooth rows, whereas those of *R. juliani* possess at least five and sometimes six. The oral disk of tadpoles of *R. maculata* is not emarginate, whereas that of *R. juliani* tadpoles is emarginate. Transformed specimens of *R. juliani* may be distinguished from specimens of the geographically close *R. vaillanti* by the presence of a dark face mask and a light supralabial stripe, the absence of vocal sacs and slits in males, and by the smaller size at sexual maturity. The tadpoles of *R. juliani* and *R. vaillanti* are easily distinguished by the number of both upper tooth rows (5–7 in *R. juliani*, 4 in *R. vaillanti*)

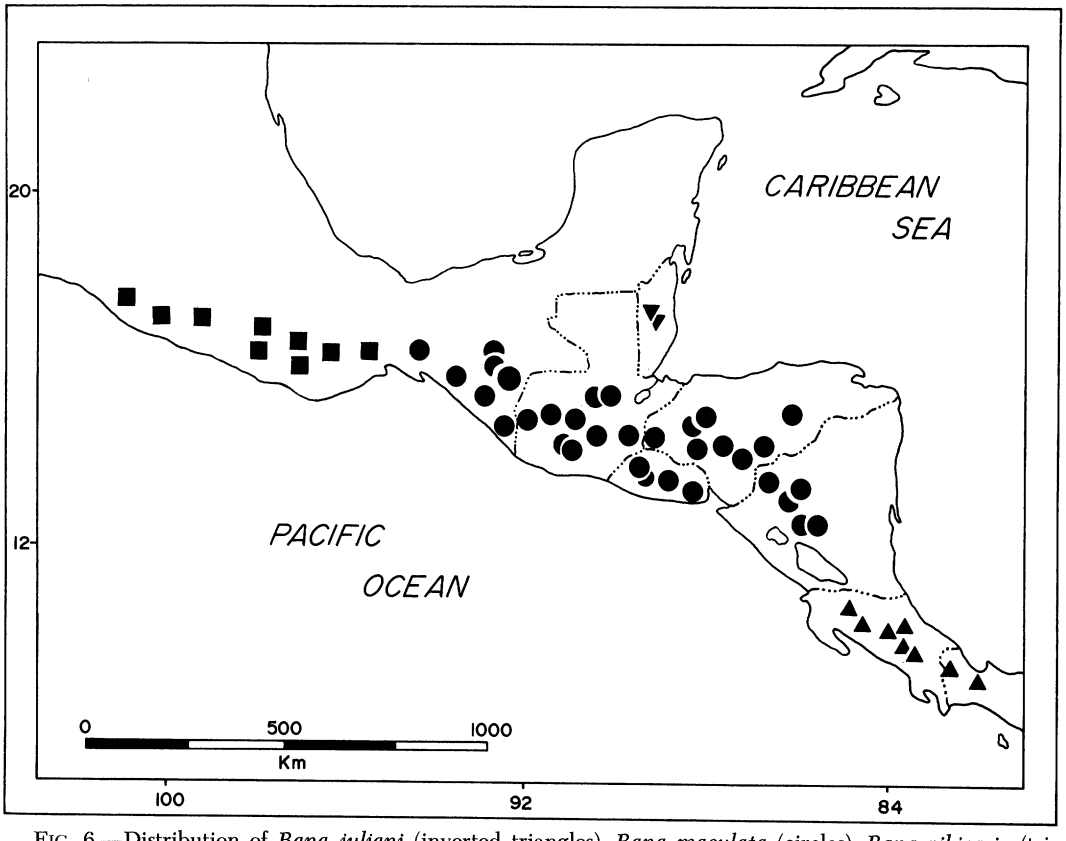

FIG. 6.—Distribution of *Rana juliani* (inverted triangles), *Rana maculata* (circles), *Rana vibicaria* (triangles), and *Rana sierramadrensis* (squares).

and lower tooth rows (5–6 in *R. juliani*, 4 in *R. vaillanti*).

Larvae.—A series of *R. juliani* tadpoles (KU 157162, 12 specimens) was described in detail by Lee (1976) as *R. maculata*. Lee (1976) also illustrated the mouth and a lateral view of one of these specimens. An additional 23 tadpoles (UTA 9069–79) were collected at the type locality along with the holotype. These specimens (stages 25–41; Gosner, 1960) agree very closely with the description provided by Lee (1976), except that the maximum number of upper tooth rows in the UTA series is seven rather than six.

Vocalizations.—None known.

Etymology.—This species is named in honor of the collector of the first specimens of the species, Julian C. Lee. This patronym is especially appropriate in view of the large toothy mouth of the tadpoles of this species.

Rana maculata Brocchi
(Frontispiece)

Rana maculata Brocchi, 1877:178 [Syntypes—Museum National d'Histoire Naturelle (MNHN) 6412, 6412A, 6412B; MNHN 6412A from "Totonicapam (Mexique)" (= Totonicapan, Guatemala) designated lectotype by Smith et al. (1966:171)].

Rana melanosoma Günther, 1900:203 [Syntypes—British Museum (Natural History) (BMNH) 1947.2.2.14–16, from "Dueñas," Guatemala, and "Hacienda Rosa de Jericho," Nicaragua].

Rana maculata krukoffi Smith, 1959:215 [Holotype—University of Illinois Museum of Natural History (UIMNH) 10526, from "Finca Juárez, 7 leagues NE Escuintla, Chiapas," México].

Definition.—1) Larval tooth formula: 5–7(2–7)/4(1); 2) larval marginal teeth

present; 3) larval oral disk not emarginate; 4) toe tips expanded; 5) internal vocal sacs and slits present; 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused; 8) tympanum small, much smaller than diameter of eye; 9) one metatarsal tubercle; 10) webbing of hindfeet: I 0–1 II 0–1 III 0–1 IV 1–0 V; 11) supralabial stripe present; 12) black border along dorsolateral folds; 13) black face mask present; 14) color in life—uniform or blotched brown to bright green dorsally, light brown (usually with dark brown blotches) laterally, dark brown crossbars on legs approximately as wide as intervening spaces; 15) adult SVL 60–113 mm females, 50–75 mm males.

Distribution.—Moderate to high elevations (800–2700 m) from eastern Oaxaca (east of the Isthmus of Tehuantepec), México, south and east to central Nicaragua (Fig. 6). Records for lowland areas of Nicaragua (Lee, 1976; Villa, 1972) represent misidentified specimens of *R. vaillanti* (Villa, 1979).

Eggs, larvae, and reproduction.—Tadpoles of this species were first described as an "unknown hylid" by Stuart (1948). Stuart (1951) corrected the identification for that description and provided excellent illustrations of the tadpole and its mouthparts. Tadpoles of *R. maculata* have thick, muscular tails and streamlined bodies. The tail and fins are usually heavily blotched.

Eggs and egg masses of *R. maculata* were described by Mertens (1952) and in more detail by Villa (1979). Mertens (1952) reported floating egg masses of *R. maculata* in ponds in El Salvador, whereas Villa (1979) found egg masses of this species only in flowing water, where they were always submerged and attached to hard substrate. Developing embryos are 2.1–2.9 mm in diameter and are surrounded by two jelly coats (2.7–3.9 mm and 3.9–4.8 mm in diameter, respectively; Villa, 1979).

Stuart (1951, 1954) noted that *R. maculata* tadpoles and calling males may be found throughout the year in montane streams in Guatemala and concluded that this species probably has an extended breeding season. Mertens (1952) found recently laid egg clutches, amplexing pairs, and large tadpoles of *R. maculata* in September in El Salvador, the height of the rainy season. In contrast, Villa (1979) reported that *R. maculata* breeds exclusively in the dry season (November–May) in Nicaragua.

Vocalizations.—Although breeding has been observed by several authors (Mertens, 1952; Stuart, 1954; Villa, 1979) and calling activity of males has been reported (Stuart, 1954), the vocalizations have not been described in the literature.

Comments.—The name *R. macroglossa* Brocchi (1877) has been used by some authors in the past for this species. The type series of *R. macroglossa* contains both *R. maculata* and *R. berlandieri* (Hillis, 1985). Smith et al. (1966) designated MNHN 6321, a specimen of *R. berlandieri*, as the lectotype for *R. macroglossa*. However, *Rana maculata* Brocchi is a junior primary homonym of *Rana maculata* Daudin (which is the senior synonym of *Eleutherodactylus richmondi* Stejneger). Smith et al. (1966) proposed suppression of *Rana maculata* Daudin in order to preserve current usage of both *Rana maculata* Brocchi and *Eleutherodactylus richmondi* Stejneger. The International Commission on Zoological Nomenclature has not yet ruled on this proposal, so current usage is followed here. If the Commission rules against the proposal, the lectotype designation of *Rana macroglossa* by Smith et al. (1966) remains valid (unless separately suppressed by the Commission), and the next available name for this species is *R. melanosoma* Günther.

Rana palmipes Spix
(Figs. 7, 8)

Rana palmipes Spix, 1824:5 [Syntypes—Zoologisches Sammlung des Bayerischen Staates (ZSM) 963/0 (2 specimens, now lost, although one is figured in Spix, 1824) from "Amazonenfluss" (= Amazon River), Brasil].

Ranula gollmerii Peters, 1859:402 [Holotype—Universität Humboldt, Zoologisches Museum (ZMB), now believed lost; from "Caracas," Venezuela; specimen described as a recently transformed

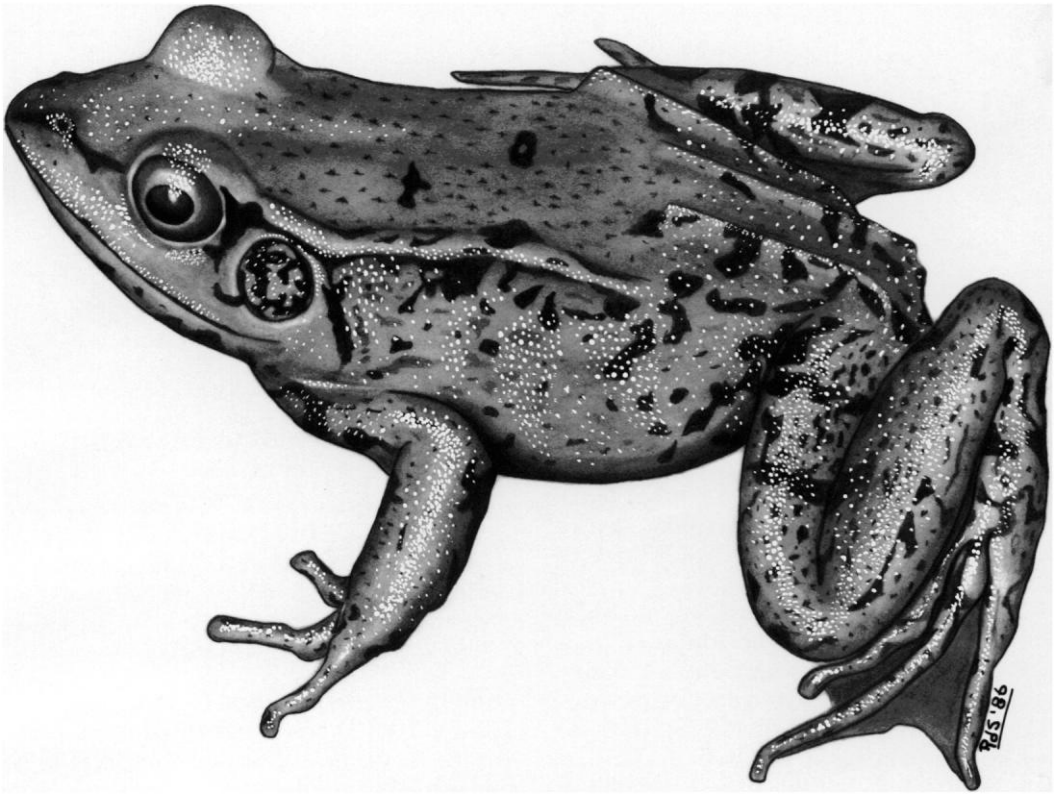

FIG. 7.—Adult specimen of *Rana palmipes* (KU 146639).

juvenile (50 mm SVL) by Boulenger, 1920:475].

