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THREE NEW SPECIES OF LEOPARD FROGS (*RANA PIPIENS* COMPLEX) FROM THE MEXICAN PLATEAU

By

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Numerous studies of the *Rana pipiens* complex over the past twenty years have shown conclusively that this group of frogs consists of many distinct species (for a review, see Hillis et al., 1983). The *R. pipiens* complex is comprised of two major sister groups (the alpha and beta divisions) the respective members of which are sympatric over large parts of North and Middle America. Within these divisions, species usually are parapatrically distributed, with or without narrow zones of overlap (Hillis et al., 1983). Where zones of contact do occur, little or no interspecific hybridization is evident (Post and Pettus, 1967; Mecham, 1968; Brown and Brown, 1972; Platz, 1972; Platz and Platz, 1973; Dunlap and Kruse, 1976; Frost and Bagnara, 1976, 1977a, b; Lynch, 1978; Hillis, 1981). Although species within this complex can usually be distinguished on a morphological basis (Post and Pettus, 1966; Pace, 1974; Frost and Bagnara, 1976; Hillis, 1982; Platz and Frost, 1984), leopard frogs are morphologically conservative and most of the species have been delineated by other techniques before their morphological distinctness became clear.

With the descriptions of *R. blairi* (Mecham et al., 1973), *R. chiricahuensis* (Platz and Mecham, 1979), and *R. yavapaiensis* (Platz and Frost, 1984), the leopard frogs of the United States are now fairly well known. This is not the case with the leopard frogs of México. Currently, four described species of the alpha division *(R. chiricahuensis, R. dunni, R. megapoda,* and *R. montezumae)* and six described species of the beta division *(R. berlandieri, R. brownorum, R. forreri, R. magnaocularis, R. omiltemana,* and *R. yavapaiensis)* are known from México. Of the beta division species, all are lowland or foothill forms except for *R.*

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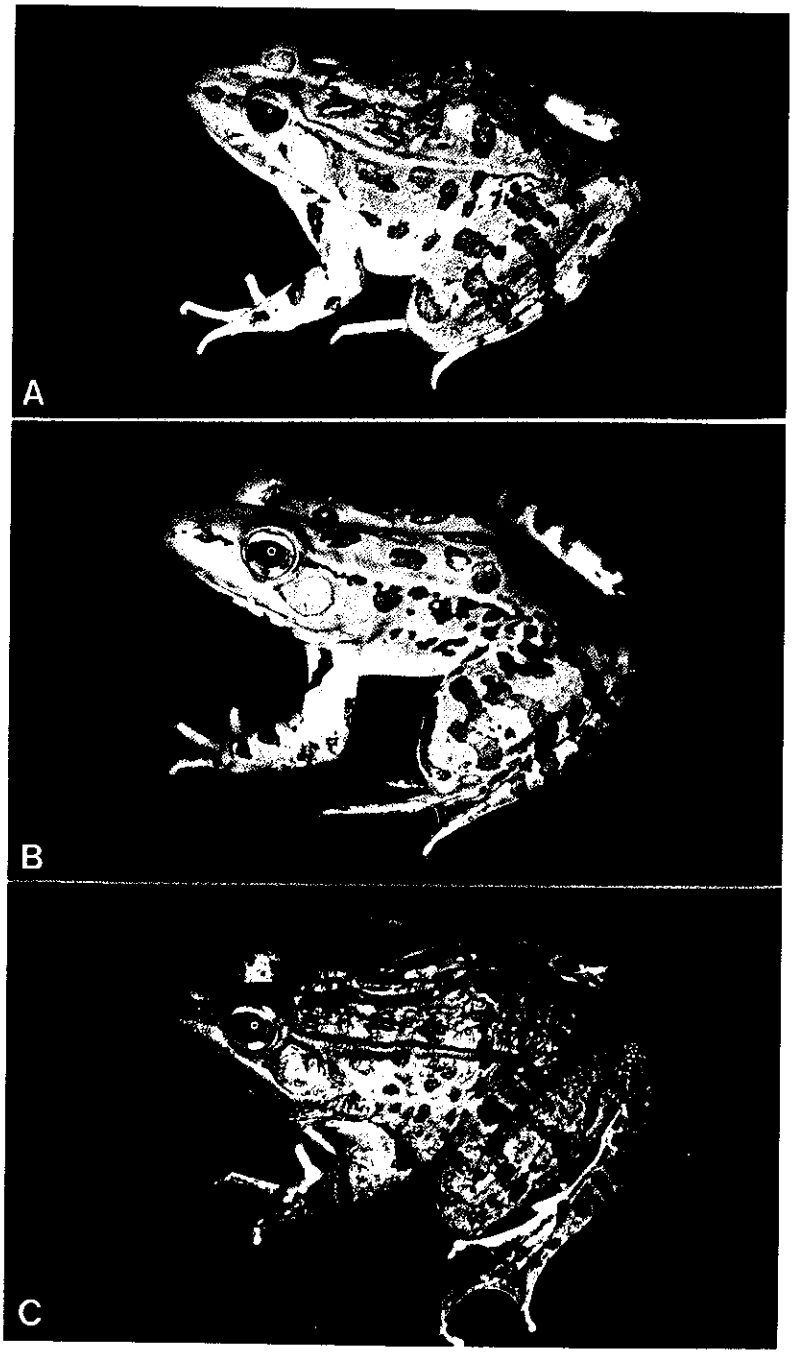