Rana affinis Peters, 1859:403 [Holotype—ZMB, now believed lost; from "Caracas," Venezuela; specimen described as a juvenile (63 mm SVL) by Boulenger, 1920:475].

Rana clamata var. *guianensis* Peters, 1863: 412 [Holotype—presumably in ZMB, but not known to exist; from "Guiana" (= Guyana)].

Ranula brevipalmata Cope, 1874:131 [Holotype—Academy of Natural Sciences, Philadelphia (ANSP) 11398 from "Nauta," Perú].

Ranula nigrilatus Cope, 1874:131 [Holotype—supposedly in ANSP, but not listed by Malnate (1971); from "Nauta," Perú].

Rana copii Boulenger, 1882:49 [substitute name for *Ranula brevipalmata* Cope, after transfer of *Ranula* into *Rana*, as *brevipalmata* is preoccupied by *Rana brevipalmata* Peters (1871)].

Rana palmipes forma *rionapensis* Andersson, 1945:3 [Holotype—Royal Museum of Natural History, Stockholm (NHRM), no number given, specimen 48 mm in total length, from "Rio Napo, 400 m," Napo Province, Ecuador].

Definition.—1) Larval tooth formula: 4(2–4)/4(1); 2) larval marginal teeth absent; 3) larval oral disk emarginate; 4) toe tips expanded; 5) vocal sacs and slits absent (52.4%), present (42.8%), or present on one side only (4.8%); 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused; 8) tympanum large, equal to or exceeding diameter of eye; 9) one metatarsal tubercle; 10) webbing of hindfeet: I 0–0 II 0–1 III 0–1 IV 0–0 V; 11) supralabial stripe absent; 12) black border along dorsolateral folds; 13) no black face mask; 14)

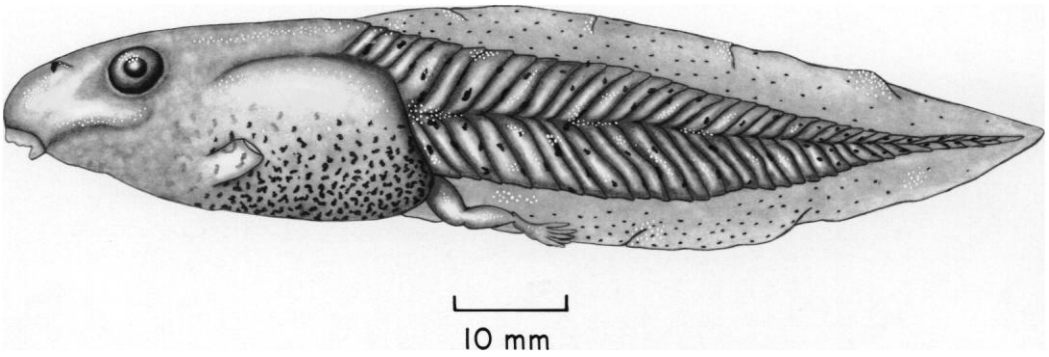

FIG. 8.—Tadpole of *Rana palmipes* (KU 202981).

color in life—dorsum olive-green to brown with irregular dark brown spots, flanks light brown with dark brown mottling, venter cream to yellow, with or without ventral melanism; 15) adult SVL 78–126 mm females, 55–101 mm males.

Distribution.—Lowlands of northern South America east of the Andes (Fig. 3).

Larvae and reproduction.—A single tadpole of *R. palmipes* from Ecuador was described by Duellman (1978). His description is similar to the Ecuadorian tadpole illustrated in Fig. 8. A series of tadpoles from Bolivia (USNM 146597) are considerably more mottled. Larvae of *R. palmipes* are approximately 50% larger than the corresponding stages of *R. vaillanti* larvae.

Gravid females of *R. palmipes* are found throughout the year. Duellman (1978) reported that 25 female *R. palmipes* (SVL 103–125 mm) contained 720–6750 ovarian eggs. Egg masses are deposited in clumps in ponds or slowly moving water.

Vocalizations.—According to Duellman (1978), the call of this species consists of ". . . a series of guttural chuckling sounds produced in water" throughout the year. The call has not been quantified.

Comments.—Boulenger (1882) and subsequent authors have included *Rana juninensis* (Tschudi, 1845; type locality, Lago de Junin, Perú) in the synonymy of *Rana palmipes*. This allocation is clearly in error; the species described by Tschudi is not a *Rana*, and the elevation of the type locality is much higher than *R. palmipes* occurs.

Rana sierramadrensis Taylor (Frontispiece)

Rana sierramadrensis Taylor, 1939:397 [Holotype—Field Museum of Natural History (FMNH) 100038 (formerly EHT-HMS 3963B), from "near Agua del Obispo, between Rincón and Cajones, Guerrero," México].

Diagnosis.—1) Larval tooth formula: 6–7(2–7)/3(1); 2) larval marginal teeth present; 3) larval oral disk not emarginate; 4) toe tips expanded; 5) vocal sacs and slits absent; 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused; 8) tympanum small and indistinct; 9) one metatarsal tubercle; 10) webbing of hindfeet: I 0–1 II 0–1 III 0–1 IV 1–0 V; 11) supralabial stripe present; 12) black border along dorsolateral folds; 13) black face mask present; 14) color in life—dorsal ground color uniform bronze or brown, with black canthal stripe, black post-tympanic bar, and black ventrolateral bar from axilla to groin; femoral crossbars narrow (intervening spaces 3–5 times as wide); dark black and yellow mottling on posterior surfaces of thighs; ventral melanism usually extensive; breeding males develop extensive white denticles on anterior venter and forearms; 15) adult SVL 60–98 mm females, 60–100 mm males.

Distribution.—Sierra Madre del Sur of Guerrero and Oaxaca, México (Fig. 6).

Larvae.—The tadpoles of this species are known from just three specimens (KU 87660) described and illustrated by Webb (1978). These specimens have very little

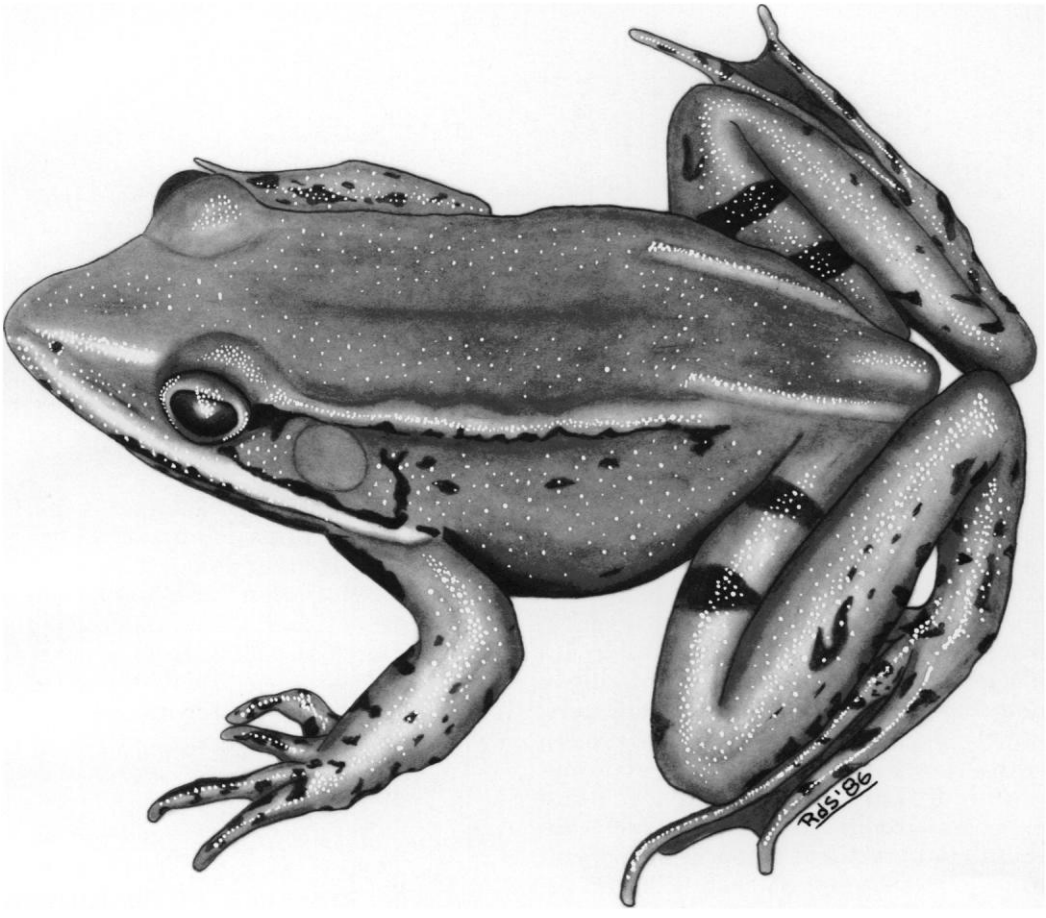

FIG. 9.—Adult specimen of *Rana vaillanti* (KU 96443).

pigmentation on the tails or fins, the bodies are uniformly pigmented, and the fins are low (Webb, 1978). The three specimens range from stages 25 to 35 (Gosner, 1960) and were collected on 8 June 1964. No breeding records are known for this species, but the above collection date for tadpoles indicates that at least some breeding occurs in the dry season.

Vocalizations.—None reported.

Rana vaillanti Brocchi
(Figs. 9, 10)

Rana vaillanti Brocchi, 1877:175 [Holotype—MNHN 6328, from "Belize, (Honduras)" (= Belize, Belize); Kellogg (1932) listed the type locality as "Mullins River, near Belize, British Honduras"].

Rana bonaccana Günther, 1900:201 [Syntypes—BMNH 1947.2.2.17–23, from "Mexico, Island of Bonacca, off the coast of Yucatan" (= Isla de Guanaja, Honduras; not Belize as suggested by Kellogg, 1932)].

Rana brevipalmata rhoadsi Fowler, 1913: 166 [Holotype—ANSP 18051, from "Bucay, Province of Guayas, Western Ecuador"].

Definition.—1) Larval tooth formula: 4(2–4)/4(1) (a few teeth occasionally form an abbreviated fifth upper row according to Volpe and Harvey, 1958); 2) larval marginal teeth absent; 3) larval oral disk emarginate; 4) toe tips expanded; 5) vocal sacs and slits usually present in males (88.7% of specimens); 6) dorsal skin denticles present; 7) sacral and presacral vertebrae fused;

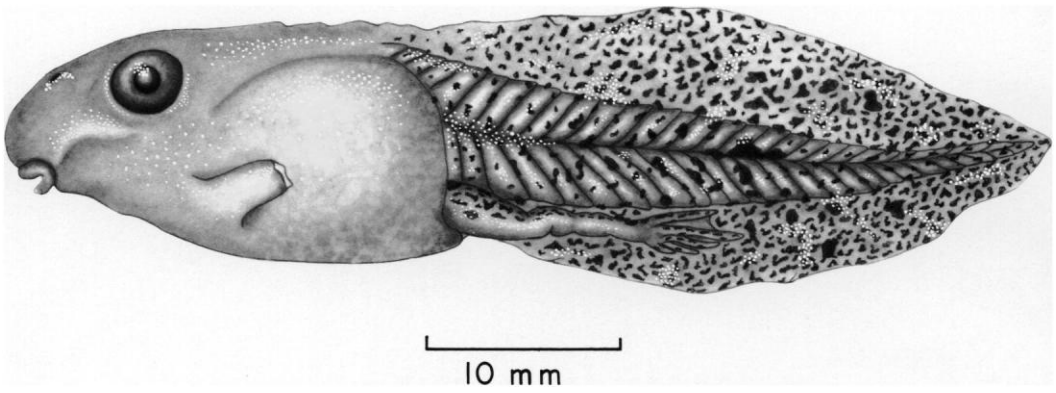

FIG. 10.—Tadpole of *Rana vaillanti* (KU 202853).

8) tympanum large, equal to or larger than diameter of eye; 9) one metatarsal tubercle; 10) webbing of hindfeet: I 0–0 II 0–1 III 0–1 IV 0–0 V; 11) supralabial stripe absent or present only posterior to eye; 12) black border along dorsolateral folds; 13) black face mask absent; 14) color in life—dorsal ground color brown posteriorly, usually changing to green anteriorly, often with a few scattered dark brown markings posterodorsally and laterally; femoral crossbars variable but usually distinct; canthus dark brown and green; venter cream to yellow; 15) adult SVL 76–125 mm females, 67–94 mm males.

Distribution.—From Veracruz, México, south along the Atlantic coastal plain (to the Pacific coast in southeastern Oaxaca and northwestern Chiapas, México) to both coasts in Nicaragua, south through Costa Rica and Panama to the Pacific coast of Colombia and Ecuador (Fig. 3).

Larvae.—Tadpoles of *R. vaillanti* from Colombia, Panama, Costa Rica, and México were described and illustrated by Volpe and Harvey (1958). All of their specimens were similar to the specimen illustrated in Fig. 10, with the exception of a collection from Colombia (FMNH 44126). The tails of the latter tadpoles were so darkly pigmented that no clear mottling pattern was apparent.

Vocalizations.—The calls of this species have been described by Greding (1972, 1976) as a series of "grunts," each about 0.2 seconds in duration, separated by intervals of 2–11 seconds. The grunts consist of 5 or 6 pulses with a dominant frequency around 1000 Hz (Greding, 1976).

Males of *R. vaillanti* call from floating vegetation or from shore. Based on the spacing of males calling from a pond in Costa Rica, Greding (1976) suggested a possible territorial role for the calls.

Rana vibicaria (Cope)
(Frontispiece)

Levirana vibicaria Cope, 1894:197 [Syntypes—Museo Nacional de Costa Rica (MNCR) 3912, 3915–16, the latter recataloged American Museum of Natural History (AMNH) 5463 and 7445; AMNH 5463, from "Rancho Redondo on the divide of the Irazu Range," San José Province, Costa Rica, was designated as lectotype by Zweifel (1964:300)].

Rana godmani Günther, 1900:204 [Syntypes—BMNH 1902-1-28,7, from "Rio Sucio," Cartago Province, Costa Rica].

Definition.—1) Larval tooth formula: 5–6(2–6)/4(1); 2) larval marginal teeth absent; 3) larval oral disk emarginate; 4) toe tips broadly expanded; 5) vocal sacs and slits absent; 6) dorsal skin denticles reduced; 7) sacral and presacral vertebrae fused; 8) tympanum smaller than eye, distinct; 9) two metatarsal tubercles; 10) webbing of hindfeet: I 1–2 II 1–2 III 1–2 IV 2–1 V; 11) supralabial stripe present; 12) black border along dorsolateral folds; 13) black face mask present; 14) color in life—

dorsal ground color of body and limbs yellow-brown to brassy to sooty brown to green, often with small dark brown spots; axilla, groin, and posterior surfaces of limbs red; vague post-tympanic bar or fold sometimes present; 15) adult SVL 66–80 mm females, 60–73 mm males.

Distribution.—Highlands (above 1200 m) of Costa Rica and western Panama (Fig. 6).

Eggs and larvae.—The tadpole of *R. vibicaria* was first described by Dunn (1922). Zweifel (1964) provided a much more thorough description and illustrated the tadpole and mouthparts and also described the eggs of this species. The following summaries are based primarily on Zweifel's descriptions, as supplemented with examined material (see Appendix).

The eggs are deposited in globular masses in pools or slow streams. The embryo is 2.3–2.6 mm in diameter and is surrounded by two jelly coats (3.7–4.2 mm and 5.4–6.4 mm in diameter, respectively). The larvae are uniformly darkly pigmented or have inconspicuous dark mottling. The tail fins are deep, and the body is short and rounded. The largest specimen recorded is the single specimen described by Dunn (1922) with a total length of 70 mm.

Vocalizations.—This species does vocalize despite its lack of vocal sacs and slits. Zweifel (1964) described two vocalizations for *R. vibicaria*: a "harsh trill" of 11–21 pulses that lasts from 0.30–0.65 seconds and an untrilled call of similar duration. Greding (1972) reported a range of 9–30 pulses for the trilled call, with durations of 0.35–0.90 seconds. The trilled calls may be given from one to five times in succession and may be followed by up to three untrilled calls (Zweifel, 1964).

Rana warszewitschii (Schmidt) (Frontispiece)

Ixalus warszewitschii Schmidt, 1857:11 [Holotype—Krakow Museum (KM) 1006/1338, from "Unweit des Vulcanes Chiriqui, zwischen 6000′ und 7000′ Höhe, in einem feuchten, nie trockenen Klima von 12–14°R," Panama, according to Schmidt, 1858:242].

Rana coeruleopunctata Steindachner, 1864:264 [Syntypes—Naturhistorisches Museum, Wien (NHMW) 20840:1–4, according to Haupl and Tiedemann, 1978; "Fundort unbekannt" (origin unknown)].

Ranula chrysoprasina Cope, 1866:129 [Holotype—a juvenile specimen in United States National Museum (USNM) collection according to Cope, but not listed by Cochran (1961); from "Arriba, Costa Rica"].

Rana zeteki Barbour, 1925:156 [Holotype—Museum of Comparative Zoology, Harvard University (MCZ) 10031, from "Barro Colorado Island, Gatun Lake, Canal Zone of Panama"].

Definition.—1) Larval tooth formula: 6(2–6)/4(1); 2) larval marginal teeth absent; 3) larval oral disk not emarginate; 4) toe tips broadly expanded; 5) vocal sacs and slits absent; 6) dorsal skin denticles reduced; 7) sacral and presacral vertebrae fused; 8) tympanum smaller than eye, distinct; 9) two metatarsal tubercles; 10) webbing of hindfeet: I 1–2 II 1–3 III 1–3 IV 3–1 V; 11) supralabial stripe present; 12) black border along dorsolateral folds; 13) black face mask present; 14) coloration in life—dorsum brown with green spots to uniform metallic green; light dorsolateral fold; darker laterally than dorsally; interspaces between tibial and femoral crossbars 1–3 times wider than crossbars; 2–4 distinct yellow spots on posterior surfaces of thighs; 1–2 yellow spots in axillae; undersurfaces of limbs usually red; males with ventral melanism; 15) adult SVL 45–63 mm females, 37–48 mm males.

Distribution.—Southeastern Honduras south and east to eastern Panama (Fig. 11).

Larvae.—*Rana warszewitschii* tadpoles were described by Starrett (1960). The tadpoles grow to a large size (115 mm), have a thick, muscular tail with low tail fins, and are heavily mottled on the tail musculature and fins. Tadpoles of this species live in small montane streams.

Vocalizations.—Greding (1972) provided the only report of vocalizations in this species. He summarized calls from five individuals recorded at an air temperature

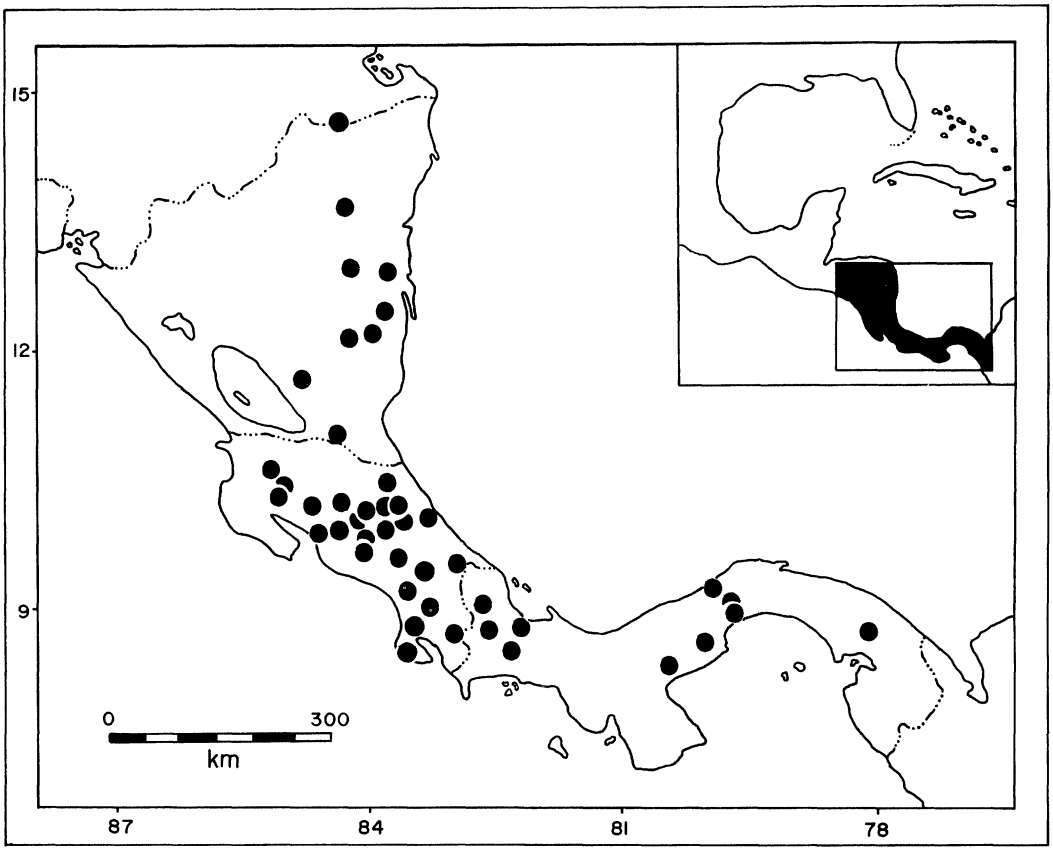

FIG. 11.—Distribution of *Rana warszewitschii*.

of 20 C; these calls were short (0.12–0.35 seconds duration) and trilled (4–9 pulses), much like a shortened version of the trilled call of *R. vibicaria*. This is the only other species besides *R. vibicaria* in the *R. palmipes* group that is known to vocalize without vocal sacs or slits.