FIGURE 1. (A): *R. neovolcanica,* KU 197185 from Ojo de Rana, Michaocán, México. (B): *R. spectabilis,* from 5 km W Ciudad Hidalgo, Michoacán, México (to be deposited at KU). (C): *R. tlaloci,* KU 194435 from Xochimilco, Distrito Federal, México.

omiltemana, which is restricted to the Sierra Madre del Sur in Guerrero. Hillis et al. (1983) reported a clade of three electrophoretically distinct species of beta division leopard frogs that occurs along the southern edge of the Mexican Plateau. As a whole this subgroup of the *R. berlandieri* species group (Hillis et al., 1983) can be distinguished from all other described leopard frogs by the following combination of morphological characters (in addition to several unique allozymic markers): presence of broken and medially deflected dorsolateral folds; presence of numerous raised dorsal tuberosities; absence of vestigial oviducts in males; absence of a complete supralabial stripe; small head; and a dark reticulate pattern on the posterior surfaces of the thighs. We here describe the species that have been informally termed the Chapala form, the Hidalgo form, and the Xochimilco form of leopard frogs:

Rana neovolcanica, n. sp.
(Fig. 1a)

Rana halecina (in part): Boulenger (1920)
Rana pipiens (in part): Kellogg (1932), Smith and Taylor (1948), Duellman (1961, 1965), Salthe (1969)
Rana berlandieri (in part): Sanders and Smith (1971), Smith and Smith (1976)
Chapala form: Hillis et al. (1983)

Holotype.—KU 200782, an adult female from 3.2 km NW Tapalpa, Jalisco, México, elevation 2088 m, collected 7 August 1984 by David M. Hillis and Jonathan A. Campbell.

Paratopotypes.—KU 200781, 200783-787, UTA 15863-67, same data as holotype.

Referred specimens.—(All distances converted to kilometers). **Guanajuato:** 16 km E Yuriria, AMNH 75256; 3.2 km W Yuriria, AMNH 75257; NW Acámbaro, KU 38239; 6.4 km W Acámbaro, UIMNH 32133, FMNH 110649, 110673; 11.2 km SE Acámbaro, UIMNH 32134, FMNH 110647; 7.2 km S Valle de Santiago, UIMNH 8274-75; 22.1 km S Valle de Santiago, UIMNH 8351-69. **Jalisco:** near Chapala, UIMNH 32070-71; Lago de Chapala, FMNH 105180; south shore Lago de Chapala, CAS 97304; 0.5 km W Michoacán-Jalisco border, Lago de Chapala, MVZ 186215-220; 3.2 km E Jocotepec, UIMNH 8258; Atemajac, CAS 71783-86; 64 km NW Ciudad Guzmán, UTA 4086; 2.4 km NW Tapalpa, KU 195229-44. **Michoacán:** near Lago de Chapala, UIMNH 32205; 1.6-8 km N Jacona, UIMNH 85274-78; 29.6 km NW Jacona, UIMNH 8290-97; 16 km W Jacona, KU 194537-51, KU 194515 (tadpoles); Jacona, UIMNH 24677-78, 24704; near La Barca, KU 197178-80, 200764; 20.5 km W Jiquilpan, KU 195245-50; Jiquilpan, KU 38236; 16 km E Jiquilpan, KU 200765-69; La Palma, USNM 113812-15; 3.2 km E La Palma, KU 29096; Tacícuaro, USNM 113816; 2.4 km N Los Reyes, KU 38237; 3.2 km SW Zacapú, KU 38238; near Zamora, CAS 97244-50,

AMNH 67474-75; 1.6 km N Zamora, MVZ 39392-93; 9.6 km E Zamora, AMNH 68054-55; 1.6 km S and 17.6 km W Zamora, KU 29082, 29084-90, 29092-93, 29095, 29097-106, 29108, 29110-12, 29115, 29117-124, 29126; 16 km NW Zamora, KU 194552-58; 20.8 km SE Zamora, KU 194516 (tadpoles); vicinity of Ixtlán, KU 197183; Ojo de Rana, W of Zamora, KU 197185; 3.2 km W Cojumatlán, AMNH 73403; 1.6 km E Cojumatlán, AMNH 73404; Lago de Pátzcuaro at Tzintzuntzán, AMNH 67473; embarcadero at Pátzcuaro, AMNH 58403-05; 4.8 km S Pátzcuaro, CAS 87178-79; 9.6 km N Pátzcuaro, UIMNH 8259; Colonia Vista Bella, Morelia, MVZ 71938; Zurumbeneo, KU 194536, 194513 (embryos), 194514 (tadpoles).