Comments.—The spelling of the name of this species usually has been *R. warschewitschii* in the literature, because this was the spelling used by Schmidt (1858). However, Schmidt's detailed description of this species in 1858 was not the original description; in the original description (Schmidt, 1857), the spelling is *R. warszewitschii*. According to the International Code of Zoological Nomenclature (1985), Articles 31–33, *R. warszewitschii* is a correct original spelling and *R. warschewitschii* is an incorrect subsequent spelling. Likewise, *Rana coeruleopunctata* has been consistently misspelled as *Rana caeruleopunctata* since Boulenger (1882), although the former spelling appeared in Steindachner (1864). This change is unjustified because both spellings are correct in Latin.

RELATIONSHIPS OF THE SPECIES

The *R. palmipes* group is the most morphologically diverse species group of New World *Rana*. Therefore, we analyzed the morphological differences of adults and larvae (see definitions) to examine the probable evolutionary history of this group. As supported by Hillis (1985) and Hillis and Davis (1986), the *R. tarahumarae* group was used as a first outgroup and the *R. pipiens* complex as a second outgroup to the *R. palmipes* group. These two groups, along with the *R. palmipes* group, compose the beta section of the subgenus *Lithobates*; the *R. tarahumarae* and *R. pal-*

TABLE 2.—Morphological characters and coded character states used in phylogenetic analysis of the *R. palmipes* group. State 0 is plesiomorphic.

Character	Character states
1. Upper rows of teeth (in larvae)	0: two 1: three 2: four 3: five to seven
2. Lower rows of teeth (in larvae)	0: three 1: four 2: five or six
3. Larval marginal teeth	0: absent 1: present
4. Larval oral disk	0: emarginate 1: not emarginate
5. Toe tips	0: not expanded 1: expanded 2: expanded, toe pads present
6. Vocal sacs and slits (in males)	0: present 1: absent
7. Skin denticles	0: absent or reduced 1: present
8. Sacral and presacral vertebrae	0: separate 1: fused
9. Tympanum	0: < eye diameter 1: > eye diameter
10. Metatarsal tubercles	0: one 1: two
11. Webbing on feet	0: I 0–0/0–1 II 0–1 III 0–0/0–1 IV 0–0/1–0 V 1: I 1–2 II 1–2/1–3 III 1–2/1–3 IV 3–1 V
12. Supralabial stripe	0: absent 1: present
13. Black border along dorsolateral folds	0: absent 1: present
14. Dark face mask	0: absent 1: present
15. Red pigment on underside of legs	0: absent 1: present

mipes groups compose the *R. palmipes* supergroup (Hillis, 1985). All characters that vary in more than one species were included in the analysis (Table 2). The characteristics for all species in the analysis are given in Table 3.

The most parsimonious phylogenetic hypothesis was constructed using D. Swofford's PAUP program, version 2.4. The branch and bound algorithm was used to insure that the shortest tree was found (Fig. 12). In addition, the lengths of all 10,395 unrooted trees were computed for the eight species in the *R. palmipes* group using the ALLTREES algorithm of PAUP. The distribution of these trees is strongly skewed, with few trees near the most parsimonious solution (Fig. 13). This finding indicates a high degree of concordance among the characters in the data matrix (Fitch, 1984).

The monophyly of the *R. palmipes* group is supported by both morphological and biochemical evidence. Fusion of the sacral and presacral vertebrae occurs as a developmental abnormality in several species of *Rana* (Lynch, 1965), but the *R. palmipes* group is unique in having this condition fixed among the contained species. As noted by Webb (1978), members of the *R. palmipes* group all have distinct dark lateral borders along the dorsolateral folds. With the exception of *R. sierramadrensis*, tadpoles of all species in the *R. palmipes* group have four or more lower rows of teeth, whereas members of the other species in the subgenus *Lithobates* have no more than three lower rows; the relationships of the *R. palmipes* group suggest that the occurrence of three lower

TABLE 3.—Character matrix for taxa in phylogenetic analysis. Character numbers refer to Table 2.

Taxon	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
R. bwana	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0
R. juliani	3	2	1	0	1	1	1	1	0	0	0	1	1	1	0
R. maculata	3	1	1	1	1	0	1	1	0	0	0	1	1	1	0
R. palmipes	2	1	0	0	1	0	1	1	1	0	0	0	1	0	0
R. sierramadrensis	3	0	1	1	1	1	1	1	0	0	0	1	1	1	0
R. vaillanti	2	1	0	0	1	0	1	1	1	0	0	0	1	0	0
R. vibicaria	3	1	0	0	2	1	0	1	0	1	1	1	1	1	1
R. warszewitschii	3	1	0	1	2	1	0	1	0	1	1	1	1	1	1
R. tarahumarae group	2	0	1	0	1	1	1	0	0	0	0	0	0	0	0
R. pipiens group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

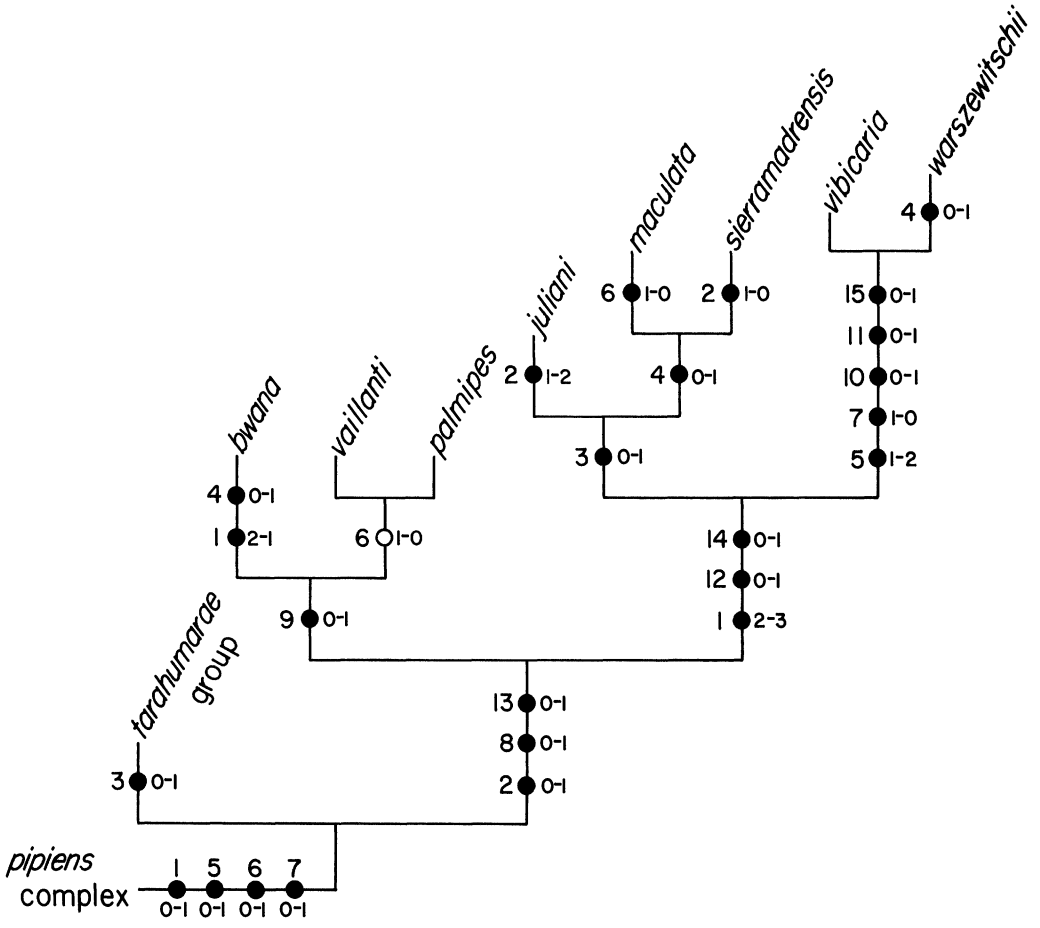

FIG. 12.—Cladogram of members of the *Rana palmipes* group. Character numbers (to the left or above circles) and changes in character states (to the right or below circles) refer to numbers in Table 2. The open circle for character 6 (synapomorphy of *Rana vaillanti* and *Rana palmipes*) indicates a polymorphic state for that character.

rows in *R. sierramadrensis* is a reversal (Fig. 12). Biochemically, members of this group are unique in the possession of a *Stu* I restriction site in the nontranscribed spacer of the ribosomal DNA array (site 11 of Hillis and Davis, 1986).

Within the *R. palmipes* group, a primary dichotomy is indicated in Fig. 12 between the lowland species (*R. bwana, R. palmipes,* and *R. vaillanti*) and the highland species of Middle America (*R. maculata, R. juliani, R. sierramadrensis, R. vibicaria,* and *R. warszewitschii*). Within the Middle American highland clade, there is a split between the species north of the Nicaraguan Depression (*R. maculata, R. juliani,* and *R. sierramadrensis*) and those south of this barrier (*R. vibicaria* and *R. warszewitschii*). The Nicaraguan Depression is a major lowland barrier to many montane groups (Duellman, 1966); the montane areas to the north and south of the barrier were separated by sea in the Miocene and were connected by only a narrow lowland pass through the Pliocene (Savage, 1966). Therefore, it is likely that the divergence of the northern species group (*R. maculata, R. juliani,* and *R. sierramadrensis*) and the lower Central American montane species group (*R. vibicaria* and *R. warszewitschii*) occurred in the Miocene. The speciation event between the ancestor of the *R. palmipes* complex (*R. bwana, R. palmipes,* and *R. vaillanti*) and the ancestor of the montane species (*R. maculata, R. juliani, R. sierramadrensis,*

R. vibicaria, and *R. warszewitschii*) must have occurred earlier if the phylogeny represented in Fig. 12 is correct. This suggests the possibility of an old Middle America–South America vicariance, rather than a recent invasion of the *R. palmipes* complex into South America.