Diagnosis.—*Rana neovolcanica* differs from other species outside the subgroup (here designated the *R. neovolcanica* subgroup) as described above. It differs from other species within the *R. neovolcanica* subgroup by the following combination of characters (also see Hillis et al., 1983, for unique allozymes): dorsolateral folds prominently raised, usually white or cream; prominent, darkly pigmented external vocal sacs; head longer than wide; snout relatively pointed; legs relatively long (distal end of tibiofibula extending to beyond snout when adpressed against body); dorsal background coloration usually a mixture of tan, brown, and light green, with each dorsal spot surrounded by a light green halo; ventral coloration white.

Description of the holotype.—Adult female with the following measurements: snout-vent length, 71.4 mm; head width, 23.5 mm; head length (angle of jaw to tip of snout), 24.5 mm; tibiofibula length, 42.0 mm; foot length, 42.5 mm; tarsus length, 22.8 mm; interorbital distance, 4.2 mm; internarial distance, 5.2 mm; eye-naris distance, 6.3 mm; tympanum diameter, 5.7 mm. Dorsolateral folds distinctly raised, broken posteriorly and inset medially. Twenty-one dorsal spots between dorsolateral folds. Dorsal spots irregular ovoids, darker around periphery, and surrounded by light halos. Dorsal ground color (in life) light brown posteriorly, grading to light green anteriorly; dorsal spots dark brown. Dorsolateral folds white. Vague light spot in center of tympanum, otherwise tympanum yellow-brown. Yellowish-white supralabial stripe terminating just anterior to eye. Dark band through eye onto canthus rostralis. Light brown laterally, with distinct white striatulations. Venter and undersurfaces of legs white; some dusky markings on throat and chin regions. Dorsal surfaces of legs with distinct crossbars; posterior surfaces of thighs with dark brown and cream reticulations. Liver and portion of thigh muscle removed for biochemical studies.

Embryos and larvae.—The eggs of *R. neovolcanica* are laid in a submerged, spherical mass. A complete egg mass of this species (KU 194513) contains approximately 4,500 embryos (late cleavage to dorsal lip) in its volume of 150 ml. The embryos are 1.7 mm in diameter, and the jelly envelopes are 4.0 mm in diameter.

The tadpoles of *R. neovolcanica* are of the pond-type (Fig. 2).

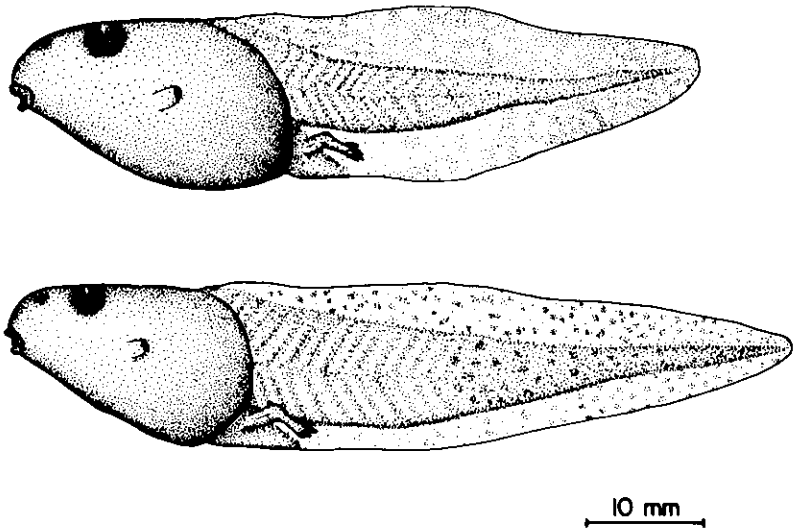

FIGURE 2. Upper: tadpole of *R. neovolcanica*, KU 194514 from Zurumbeneo, Michoacán, México; lower: tadpole of *R. spectabilis*, KU 194517 from 5 km W Ciudad Hidalgo, Michoacán, México. Both are in stage 35 of Gosner, 1960.

Compared to other members of the *R. berlandieri* group, the tail is relatively shorter, less muscular, and has higher fins.