The evolution of *R. vibicaria* and *R. warszewitschii* may have been associated with an elevational isolation. Although the two species now overlap in elevational distribution, *R. warszewitschii* occurs at lower elevations (nearly to sea level) whereas *R. vibicaria* is restricted to high elevations (above 1200 m). Except for elevational considerations, the range of *R. vibicaria* is completely encompassed by that of *R. warszewitschii* (Figs. 6, 11).

The sister species *R. maculata* and *R. sierramadrensis* display a common geographic pattern (Fig. 6): one species (*R. sierramadrensis*) in the highlands of southwestern Mexico and the other (*R. maculata*) in the highlands of nuclear Central America. These two highland areas are separated by the lowlands of the Isthmus of Tehuantepec. Many other sister species of frogs show a trans-Isthmian highland distribution (e.g., *Ptychohyla schmidtorum* and *P. ignicolor*; *Hyla bromeliacea* and *H. dendroscarta*; and *Hyla euphorbiacea* and *H. walkeri*; Duellman, 1970). *Rana juliani* of the Maya Mountains is the sister species to the *R. maculata–sierramadrensis* species-pair. The Maya Mountains are not noted for endemism of terrestrial vertebrates; *R. juliani* is the only amphibian restricted to the area (Lee, 1980). However, several other montane or premontane amphibians do have isolated populations in the Maya Mountains (e.g., *Centrolenella fleischmanni* and *Agalychnis moreleti*; Lee, 1980).

The primary geographic barrier among the lowland members of the *R. palmipes* complex are the Andes of South America (Fig. 3). *Rana palmipes* is restricted to the lowland tropical forests east of the Andes, whereas *R. vaillanti* is distributed in the lowland tropical areas west of the Andes and north into Middle America. *Rana bwana* is also found west of the Andes, but is ecologically separated from *R. vaillanti*, as the former species is found only in a few desert streams that drain the Pacific versant of the Huancabamba Depression in northwestern Perú and southwestern Ecuador (Fig. 3).

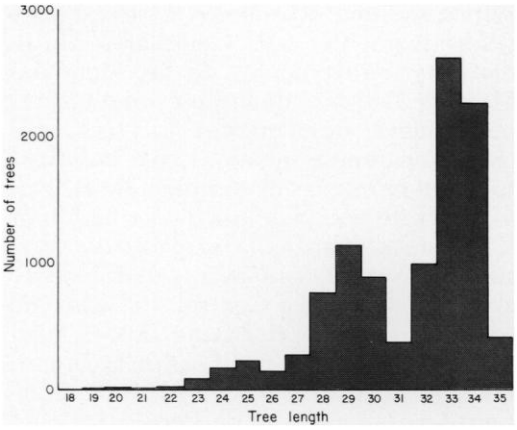

FIG. 13.—Distribution of all 10,395 unrooted trees for the eight species in the *Rana palmipes* group.

The phylogeny of the *R. palmipes* group presented in Fig. 12 provides a framework upon which future studies of these frogs can be based. The *R. palmipes* group is especially appropriate for studies of the evolution of vocalization in frogs. Several of the species have lost vocal slits and sacs, although at least two of the species without these structures (*R. vibicaria* and *R. warszewitschii*) have retained or regained vocalizing behavior. Vocalizations are diverse among the species, and multiple types of calls are present within some species. Some species (*R. palmipes* and *R. vaillanti*) appear to be polymorphic for the presence or absence of vocal slits. Both mate-attraction and territoriality have been proposed as functions of vocalizations in this group. Combined with knowledge of the phylogenetic relationships, the diversity of vocalizations and vocalization apparati in these frogs provide an excellent opportunity to study the evolution of anuran calling behavior and its morphological basis.

RESUMEN

El grupo de *Rana palmipes* consiste de ocho especies. La distribución combinada de estas especies se extiende desde el sur de México hasta Perú, Bolivia, y Brasil. Bajo el nombre de *R. maculata* y *R. pal-*

mipes, se identificaron dos y tres especies respectivamente. Los ejemplares de *R. maculata* provenientes de las Montañas Maya de Belize se describen como una especie nueva, *Rana juliani*. Las tres especies previamente incluídas bajo *palmipes* son denominandas el complejo de *R. palmipes*. Este complejo queda formado por *R.palmipes*, distribuída en el este de América del Sur, *R. vaillanti*, extendiéndose atraves de América Central y el oeste de América del Sur, y *R. bwana*, especie nueva, de las vertientes pacíficas de la Depresión de Huancabamba en el suroeste de Ecuador y el noroeste de Perú.

La variación morfológica en el grupo de *R. palmipes* (*bwana, juliani, maculata, palmipes, sierramadrensis, vaillanti, vibicaria*, y *warszewitschii*) provee información sobre la filogenía de las especies. El grupo se define fácilmente en base a caracteres morfológicos y bioquímicos. Dentro del grupo *palmipes* hay una dicotomía principal: especies de baja altitud (*bwana, palmipes*, y *vaillanti*) y especies de montaña (*juliani, maculata, vibicaria sierramadrensis*, y *warszewitschii*). Entre las últimas, las especies del sur de América Central (*vibicaria* y *warszewitschii*) forman un grupo monofilético, mientras que las especies del norte de América Central (*sierramadrensis, juliani*, y *maculata*) forman otro grupo monofilético. Las especies *maculata* y *sierramadrensis*, actualmente separadas por el Istmo de Tehuantepec, son especies hermanas.

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APPENDIX

Specimens Examined

Rana bwana.—**Ecuador:** Loja, 24 km N Macará, TNHC 37414–15. **Perú:** Piura, 1.5 km S Las Lomas, Río Chipillico; LACM 49190–212, 49213 (tadpoles), 49214, 49282, TCWC 28769–800, 28922; 3 km SE Las Lomas, MVZ 82523, 82524 (skeleton), 82525–27; 4.6 km ESE Las Lomas, TCWC 28801–02; 5 km SE Las Lomas, MVZ 82528–30; 4.6 km W Suyo, TCWC 28801–02.

Rana juliani.—**Belize:** Cayo, 23.2 km S Georgeville, Little Vaquero Creek, KU 157161, 157162 (tadpoles); Toledo, SW end Little Quartz Ridge, 16°24′ N, 89°06′ W, UTA 9067–68, 9069–79 (tadpoles).

Rana maculata.—**El Salvador:** Ahuachapán, 3.2 km NW Apaneca, MVZ 39894, 39897; Cabanas, 4.5 km SW Tejutepeque, Cantón El Huilihuiste, KU 184908–12; Chalatenango, 10 km NE La Palma, Cantón Las Pilas, KU 184907; Cerro El Pital, KU 184949; E slope Los Esesmiles, MVZ 39887–91; Cuscatlán: 1.2 km N Tenancingo, KU 184857–902; 1.3 km N Tenancingo, KU 184856; La Libertad, 2 km SE Colón, KU 61993; Morazán, N slope Mt. Cacaguatique, MVZ 39886; 12 km NE Perquín, Cantón El Zancudo, KU 184903–06; Santa Ana, Rancho San José, KU 66092–93, 68568 (tadpoles); Sonsonate, Hacienda Chilata, MVZ 39872–77. **Guatemala:** Alta Verapaz, Tactic, KU 190423; 8 km E Tactic, MVZ 150937; 10 km S, 2 km W Cobán, MVZ 104645–47; Baja Verapaz, 32 km N Morazán, KU 68569 (tadpoles); W slope Cerro Verde, KU 190422; Plantación Santa Teresa, along Río Chipilin, KU 186677; 1.6 km ESE Purulhá, KU 186675; 2 km ESE Purulhá, KU 186676; 2 km E Purulhá, MVZ 143395–97, 143399; 3.2–5.3 km W Purulhá, KU 186674; 8 km W San Jerónimo, AMNH 81640; 5 km ENE Chilascó, MVZ 150938; 2 km SE Salamá, TCWC 23708–09; 21 km S Salamá, UIMNH 52139; Chilmaltenango, near Chocoyos, TNHC 29627; Chiquimula, 20 km SSE Chiquimula, TCWC 23707; El Quiché, 4 km N Chichicastenango, AMNH 70232 (tadpoles); Escuintla, Finca El Salto, MVZ 88357–62; 4 km NE Finca El Salto, AMNH 70231; 6.4 km N Esquintla, AMNH 80021–23, 79912 (skeleton); 9 km N, 3 km E Escuintla, MVZ 88356, 104636–38; Guatemala, 14.5 km S Guatemala City, MVZ 149073, 149075–76; 20 km NE Guatemala City on Puerto Barrios Hwy., KU 145760; San Jorge Muxbal, KU 186674; Quetzaltenango, Salcajá, TNHC 29628–29; Quetzaltenango, AMNH 78419–32, TNHC 38159–68, 32070–74; San Marcos, Finca La Paz, near La Reforma, KU 58880–82, 60040–41 (tadpoles); Finca Santa Julia, 1.25 km E, 0.75 km S San Rafael Pie de la Cuesta, CAS 144672–75, MVZ 113617, 132360–61, 144020, 159530, 180395; Suchitepéquez, Finca El Naranjo, W slope Volcán Santa Clara, AMNH 74524, UIMNH 46211–15; Río Ixtacap, CAS 69754; Volcán Zunil, CAS 69751–53; 10.7 km N. Patulul, KU 195106; Volcán Atitlán, Finca Los Andes, MVZ 160713–15; Totonicapán, near Santa Lucía La Reforma, KU 190427; Zacapa, Sierra de las Minas, 6.4 km N jct. Hwy. CA-9 and road to San Lorenzo, KU 190424, 191296 (tadpoles); Sierra de las Minas, 1.6 km NNW San Lorenzo, KU 190426; Sierra de las Minas, Finca Sitio Nuevo on Río Portón, KU 190425. **Honduras:** Comayagua, between Siguatepeque and La Mision, AMNH 54895; Cortés, Agua Azul Research Station, AMNH 54909; Cerro Cusuco, KU 194242; Quebrada de Colorado, near Buenos Aires, KU 194243; El Paraíso, Agua Fría, AMNH 54773; Portillo de los Arados, near Guinope, AMNH 54753; Montaña La Burra, Aldea La Máquina, Danlí, KU 192308; 7 km E Danlí, TCWC 23809; Francisco Morazán, Tatumbla, AMNH 54754; Tegucigalpa, AMNH 54896, TNHC 48847; 83 km N Tegucigalpa, AMNH 53934–38; Cerro Uyuca, AMNH 54768; W slope Cerro Uyuca, KU 103226; 5 km WNW El Zamorano, KU 103227; Intibucá, 5 km NE Jesús de Otoro TCWC 23808; La Paz, Santa Elena, KU 194274; 5 km S Santa Elena, KU 194244–45; Ocotepeque, Nueva Ocotepeque, TCWC 23710–12. **México:** Chiapas, 6.6 mi N Arriaga, KU 148647 (tadpoles); 17.6 km S Arriaga, UIMNH 57101–04; Bochil, AMNH 60687; 8 km N Bochil, UIMNH 78843–47; 6.4 km NE Chiapa de Corzo, TCWC 20942–49; 8 km N Chiapa de Corzo, MVZ 99531; 11 km NE Chiapa de Corzo, SM 4874–76, SM 4890–91, 4898–900, BCB 10530–33, BCB 16749–53; Laguna Chamula Microwave Station, 15 km SE Amatenango, CAS 139874; Linda Vista, 2 km NW Pueblo Nuevo Solistahuacan, KU 58877; 41 km S Pueblo Nuevo Solistahuacan, TNHC 27053; San Cristóbal de las Casas, AMNH 80663; Río Navillero, UIMNH 55278–79; Intersection Mex. Hwy. 190 and 195, KU 195160–64, 200857; 14.6 km N jct. Mex. Hwy. 200 on road to Nueva Alemania, MVZ 132899; 3.2 km N Hastlan, AMNH 80666; Finca San Jerónimo, 7.5 km N Cacaohatán, UIMNH 55260–77, 55280, 55979, MVZ 159330–44, 165171–80, 167169, 177586–89, 177684–85; Finca Juarez, 7 leguas NE Escuintla, UIMNH 10512–31; Finca Las Nubes, 20 km NE Escuintla, MVZ 104701; Rancho San Bartóla, UIMNH 9847–48; Oaxaca, Colonia Rodulfo Figueroa, 20 km W Rizo de Oro, KU 195258–95, 200849–52 (tadpoles), UTA 4816; 1.6 km N Colonia Rodulfo Figueroa, UTA 4887–88; Río Navillero, UIMNH 55255; N Zanatepec,

UIMNH 56884. **Nicaragua:** Boaco, 30 km E Boaco near Cerro Masigue, KU 173868–69; Chontales, Santo Domingo, KU 173867; Estelí: Finca Daraili, 5 km N, 14 km E Condega, KU 85513–16; Jinotega, Jinotega, KU 173859–66; Matagalpa, Hacienda La Cumplida; KU 68567 (tadpoles); San José de la Montaña, KU 173870–79; Finca Tepeyac, 10.5 km N, 9 km E Matagalpa, KU 85500–11, 87714 (tadpoles), 98591 (tadpoles) 98592–94.

Rana palmipes.—**Bolivia:** Beni: Río Mamoré at Cachuela, AMNH 98154–55; Río Mamoré, Guayaramerín, AMNH 79364–71, 79373–89; Guayaramerín, AMNH 72297–309, 118183–89; Río Iténez, Bahía de Onca, AMNH 79372; Cochabamba, Chaparé, USNM 146597 (tadpoles). **Brasil:** Amazonas, Igarapé, Belém, AMNH 97378–507; Paraíba, USNM 109125–28; Pernambuco, Recife, USNM 119080–82; Río Grande do Norte, Ceara Mirim, CAS 49627; Natal, CAS 49671; Lake Papery, CAS 49848, FMNH 64249–50. **Colombia:** Amazonas, Leticia, AMNH 71583–87, USNM 142198–205, 146253–54, 147123–24; Puerto Narino: USNM 144531; Caqueta, mouth of Río Mecaya, USNM 144532–33; Meta, Angostura, USNM 144540; Sierra de la Macarena, Cana Guapaya, USNM 147271; 30 km WSW Vista Hermosa, Cano Sardinata, Sierra de la Macarena, UTA 5174; Quebrada Honda, USNM 144538–39; Río Duda, Sierra de la Macarena, AMNH 81648; south end Cordillera Macarena, CAS 19014; Villavicencio, AMNH 22599, MVZ 63288–95, USNM 144541–42; Finca el Buque, south edge Villavicencio, MCZ 96985; Granada on Río Ariari, south of Villavicencio, USNM 151473–75; Upper Río Guejar, USNM 150522–24; Putumayo, 7 km SE Mocoa, AMNH 84878; Santa Rosa de Sucumbios, upper Río San Miguel, AMNH 116330–96; Puerto Asís, Río Putumayo, MCZ 80500; Vaupés, jct. Río Ariari and Río Guaviare, UTA 2658–59, 5171–73. **Ecuador:** Napo, Campana Cocha, KU 124019; Cuyabeno, UIMNH 62915–32, 92372–76; Dureno, KU 175507, UIMNH 63511–12; Lago Agrio, UF 43167, UMRC 79.140; Limón Cocha, KU 99122, UIMNH 66349–59, 93223–25, 93229–30; Misahuallí, KU 202894–903, 202981 (tadpole); 2 km W Puerto Napo, USNM 196888–89 (9); Puerto Libre, Río Aguarico, KU 124018; Puerto Ore, Río Aguarico, KU 124020–24, 124224 (tadpoles); Río Cotopino, USNM 196891; Río Jivino, UIMNH 92657–59; 3.1 km south of Río Tiputini, UF 43168, UMRC 79.141; 7 km S Río Tiputini, UMRC 79.142; 10.9 km north of Río Tiputini, UF 43166; San José, Viejo de Sumaco, USNM 196890 (2); Santa Cecilia, KU 105257–82, 109569, 111983–87, 112365–67 (tadpoles), 124013–17, 12422 (tadpoles), 126669, 136317, 146639, 150666–71, 152322 (tadpoles), 152565 (tadpoles), 152842–87 (skeletons); Tena, UIMNH 62933–36, 63725, 66346–48, 90318, 90790–93; 1.6 km NE Tena, USNM 196909; Pastaza, Anga Cocha, Río Bobonaza, AMNH 53503; Chichirota, USNM 196902 (2), 196911 (2); Río Bobonaza, USNM 196899; Río Capahuari, USNM 196902 (4); Río Capaguaria, AMNH 53502; Río Conambo, USNM 196904; Río Capataza, USNM 196908 (2); Río Lipuno, tributary of Río Villano, USNM 196912; Río Pastaza, AMNH 53504–05, MCZ 19691; Río Pindo, near Río Tigre, USNM 196903 (3); 196906; Río Rutuno, tributary of Río Bobonaza, USNM 196900 (3), 196905; mouth of Río Shyona at Río Conambo, USNM 196901 (3); Río Villano, USNM 196910 (2); Zamora, Macuma, UIMNH 62910–14. **Guyana:** no other data, AMNH 53189–203, 118203–07; Kamakusa, AMNH 21402; Kartabo, AMNH 11655, 11669–71, 24915, 71006–08, 39598, 39727, 39731. **French Guyana:** Crique Jean Pierre, LACM 44634 (plotted but not examined). **Perú:** Amazonas, Río Cenepa, AMNH 43228; Río Cenepa, vicinity of Huampami, MVZ 176520; Río Cenepa, vicinity of San Antonio, MVZ 163035; Río Cenepa, vicinity of Sua, MVZ 163003–34; Loreto, Colonia Calleria, Río Calleria, CAS 93136–37, 93139, 93187; Estirón, Río Ampiaca, CAS 93313–15, 93346, 93348–52; Iquitos, AMNH 42010; Lagada Mirano, AMNH 43188; vicinity of Pevas, CAS 3148–49; Pernambuco, MCZ 2060 (2); Purtitania, AMNH 42115; Río Ampiyacu, Estirón, AMNH 115787–800; Río Tamayo, AMNH 43239; Yahuarmayo, MCZ 4901. **Trinidad:** Guayaguayare, UF 16533–34. **Venezuela:** Amazonas, Cerro de la Neblina region, AMNH 57981; Barinas, Agua Fría 7 km NNE Altamira, USNM 216873; Cojedes, Río Oriota, 2 km E Aparlade, UIMNH 62027–28; Guárico, Río Orituco, 10 km N Altagracia, USNM 216874; Miranda, Boleita, UIMNH 62009–14; Caripe, UIMNH 62015–26; Petare, USNM 121131–34; Monagas, Aragua de Maturia, UIMNH 61998–2008; 6.5 km S Guanaguana, KU 167429–35, 167850 (tadpoles); Sucre, Santa Rosa, 20 km (by road) SE Casanay, KU 117343.

Rana sierramadrensis.—**México:** Guerrero, Acahuizotla, TCWC 8533–37, 8540–41, 10220–27; Agua del Obispo, FMNH 102197–200, 102202, 103917, 124485, KU 87282, 195181, UIMNH 27053, 32442, 32444, TCWC 10991, USNM 114009–12, 139724; 1.6 km SW Colotlipa, TCWC 10228; S of Chilpancingo, FMNH 100038; 22.4 km S Chilpancingo, CAS 87189; 37 km S Chilpancingo, KU 87281; 1.7 km S Río Santiago, KU 87659 (tadpoles); 3.3 km N San Vicente, KU 84924 (skeleton), 87276–80, 87660 (tadpoles); Oaxaca, Cacahuatepec, FMNH 207926, UIMNH 52782; Río Jalatengo, 0.8 km S Jalatengo, KU 137538; 5.1 km S Jalatengo, KU 137537; 13.1 km N Juchatengo, KU 137541; 4.8 km S Putla de Guerrero, UIMNH 52783–84; 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, 139946–47 (tadpoles); Santa Lucía, AMNH 52624.

Rana vaillanti.—**Belize:** Belize, Belize, FMNH 4408–09; Manatee, FMNH 6286–87; Orange Walk, Kate's Lagoon, FMNH 49096; Stann Creek, 28 km SE Blue Hole, KU 157013–16. **Colombia:** Antioquia, Chigorodo, near Turbo, USNM 153918; Envigado, AMNH 39256 (tadpoles), 39258–64, 39266, 39273, 39275–76, 39279; Medellín, MCZ 7770; Medellín Valley, AMNH 39463–64; Sonsón, AMNH 22600–02 (tadpoles); Cauca, near Moscopán, USNM 146418–20; Quebrada Guangui, Río Patía, AMNH 86394–484, 86485 (tadpoles); Quebrada Guangui, 0.5 km above Río Patía, AMNH 88978; Chocó, Andagoya, USNM 144534–36; Atrato region, 37 km up Río Puné, AMNH 13682, 13720 (tadpoles); Boca de la Raspadura, AMNH 13721 (tadpoles); Cano Docordo, between Cucurrupí and Noanamá, on Río San Juan, CAS 119561, 119575, 119665–71, 119673–82, 119684; about 17 km SSW Noanamá, AMNH 109489–506;