Distribution.—*Rana neovolcanica* occurs in open areas of pine-oak forest and mesquite-grassland at elevations of 1500 to 2500 m along the southern edge of the Mexican Plateau *(Cordillera Neovolcánica)* in parts of the Mexican states of Guanajuato, Jalisco, and Michoacán (Fig. 3). It occurs primarily in lakes, ponds, and slow moving streams.

Remarks.—We have found this species breeding in May, but its tadpoles may be found throughout the year, which suggests an extended breeding season. The ranges of *R. neovolcanica* and *R. spectabilis* are parapatric along the northwest-facing slopes south and east of Morelia, Michoacán. In this area, *R. spectabilis* occurs at higher elevations in fir forest, whereas *R. neovolcanica* occurs at lower elevations in open valleys. *Rana neovolcanica* has a chuckle-type call.

Etymology.—The species name is an adjective in reference to the *Cordillera Neovolcánica,* the volcanic axis of mountains along which this species is distributed.

Rana spectabilis, n. sp.
(Fig. 1b)

Rana halecina (in part): Boulenger (1920)
Rana pipiens (in part): Kellogg (1932), Smith and Taylor (1948), Ruibal (1955, 1957), Duellman (1961, 1965), Salthe (1969)

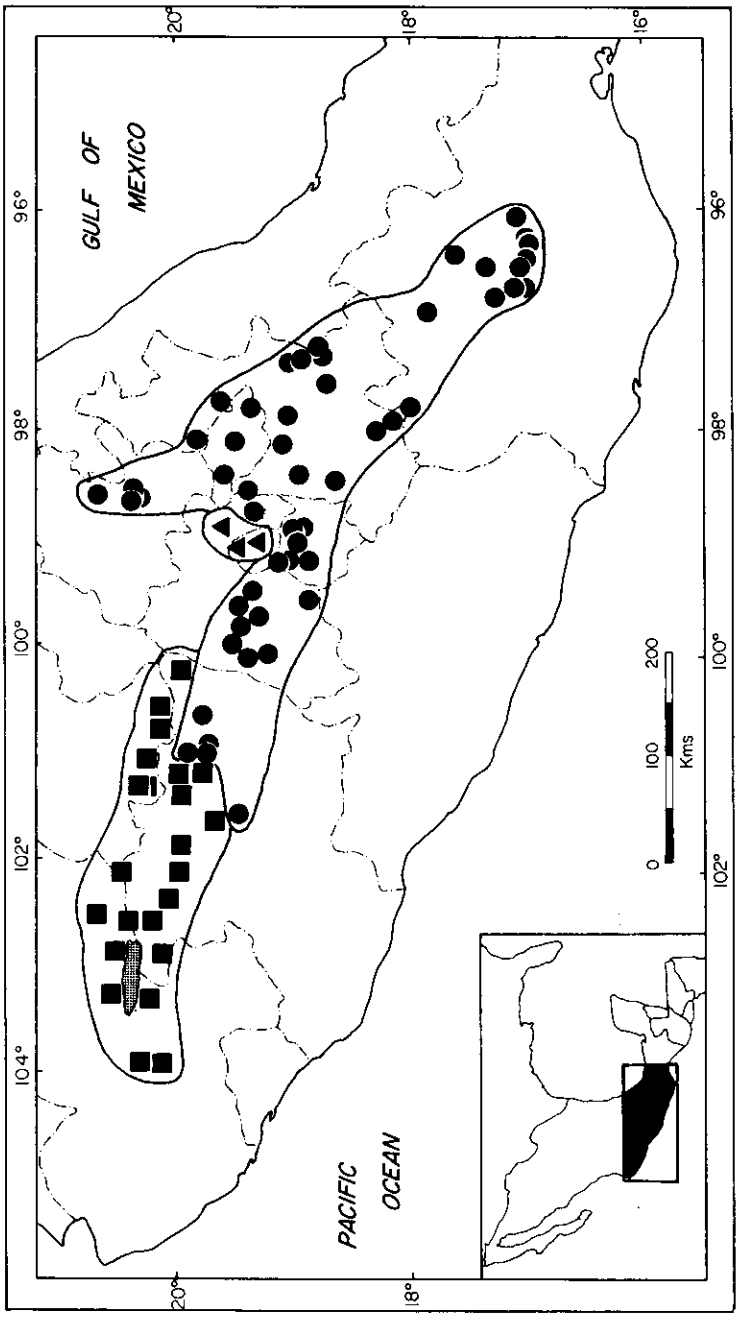

FIGURE 3. Distribution of *R. neovolcanica* (squares), *R. spectabilis* (circles), and *R. tlaloci* (triangles). The shaded area represents Lago de Chapala.