about 7 km NE Palestina, AMNH 109507–14; about 17 km NE Palestina, AMNH 109515–30; 2 km above Playa de Oro, upper Río San Juan, AMNH 87192–93; Quebrada Docordo, Middle Río San Juan, AMNH 104989–5006; Quebrada Pangala, lower Río San Juan, AMNH 109515–30; Quebrada Taparal, lower Río San Juan, AMNH 109507–14; Quebrada Taparal, 20 km N Palestina, on Río San Juan, CAS 119909; Río San Juan, 10–15 km W Playa de Oro, USNM 147217–20; Cundinamarca, Fusagasugá, AMNH 71582, USNM 144537, 151875, 153945, CAS 22990–94, 23010–12; Magdalena, Pueblo Bello, Sierra Nevada de Santa Marta, CAS 116221; Santander, 4.7 km SE Bucaramanga, USNM 146249; El Centro, USNM 144543; Lebrija, USNM 144544–52; Tolima, 8 km N Chaparral, MVZ 41996; Mariquita, USNM 144554–55; Valle, 29 km SE Buenaventura, Río Zabaletas, KU 154619; El Tigre, USNM 151476; Llano Bajo, KU 158595; Camp Carton de Colombia, lower Río Calima, USNM 149738–40; Río Calima, near Córdoba, USNM 145746–55; Río Calima, USNM 150758; Río Raposo, CAS 21866, USNM 151464–78. **Costa Rica:** Alajuela, 4 km E Aguas Zarcas, CRE 517; 1.6 km N Florencia, MVZ 76081–82; La Fortuna, CRE 7153; Río Sardinal, 5 km W Cariblanco, KU 66099–102, 68189 (skeleton); Cartago, Chitaria, KU 103821, 104295 (tadpoles); Hacienda Florencia, CRE 7195; Peralta, KU 28226–27, 30459–63, 32503 (skeleton), 32504, 32616–24; junction Río Tuis and Río Reventazon, KU 66095–98; La Suiza, KU 28225; Turrialba, CRE 28, 32, 58, 84, 293, 381, 407, 413, 440, 567, 578, 592, 2806, KU 25218 (skeleton), 28223–24, 28228, 30468–83, 32492–98, 32500–02, 32614–15, 34881, 41121–24 (skeletons), MVZ 81303, 186416, TNHC 35967–81; 3 km W Turrialba, KU 68570 (tadpoles); Guanacaste, Bagaces, CRE 7124; 0.6 km S Bagaces, MVZ 79739; Cañas, CRE 7164; 20 km SE Cañas, KU 102350–51; Carrizales, CRE 9003; 0.5 km S Carrizales, CRE 9004; Finca Jiménez, CRE 3095, 3097; 0.8 km E Finca Jiménez, CRE 842; 0.8 km W Guayaba, CRE 7025; Hacienda La Pacífica, KU 157787; 0.9 km SE Liberia, CRE 9877; 2 km W Liberia, CRE 728; 9 km N Liberia, CRE 8097; 9 km N, 4 km E Liberia, CRE 714; 42 km S Liberia, CRE 8169; 6 km N Nicoya, CRE 8229; intersection Pan American Hwy. and Rt. 145, MVZ 149009–10; 3.7 km ENE Potrerillos, CRE 8454; 0.8 km E Santa Cruz, CRE 7126; 2 km NW Tilarán, CRE 521; 6 km NE Tilarán, CRE 523, 8020; vicinity Vueltas, CRE 9005, 9008; Heredia, La Selva, CRE 65, 70, 6300, 6370; Puerto Viejo, CRE 4913, KU 35931–32, 66103–04, 68190–201 (skeletons), 117445–50 (skeletons); 1 km S Puerto Viejo, KU 86547; 7.5 km W Puerto Viejo, KU 6892–98 (skeletons), 86546; Limón, 1 km E Cuadrante, CRE 85; El Tigre, CRE 290; Guacimo, CRE 611; La Lola, CRE 201–02, 286, 4761–66, 4794–802, 8060; Laguna Penitencia, MVZ 128712; Los Diamantes, CRE 210, 212, 8051, KU 30464–67, 66105; Pandora, CRE 505, KU 86535–45; Suretka, KU 35933; Puntarenas, 3.2 km NE Boca de Barranca, CRE 8017; 12 km WNW Esparza, KU 66106–07; Maribella, KU 32499; mouth of Río Barranca, 10 km E Puntarenas, CRE 4921, 4952–55. **Ecuador:** Cotopaxi, region of Sigchos, USNM 196892; El Oro, Bucay, MCZ 3216; 7 km ESE Machalá, USNM 196886 (3); Puertovelo, AMNH 13971–72; Santa Rosa, AMNH 16185, USNM 196885 (2); Esmeraldas, 1 km N Cacnaui, USNM 196895 (5); El Placer, USNM 196894 (2); 1 km W El Placer, USNM 196893; Río Bogotá, USNM 196897; Río Palabí, USNM 196896 (4); San Lorenzo, USNM 196898; Guayas, Cochancay, MVZ 77190; 11.2 km east of San José, UF 34058, 34060–63; Loja, Río Puyango, AMNH 16198–205, 16225–27, 16229; Los Ríos: Estación Biológica Río Palenque, 56 km N Quevedo, KU 146640; Hacienda Camarones, W of Quevedo, USNM 196884; Pichincha, Santo Domingo de los Colorados, KU 121086–87, 121444; 0.5 km S Santo Domingo de los Colorados, USNM 196887 (5); 9 km W Santo Domingo de los Colorados, CAS 10598–600; 16 km W Santo Domingo de los Colorados, MCZ 90383; Tinalandia, 15.5 km SE Santo Domingo de los Colorados, AMNH 102777, KU 202905–07, 202982 (embryos). **Guatemala:** Alta Verapaz, Chinajá, KU 55957, 58878; 4 km E Sebol, AMNH 80043–43; 13 km SW Sebol, AMNH 81641; El Petén, 1.6 km W El Ceibal, KU 157022–27, UMRC 80.6; 5 km NNW Chinajá, KU 55948–49; 8 km NNW Chinajá, KU 55959–60; 10 km NNW Chinajá, KU 55956; 11 km NNW Chinajá, KU 55951–54; 15 km NW Chinajá, KU 55955; 20 km NNW Chinajá, KU 55950; 6.4 km N Poptún, KU 157017–21; Toocog, 15 km SE of La Libertad, KU 58879; Izabal, 4 km WSW Puerto Santo Tomas, KU 190428–31; Río Blanco, KU 190432–34; 8 km W Santo Tomás, KU 186678. **Honduras:** Atlántida, Lacetilla, AMNH 54755, 54797; Colón, Balfate, AMNH 45705, 45714–15; Barra de Caratasca, KU 125871–74; 48.5 km W La Ceiba, AMNH 55287; Salamá, USNM 242016, 242019–20, 242024–25; 242028–31; Lago de Yojoa, AMNH 54776, 54953–54; Gracias a Dios, Tancin, LACM 48279–82; Islas de Bahía, Island of Bonacca (= Isla de Guanaja), BMNH 1947.2.2.17–23; Santa Bárbara, Santa Bárbara, TNHC 32621; Yoro, Yoro, AMNH 16181–83. **México:** Campeche, Laguna Chumpich, 28 km S La Esperanza, KU 75100; Tres Brazos, UIMNH 32396–97; Chiapas, 32 km S Arriaga, UIMNH 56998; Asunción, UIMNH 32393–95; Bochil, UIMNH 51175; 22 km S Palenque, UMRC 85.28; Rancho Monserrata, Río Grande, UIMNH 9850–63; Rizo de Oro, MVZ 145468; 3.4 km NW Rizo de Oro, CAS 142603–04; Salto de Agua, UIMNH 10500; San Juanito, Palenque, UIMNH 49238; 6.4 km NE Tapanatepec, KU 186702–03; 18.6 km E Tierra y Libertad, MVZ 104544–50; Cosolapa, CAS 74363; Oaxaca, 15 km SW Jalapa de Diaz, KU 195296–98, 200853–54 (tadpoles); Matias Romero, AMNH 53864, UIMNH 41044–50; 27 km S Oaxaca/Veracruz border on Hwy. 185, TNHC 48821–24; 6 km N of Palomares, KU 58876; Santa María Chimalapa, AMNH 51818–19; 8.9 km NE Tapanatepec, KU 7845–49, UTA 4175–76; 4.3 km W Tapanatepec, KU 75440; Tehuantepec, USNM 30329–31; 9.4 km W Tuxtepec, KU 137542–43; 12.8 km S Zanatepec, UIMNH 40872–74, 436839–40; between Zanatepec and Tapanatepec, UIMNH 42645–46; Tabasco, Tenosique, USNM 113752–58; 0.5 mi E Río Tonala, Hwy. 180, TNHC 25176–77; 27.2 km S Villahermosa, AMNH 69004; Veracruz, 21 km N Acayucan, UIMNH 42643–44; Alvarado, TNHC 21959–60; 3.5 km SE, 2.4 km W Catemaco, UIMNH 72826–28; 5.9 km S Catemaco, UIMNH 72824–25; 9.6 km S Catemaco, UIMNH 72835; 13.3 km E Ca-

temaco, UIMNH 72829–32; 21.8 km E Catemaco, UIMNH 72833–34; Lago de Catemaco, TNHC 35982, UTA 2221, 2287; Dos Chaneques, UIMNH 59871; 16 km ESE Cardoba, TNHC 25119; Coyame, UIMNH 38152–54, 82044; 62 km E Huatusco, TNHC 27539; 25 km SE Jesús Carranza, KU 27368–71; 3 km S Juan Diaz Corarrubias, UTA 6337; 2 km ENE Mata Oscura, KU 105683–84; Metlac, UIMNH 49237; Mirador, KU 23872–73, 23875–76; Potrero Viejo, KU 26433, UIMNH 10501–11, 15125, 32391–92, 49236, 57105, USNM 113736–50; 5 km S Potrero Viejo, KU 26432; Puente Nacional, UIMNH 21789–90; Río Blanco, 27.2 km E Córdoba, KU 194619; Río Blanco, 20 km WNW Piedras Negras, KU 23255; Río Blanco, 3 km W Plan del Río, KU 23719–21; Río Blanco, 15 km ENE Tlacotepec, KU 23871; vicinity San Andrés Tuxtla, UIMNH 27132–33, 32378–79, 57788–92; San José de Gracia, UIMNH 32380–90; 2–3 km SW San Marcos, KU 24422–24; near Siguapan, UIMNH 42639–41; Tierra Colorada, UIMNH 32376–77; 15 km ENE Tlacotepec, KU 23874. **Nicaragua:** Boaco, Boaco, KU 173846–56; Santa Rosa, 17 km N, 15 km E Boaco, KU 112936–37; Chontales, 1 km N, 2.5 km W Villa Somoza, KU 112943–45; Estelí, Condega, MVZ 78677–79; 12.8 km S Condega, KU 43164–206; Jinotega, Jinotega, KU 173845, 173858; Yalí, KU 101857; Managua, Tipitapa, KU 85517–18, 173842–43; 4 km SW Tipitapa, KU 85512; Hacienda La Cumplida, KU 66094; Nuevo Segovia, 1.5 km N, 1 km E Jalapa, KU 112941–42; 5 km N, 2.5 km E Jalapa, KU 112938, 112940; Río San Juan, Machuca, KU 173857; Rivas, 4.2 km SW Rivas, KU 85499; Zelaya, Bluefields, AMNH 75586; Bonanza, KU 84863, 85493–98, 101193; 1 km SW Bonanza, KU 101194; 5 km W Rama, KU 173844; El Recreo, S side Río Mico, KU 112933–35. **Panama:** Bocas del Toro, Almirante, KU 80083–92, 96415–29, MVZ 149561–63, USNM 142835; 3 km W Almirante, KU 108918–19, 108933; 4.0 km NW Almirante, KU 96430; Cayo de Agua, KU 96433, USNM 148261–63; 7.5 km WSW Chiriquí Grande, AMNH 113994; Fish Creek, KU 96436; Isla Bastimentos, AMNH 113995, KU 96434; Isla de Colon, La Gruta, KU 96431–32; E end Isla Escudo de Veraguas, KU 108920–22; S end Isla Popa, KU 96435; mouth of Río Cahuita, KU 108923–25; Chiriquí, 12.0 km WNW David, Río Platanal, KU 96437; N of Nueva California, USNM 167738 (tadpoles); Colon, Achiote, KU 77581–82; Darien, Camp Creek, Camp Townsend, AMNH 41023, 41137, 41156, 41728–30; Chalichimans Creek, Río Sucubti, AMNH 40515–18, 40532, 40537, 40556–58, 40794, 40878–79, 41059, 41062; Río Chucunaque, 7 km above Río Morti, KU 108932; Río Mono, 5 km above Río Tuira, KU 96438; Río Sucubti, AMNH 40563, 40824, 40826, 40830, 40832, 40835, 40840, 40843, 40845, 40847, 40852–53; Río Tuira at Río Mono: KU 96439–45; Three Falls Creek, AMNH 40878–79, 41064, 41685–86, 41706. Panama, Barro Colorado Island, AMNH 60528, 69850–55, KU 77580, 77653 (tadpoles); Juan Mina, FMNH 154370; Three Rivers Plantation, Gatun Lake, CAS 2906 (tadpoles); Veraguas, mouth of Río Concepción, KU 108926–31.

Rana vibicaria.—**Costa Rica:** Alajuela, Volcán Poás, CAS 64115–16, CRE 494, KU 86549–54, 103834, 104212 (tadpoles), MVZ 76079–80, 162034, TCWC 21758–64, TNHC 3595156; 3 km SE Volcán Poás, CRE 495, 698, 768; 16.6 km NW Los Cartagos, TNHC 31885–96; near Palmira, CRE 2654; Cartago, El Empalme, CRE 4816–17, MVZ 149033–34, 162035–36 (tadpoles); 9.8 km by road above Santa Cruz, on S slope of Volcán Turrialba, TNHC 36000–11; Volcán Irazú, AMNH 11746–47; Heredia, Alto del Roble, CRE 7094, 8160; 28.2 km N Heredia, KU 86548; Rama Sur, Río Las Vueltas, KU 103835–53, 104210 (embryos), 104211 (tadpole), 117451–56 (skeletons); Varablanca, CRE 6306, KU 37023; Volcán Barva, KU 30355–60, 100621; 7 km SE Volcán Barva, Río Las Vueltas, TCWC 21755–57; pass between Volcán Poás and Volcán Barva, KU 25028–30, 25032–37, 35039 (tadpoles), 35176–79; Puntarenas, SE Monteverde, CRE 6491; San José, Cascal de Las Nubes, CRE 174; Rancho Redondo, AMNH 5463. **Panama:** Bocas del Toro, N slope Cerro Pando, 1450 m, KU 116515; N slope Cerro Pando, 1810 m, KU 116516–17; Chiriquí, 4.5 km E Cerro Respingo, MVZ 128592–93; Cerro Punta, AMNH 69860–69, KU 77584–85; 3 km E Cerro Punta, MVZ 128591; 3.2 km W Cerro Punta, AMNH 69856; 4.8 km W Cerro Punta, AMNH 69857–59; 11.2 km E Volcán, CAS 143323–26.

Rana warszewitschii.—**Costa Rica:** Alajuela, 9.1 km W Atenas, CRE 6302; 2 km W Cariblanco, KU 66158; Cinchona, CRE 7017, KU 32705–08, 66159–60, 68588–90 (tadpoles), 104215 (tadpoles); Isla Bonita, KU 32699–700, 68591 (tadpoles), 25008, 25026–27; La Balsa, KU 140022; San Ramón, KU 140020–21; Sarchí, KU 32709–10; 4.8 km S Tanque San Carlos, CRE 7154; 4.8 km S Quesada, CRE 8077; 8 km N Quesada, CRE 7155; Cartago, 1.9 km E Cachí, CRE 6286; 2.5 km W Cachí, CRE 6287; 5 km S Cartago, CRE 163; 6.4 km SW Cartago, KU 32692; 11.2 km S Cartago, KU 35186; Río Chirripó, 2 km upriver from Quebrada Sueo, CRE 10082; Río Chitaria, CRE 282, 7073, KU 68580–81 (tadpoles); El Silencio de Sitio Mata, CRE 232, 235–37, TNHC 31897; 8 km N Entronque de la Sierra, KU 66157; Moravia de Chirripó, CRE 785, KU 32629–64, 32667–91, 32693–96, 41125–28 (skeletons), 66152–56, 68582 (tadpoles), TNHC 35984–93, 36012–36; Pavones, KU 140023–24; 3 km S Pavones, KU 66129, 66151, 68576 (tadpoles), 68577; Río Grande Tapantí, MVZ 76077–78; Río Playas, 5 km NE Capellades, CRE 7055; 1.6 km S San Isidro de Tejar, CRE 7061; vicinity Tapantí, CRE 682–83, 6157, 6309, 6455–56, 6497, KU 66128, 66130–49, 68199–205 (skeletons), 68578–79 (tadpoles), 68661 (tadpoles), 104213–14 (tadpoles); between Tejar and Cangreja, CRE 7160; Turrialba, KU 30398, 35187; 3 km W Turrialba, MVZ 186445–48; 6 km W Turrialba, KU 68584; 6.4 km S Turrialba, KU 25002–05, 25007; 8 km W Turrialba, KU 68583 (tadpoles); La Suiza, 8 km S Turrialba, KU 25006; Volcán Irazú, KU 30362–64; Guanacaste, El Silencio, CRE 6217, 6225, 6228–31, 6237–38, 6245, 7068; Hacienda La Pacífica, KU 157788; Las Flores, KU 32712; Los Angeles de Tilarán, KU 125516; San Bosco, CRE 6272; 2 km W Tilarán, CRE 731; 3 km E Tilarán, CRE 7069; 5 km NE Tilarán, KU 36565–68; 5 km NW Tilarán, CRE 730; Heredia, Cariblanco, KU 32701–04; 0.7 km N La Concordia, KU 68592–93 (tadpoles); Finca La Selva, KU 157789; 5 km S Los Cartagos, KU 68662 (tadpoles); 1 km N Montana

Azul, KU 68594–95; 1.6 km NNE Uvita, CRE 7010; Limón, Bambú, CRE 7182; El Tigre, CRE 290; 4 km W Guápiles, CRE 850; Los Diamantes, CRE 7002, KU 25010–25, 25031; Río Toro Amarillo, 7 km W Guápiles, KU 87688 (tadpoles); Suretka, KU 36572, 36580–81; Puntarenas, Agua Buena, KU 36569–71, 36573–79, 36582; near Barranca, KU 32711; Finca El Helechales, CRE 8268, 8277, 8280; Finca Las Mesillas, Río Negro, KU 91767–68; Finca Loma Linda, CRE 7224; Las Cruces, CRE 3117, 6367; Monteverde, CRE 4927–31 (tadpoles), 7040, 7203; 3 km E Palmar Norte, CRE 10025; 5 km S Santa Elena, CRE 4932–39 (tadpoles); Sirena Station, Parque Nacional Corcovado, CRE 8947; San José, El Cerrito, CRE 514; Curridabat, CRE 6473–74; between Tres Ríos and Curridabat, CRE 225 (3), 226 (6); 3.2 km WSW Escazú, CRE 7186; Guadelupe, CRE 244, 7011; La Palma, CRE 243, 301, 502, 527, 766, 6310, 7144, KU 36315–36, 41129 (skeleton), 66161–63, 68587 (tadpoles), MVZ 98035; Río Claro, CRE 7035, 7048, 8081; Río Claro and Río La Hondura, CRE 2823, 6380; Río Jorco, 2 km S Desamparados, KU 91770–71; Salitral de Santa Ana, CRE 229 (5); 2 km W Santa Ana, Río de Oro, CRE 222 (17); 1 km S San Cristóbal Sur, CRE 7062; San Isidro del General, KU 32697–98; 3.2 km SW San Isidro del General, KU 25009; 14.4 km SW San Isidro del General, CRE 7098; 15 km SW San Isidro del General, AMNH 86490–91, KU 91769; 20 km SW San Isidro del General, KU 68585 (tadpoles), 68586; vicinity San José, AMNH 11744–45, CRE 298, 477, 769, 1012–20, 7049; San Pedro, CRE 3049, 7036; San Ramón, MVZ 186449–50. **Honduras:** Gracias a Dios, Moca, LACM 13946. **Nicaragua:** Río San Juan, El Castillo, TCWC 23621; Tule Creek (= Río Tule), AMNH 7130–38; Zelaya, Camp Corozo, Río Huahuashán, AMNH 54973–74; Camp Santa Ana, Río Huahuashán, AMNH 54991–92; Cupitna Camp, AMNH 7122–24; Edén Mine, AMNH 7125–29; Maselina Creek, AMNH 7120; near Pia Creek, AMNH 7121; 2.4 km NW and 1.6 km NE Rama, TCWC 55562–64; 3.0 km NW Rama, MPM 12923; Río Pichinga, back of Pearl Lagoon, AMNH 55012–16. **Panama:** Bocas del Toro, 12.8 km W Almirante, KU 96453–68, 116795 (embryos); N slope Cerro Pando, KU 116510–11; Río Claro near Río Changena, KU 104270–71 (tadpoles), 116506–09; Chiriquí, Boquete, AMNH 69875; north of Boquete, CAS 79457–551; El Volcán, KU 96469–70; 6 km ENE El Volcán, KU 77656 (tadpoles); 6 km WNW El Volcán: KU 77655 (tadpoles); 8 km NW El Volcán, KU 77586, 77657 (tadpoles); Quebrada Chevo, S slope Cerro La Pelota, KU 116796 (tadpoles); Cocle, El Valle de Antón, CAS 98236, 98265, 98339–42, KU 77587, 116505; Darién, Chalichiman's Creek, Río Sucubti, AMNH 40519, 40539, 40918; Panama, Fort Clayton Reservation, UIMNH 42036–42; Madden Forest, George Creek Park, AMNH 81529–44; 7 km N Paraíso: KU 68017–39; Pipeline Road at Río Frijolita, KU 172865–67; near Three Rivers Plantation, CAS 2907 (tadpoles); south slope Cerro la Campana, KU 77654 (tadpoles), 116797 (tadpoles).