Rana pipiens trilobata: Smith (1947)
Rana berlandieri (in part): Sanders and Smith (1971)
Rana berlandieri brownorum (in part): Sanders (1973)
Rana berlandieri trilobata (in part): Smith and Smith (1976)
Hidalgo form: Hillis et al. (1983)

Holotype.—KU 195186, an adult female from La Estanzuela, Hidalgo, México, elevation 2900 m, collected 17 June 1983 by David M. Hillis, Jonathan A. Campbell, and William W. Lamar.

Paratopotypes.—KU 195187-211, 195331-33, UTA 15868-872 (adults), KU 200842 (tadpoles), KU 200841 (embryos), same data as holotype. KU 200828-830, 24 January 1984, David M. Hillis and Richard L. Mayden.

Referred specimens.—(All distances converted to kilometers). **Hidalgo:** Parque Nacional El Chico, UIMNH 32270, 32064, USNM 113833-38, MVZ 104571, 104534-39, FMNH 102891, 107814, 107817, KU 58883, 71570-71, 195405-418; 19.2 km NE Pachuca, BCB 12524-29; Presa Arroyo Zarco, 10.4 km NE Mexquititlan, KU 195217-23, 200845 (tadpoles); 7 km SE Zacualtipán, KU 195228, 200844 (tadpoles). **México:** between Puebla and México City, 33.6 km E México City, UIMNH 32146-50; Atotonilco Grande, UIMNH 32151, 32283; 12.8 km W Villa Victoria, UIMNH 32152, 32284, FMNH 107776, 107778, 107782; 11.2 km W Villa Victoria, USNM 113808; 3.2 km S San Martín, UIMNH 32153, FMNH 110662; 15 km W Toluca, USNM 113800-07; 3.2 km W Toluca, AMNH 89342; 8 km N Toluca, AMNH 89343; 4 km W Toluca, FMNH 65540; Lagunilla Ojuelos, 8 km W Toluca, AMNH 58926-27; Lerma, AMNH 53238, FMNH 110654, 110683; Ixtapan de la Sal, AMNH 55213-15, FMNH 65530-39, 65541-53; Lagunas de Zempoala, AMNH 57701-05, 57706-710; Valle de Bravo, FMNH 65544; 1.6 km S Tonatico, KU 62396. **Michoacán:** 29.8 km E Morelia, UIMNH 40352; 40 km E Morelia, CAS 132172-185; San José Lagunillas, MVZ 186210-14; 11.4 km E junction México Hwy. 15 and 51, W of Ciudad Hidalgo, KU 194559-63, 194565, 194517 (tadpoles); Presa Pucuato, KU 194564; 3.2 km E San Gregorio, KU 50542-79; 4.8 km SE Opopeo, KU 37994-96; 19.2 km W Ciudad Hidalgo, KU 43653; 5 km W Ciudad Hidalgo, KU 192987-89. **Morelos:** Lagunas de Zempoala, UIMNH 10547-51, 32092-99, 32221-29, 63793, USNM 148915-16, 113840-54, FMNH 105785, 107767, 107772, 107781, 107804, 107806-08, 108861, 108864, 108878, 108880, 108887-88, 110709-720, 110722-24, 110726-29, 110733-34, 110793, 110864, 110869, 122565, 122567-570, 126303-04, 126310, KU 195255, 195419-432; Cuernavaca, UIMNH 32082, 16798-800, USNM 20160-64, FMNH 108865, 108889; 3.2 km N Cuernavaca, UIMNH 32086; FMNH 108866, 108881; 4.8 km N Cuernavaca, UIMNH 32087, FMNH 108886; near Temixco, UIMNH 32083-85, 32211, 32216; Progreso, UIMNH 35261-300; near Yautepec, UIMNH 32230; 3.5 km W Cuautlixco, KU 87264-272; 1.6 km E Cuautla, KU 194578-79. **Oaxaca:** Oaxaca, UIMNH 32172-73, USNM 46972, 47058-59, 47075-76, AMNH 53616, 64690-93, 96569-572, FMNH

38668, 102896, 102905, 107741, 107771, BCB 11008-09; 3 km from Oaxaca on road to airport, AMNH 68224-25; 4.8 km ESE Oaxaca, KU 37992-93; 6.4 km S Oaxaca, UIMNH 9244-48; 20.8 km S Oaxaca, CAS 11054-56; between Oaxaca and Tlacalula, UIMNH 26552; San Felipe de Agua, UIMNH 53075, 57726; W of San Felipe de Agua, UIMNH 57775-78; 1.6 km W San Felipe de Agua, UIMNH 57739-45, 58053-56; 1.6 km S San Felipe de Agua, UIMNH 57734-38; 3.2 km SW San Felipe de Agua, UIMNH 57727-733; Mitla, USNM 47060-62; 4 km W Mitla, UTA 2906-07; 4.8 km W Mitla, KU 50541; 6.4 km W Mitla, KU 43333-35; 8 km W Mitla, AMNH 78464-65; 3.7 km N Mitla, KU 200779; near El Tule, AMNH 68226-27; 11.2 km S Tamazulapan, UIMNH 9354-55; Río de la Y, Cofradía, CAS 113957; Tlalixtac de Cabrera, AMNH 68218-223; 4 km NW Sta. María Albarradas, AMNH 80657; below Tejocotes, Río Temascal, AMNH 80658-59; Cuicatlán, USNM 46969; Ixtlán de Juárez, CAS 103429; 2.6 km W Ixtlán de Juárez, AMNH 78475-78; 3.2 km E Ixtlán de Juárez, AMNH 106558; 4.8 km S Ixtlán de Juárez, UIMNH 59873-75; Llano de las Flores, UIMNH 58059-68, AMNH 68228-239, 78471-74, KU 71572-75, 129172, 137544-46, 139948-952 (tadpoles). **Puebla:** 1.6 km E Hidalgo-Puebla state line above Huauchinango, INHS 9621; Puebla, UIMNH 32232-35, AMNH 64687-88, 65687-695, FMNH 107774, 107789-93, 107795-96, 110774, 110776, 110783, 110789, 110792, 110796; N Alseseca, UIMNH 32231; 11.2 km S and 4.8 km E Puebla, KU 39874; 14.4 km N Izúcar de Matamoros, UIMNH 9352-53; 10.4 km SW Izúcar de Matamoros, KU 39580-85; 4.5 km W Tepeaca, UIMNH 38112-124, 72945-56, 82062; Santa Inés, UIMNH 49239; near Acatlán, UIMNH 55247-48; 17.6 km S Acatlán, UIMNH 57746; Atlixco, USNM 47923; between San Sebastián and Venta Salada, AMNH 6295-97; Los Reyes, near Catarina, AMNH 13878-882; Santa Catarina, AMNH 13868-69; Laguna de Santa Catarina, AMNH 13872-77; 19.2 km S Chignahuapan, AMNH 107109; 3.2 km E Río Frío, BCB 12523; 22.4 km S Tecamachalco, BCB 12511-522; Río Pesmatlán, 8.6 km W Teteles, KU 195337-345, 200843 (tadpoles). **Tlaxcala:** 1 km W Apizaco, UIMNH 40869-870; 32 km E Huamantla, TNHC 36663-71; 3.2 km E El Carmen, AMNH 73392-95; Laguna del Carmen, AMNH 75255. **Veracruz:** Acultzingo, UIMNH 49241, 58076-98; 9.6 km SW Acultzingo, BCB 12501-510; Cumbres, FMNH 102869, 102892; 0.8 km W Cumbres, BCB 9039.

Diagnosis.—R. spectabilis differs from species outside of the *R. neovolcanica* subgroup as described above. This species can be distinguished from the other members of the *R. neovolcanica* subgroup by the following combination of characters (in addition to a number of unique allozymes, Hillis et al., 1983): dorsolateral folds flattened, broad, usually bronze; vocal sacs small, eversible; head short and rounded; legs short, distal end of tibiofibula not reaching snout; dorsal ground color metallic green to yellowish green, usually without any light halos around spots; undersurfaces of legs and posterior portion of venter sulphur yellow.

Description of the holotype.—Adult female with the following measurements: snout-vent length, 67.0 mm; head width, 23.7 mm; head length, 21.1 mm; tibiofibula length, 35.6 mm; foot length, 36.7 mm; tarsus length, 19.4 mm; interorbital distance, 3.9 mm; internarial distance, 5.0 mm; eye-naris distance, 4.7 mm; tympanum diameter, 5.9 mm. Dorsolateral folds broad, flattened; small posterior section of dorsolateral fold broken and inset medially. Eighteen small dorsal spots between dorsolateral folds. Numerous distinctly raised striatulations between dorsolateral folds. Dorsal spots small ovoids, darker around periphery. Dorsal and lateral ground color (in life) bright metallic green; dorsal spots bronze. Dorsolateral fold greenish-bronze, not distinct from ground color. Tympanum bronze. No supralabial stripe; snout green. Posterior portion of venter and undersurfaces of legs sulphur yellow, with numerous melanistic markings on chin, throat, and chest. Dorsal surfaces of legs with distinct crossbars; posterior surfaces of thighs with black and yellow reticulations. Liver and portion of thigh muscle removed for biochemical studies.

Embryos and larvae.—The eggs of *R. spectabilis* typically are laid in a quiet pool of a stream in a submerged, spherical mass. A complete egg mass of this species (KU 200841) contains approximately 3,000 embryos (dorsal lip to mid-gastrula) in its volume of 250 ml. The embryos are 2.5 mm in diameter, and the jelly envelopes are 6.0 mm in diameter. With the limited data available, the eggs of *R. spectabilis* appear to be much larger and less numerous than those of *R. neovolcanica.*

The tadpoles of *R. spectabilis* are of the stream-type (Fig. 2). The tail is long and muscular, with low fins. Tadpoles of this species grow to be quite large; individuals with a total length of over 100 mm are common (e.g., KU 200842, 200843).

Distribution.—Rana spectabilis primarily occurs in oak, pine-oak, and fir forest at elevations of 1200 to 3200 m from eastern Michoacán east through central México (state) and Morelos, north through Tlaxcala to eastern Hidalgo, and south through central Puebla and a small portion of western Veracruz to the highlands of northwestern Oaxaca (Fig. 3). It occurs around the marshy edges of ponds and lakes, but it primarily inhabits the edges of mountain streams.

Remarks.—Rana spectabilis is sympatric with *R. forreri* in the vicinity of Yautepec, Morelos, and with *R. berlandieri* in parts of eastern Hidalgo. Sanders (1973) listed BCB 12501, 12503-05, and 12507 (from 6 mi [=9.6 km] SW Acultzingo, Veracruz) as juvenile paratypes of *R. berlandieri brownorum.* These specimens are in fact adult *R. spectabilis;* they can be distinguished from *R. brownorum* by the lack of oviducts in the males (present in *R. brownorum*); short, rounded snouts; short legs; and much smaller size at sexual maturity.

We have found this species breeding at the type locality in January and in July; an extended breeding season is probable. *Rana spectabilis* has a chuckle-type call.

Etymology.—The specific name is a Latin adjective, in reference to its remarkably brilliant coloration.

Rana tlaloci, n. sp.
(Fig. 1c)

Rana pipiens (in part): Smith and Taylor (1948)
Rana berlandieri (in part): Sanders and Smith (1971); Smith and Smith (1976)
Xochimilco form: Hillis et al. (1983)

Holotype.—KU 194434, an adult female from Xochimilco, Distrito Federal, México, collected in March 1981 by John S. Frost and Thomas J. Berger.

Paratopotypes.—KU 194435-36, same data as the holotype. KU 174481-82, 5 December 1963, Jaime Villa. USNM 113796-99, 25 January 1939, Hobart M. Smith. MVZ 186221, 26 January 1981, H. Bradley Shaffer.

Referred specimens.—**Distrito Federal:** Tacubaya, MVZ 8843; 1.6 km W Tlalpan, AMNH 12213-14; San Juanico, AMNH 12215; Lago de Guadalupe, AMNH 59873. **México:** San Juan Teotihuacán, TNHC 31869.

Diagnosis.—*Rana tlaloci* differs from species outside of the *R. neovolcanica* subgroup as described above. It can be distinguished from the other members of the *R. neovolcanica* subgroup by the following combination of characters (in addition to a number of unique allozymes, Hillis et al., 1983): dorsolateral folds prominently raised, bronze; vocal sacs external, prominent, darkly pigmented; snout short and rounded; legs relatively long, distal end of tibiofibula extending beyond snout when adpressed along body; dorsal coloration dusky brown, without light halos around dorsal spots; venter and undersurfaces of legs white.

Description of the holotype.—Adult female with the following measurements: snout-vent length, 66.3 mm; head width, 23.5 mm; head length, 20.9 mm; tibiofibula length, 39.1 mm; foot length, 38.5 mm; tarsus length, 19.5 mm; interorbital distance, 4.0 mm; internarial distance, 4.7 mm; eye-naris distance, 5.0; tympanum diameter, 5.4 mm. Dorsolateral folds distinctly raised, broken posteriorly and inset medially. Fifteen dorsal spots between dorsolateral folds. Dorsal spots irregular ovoids, darker around periphery. Dorsal ground color (in life) golden tan; dorsal spots dark brown. Dorsolateral folds bronze. Tympanum bronze. Indistinct supralabial stripe terminating under eye. Distinct striatulations on dorsal and lateral surfaces. Venter and undersides of legs cream to white, dusky anteriorly. Dorsal surfaces of legs with distinct crossbars; posterior surfaces of thighs with cream and dark brown reticulations. Liver and portion of thigh muscle removed for biochemical studies.

Distribution.—Historically known from throughout the Valley of México

(Fig. 3). Recently, however, this species has been found only at Xochimilco.

Remarks.—This species is probably in danger of extinction as a result of the growth of México City. The type locality is now badly polluted, and most of the former range of this species is now uninhabitable for frogs.

Four paratypes (USNM 113796-99) seem to have extremely short legs, but this is a result of leg fractures and preservation distortion. TNHC 31869 from San Juan Teotihuacán is the only specimen of this species that did not come from around one of the lakes of the Valley of México.

Etymology.— This species is named for Tlaloc, Aztec god of water, rain, and thunder. The recently excavated Great Temple of the Mexicas at Tenochtitlán (just north of Xochimilco in México City) features the Altar of the Frogs below the Sanctuary of Tlaloc, who was symbolized by all things aquatic (Matos Moctezuma, 1984). Therefore, it is fitting that this species of frog, which occurs only in the Valley of México and may have been the species represented by the Aztecs in sculpture, bears Tlaloc's name.

EXPERIMENTAL HYBRIDIZATION

Laboratory crosses were made involving two of the new species and other leopard frogs of the complex from México. Although the genetic compatibility data are meager, they are nonetheless informative. In a single cross of species within the *R. neovolcanica* subgroup (Table 1, cross 2), a male of *R. neovolcanica* affected outwardly normal embryonic development in 213 of 226 eggs of *R. spectabilis* (94% with respect to parallel control). This finding is suggestive of very high genetic compatibility. Similarly, high compatibility was indicated in a cross (Table 1, cross 11) of a male *R. neovolcanica* against a female *R. magnaocularis* (95% normal), whereas, in a single reciprocal cross (Table 1, cross 9) of these species, hybrid embryonic development was 77% of normal. Compatibility seemed to be substantial (76%) in the cross of a male *R. forreri* and a female *R. neovolcanica* (Table 1, cross 8). In contrast, two reciprocal crosses (Table 1, crosses 4 and 6) proved to be entirely lethal to the hybrid embryos, whereas development in control embryos was near normal (97% and 88%). With the exception of crosses 4 and 6, these data on genetic compatibility are in general agreement with allozyme data (Hillis et al., 1983) concerning genetic similarity among these species. The striking and uniform genetic defects observed in the hybrid embryos of crosses between males of *R. neovolcanica* and females of *R. forreri* reflect a developmental syndrome associated with the *R. forreri* genome that affects development in a manner disproportionate to interspecific genetic compatibility *per se.* The syndrome has been observed previously in interspecific crosses involving the eggs of *R. forreri* and sperm from *R. magnaocularis* (Frost and Bagnara, 1977a), *R. berlandieri* (Frost, 1982), and *R. yavapaiensis* (Platz and Frost, 1984). We have not attempted crosses involving *R. tlaloci* to date.

TABLE 1. Genetic Compatibility Between Leopard Frogs Considered in This Study.

(N)	Specimens* (Females)		(Males	A Eggs exhibiting 1st cleavage (N)	B Embryos normal at hatching 50% +24 hr (N)	"B"/"A" (%)	Hybrids vs. controls (%)
1.	*R. spectabilis*, Michoacan (1)	×	*R. spectabilis* Michoacan (2)	125	123	98	100
2.	*R. spectabilis*, Michoacan (1)	×	*R. neovolcanica*, Jalisco (3)	226	213	94	96
3.	*R. forreri*, Sinaloa (4)	×	*R. forreri*, Sinaloa (5)	117	113	97	100
4.	*R. forreri*, Sinaloa (4)	×	*R. neovolcanica*, Jalisco (6)	244	0	0	0
5.	*R. forreri*, Sinaloa (7)	×	*R. forreri*, Sinaloa (8)	325	285	88	100
6.	*R. forreri*, Sinaloa (7)	×	*R. neovolcanica*, Jalisco (9)	124	0	0	0
7.	*R. neovolcanica*, Jalisco (10)	×	*R. neovolcanica*, Jalisco (11)	116	105	91	100
8.	*R. neovolcanica*, Jalisco (10)	×	*R. forreri*, Sinaloa (12)	141	107	76	84
9.	*R. neovolcanica*, Jalisco (10)	×	*R. magnaocularis*, Sinaloa (13)	20	14	70	77
10.	*R. magnaocularis*, Sinaloa (14)	×	*R. magnaocularis*, Sinaloa (15)	207	196	95	100
11.	*R. magnaocularis*, Sinaloa (14)	×	*R. neovolcanica*, Jalisco (16)	236	213	90	95

* Number in parentheses following specimen identifies individual.

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RESUMEN

Tres nuevas especies de "ranas pintas" (*Rana pipiens* complex) son descritas de México. *R. neovolcanica* distribuída en Jalisco, Michoacán, y Guanajuato; *R. spectabilis* distribuída en Hidalgo, México, Michoacán, Morelos, Oaxaca, Puebla, Tlaxcala, y Veracruz; y *R. tlaloci* distribuída en el Distrito Federal y alrededores del estado de México. Estas tres nuevas especies se distínguen entre sí, y de las otras especies de *Rana* de México, por sus características electroforéticas y morfológicas. Las nuevas especies conforman al subgrupo de *R. neovolcanica* dentro del grupo de *R. berlandieri*.

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