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New Species of Stream-breeding Hylid Frogs from the Northern Versant of the Highlands of Oaxaca, Mexico

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ABSTRACT Five new species of hylid frogs are described from cloud forests on the northern versant of Oaxaca, Mexico. *Hyla abdivita* is a member of the *Hyla pinorum* group and occurs in the Sierra Mazateca. Another member of the *Hyla pinorum* group, *H. melanomma bivocata* Duellman and Hoyt, is elevated to specific level. Populations of frogs from the Sierra Mazateca, Sierra Juárez, and the Sierra Mixes, formerly associated with *H. arborescandens* in the *Hyla miotympanum* Group, are recognized as a new species, *H. cyclada*. *Hyla psarosema* is a member of the *Hyla bistincta* Group and is found in the Sierra Mixes and seems to be closely related to *H. sabrina* of the Sierra Juárez. Frogs

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from the Atlantic versant, formerly referred to as *P. erythromma* and *P. leonhardschultzei*, are described as *Ptychohyla acrochorda* and *P. zophodes*, respectively; *Hyla milleri* Shannon is a junior synonym of *P. leonhardschultzei*. *Ptychohyla erythromma* and *P. leonhardschultzei* (sensu stricto) are restricted to the Pacific slopes of the Sierra Madre del Sur in Guerrero and Oaxaca.

KEY WORDS: Amphibia; Anura; Hylidae; *Hyla*; *Ptychohyla*; new species; cloud forests; Oaxaca, Mexico.

RESUMEN Se describen cinco nuevas especies de ranas hílidos de los bosques nubosos de la vertiente norte de Oaxaca, México. *Hyla abdivita* es un miembro del grupo de *Hyla pinorum* y ocurre en la Sierra Mazateca. Otro miembro del grupo de *Hyla pinorum*, *H. melanomma bivocata* Duellman y Hoyt, se eleva a nivel específico. Poblaciones de ranas de la Sierra Mazateca, Sierra Juárez, y la Sierra Mixes que previamente se asociaban con *Hyla arborescandens* en el grupo de *Hyla miotympanum*, son reconocidos como una nueva especie, *Hyla cyclada*. *Hyla psarosema* es un miembro del grupo de *Hyla bistincta* y se encuentra en la Sierra Mixes y aparentemente está cercanamente relacionada a *H. sabrina* de la Sierra Juárez. Ranas de la vertiente Atlántica previamente conocida como *Ptychohyla erythromma* y *P. leonhardschultzei*, se describe como *P. acrochorda* y *P. zophodes*, respectivamente; *Hyla milleri* Shannon es un sinónimo secundario de *P. leonhardschultzei*. *Ptychohyla erythromma* y *P. leonhardschultzei* (sensu stricto) están restringidas a la ladera pacífica de la Sierra Madre del Sur en Guerrero y Oaxaca.

PALABRAS CLAVES: Amphibia; Anura; Hylidae; *Hyla*; *Ptychohyla*; nuevas especies; Oaxaca; Mexico.

INTRODUCTION

The northern slopes of the highlands in the state of Oaxaca in southern Mexico support humid cloud forest at moderate and intermediate elevations (600–2700 m) and pine-oak forest, with fir mixed with pine, occurs at the highest elevations (e.g., Cerro Pelón). Because of the rugged nature of these mountains, unstable soils, and wet climate, few roads traversed the northern escarpments until recent decades. The first road across the Sierra Juárez was constructed in the late 1950's, and Duellman traveled across the road for the first time in April 1959. The roads between Tamazulapan and Totontepec in the Sierra Mixes and between Huautla de Jiménez and Jalapa de Díaz in the Sierra Mazateca were passable by motor vehicle only sporadically and at considerable risk until the late 1970's and early 1980's, respectively. Both of us have worked the transect between Valle Nacional on the Atlantic lowlands across the Sierra Juárez many times, and Campbell worked in the Sierra Mixes in 1978, 1979, and 1983, and in the Sierra Mazateca in 1983 (Fig. 1).

The northern escarpment in Oaxaca is a haven for amphibians and is exceptional in Middle America for its biodiversity and high degree of endemism (Campbell, 1999; Casas-Andreu et al., 1996; Hanken and Wake, 1994). In his work on the hylid frogs of Middle America, Duellman (1970) recognized seven species of stream-breeding hylids in the region: *Hyla arborescandens*, *H. chaneque*, *H. crassa*, *H. erythromma*, *H. hazelae*, *H. mixe*, *Ptychohyla ignicolor*, and *P. leonhardschultzei*. His taxonomy was conservative and included allocation of populations in the Sierra Juárez to some widespread species (e.g., *H. arborescandens* throughout the Sierra Madre Oriental, *H.*

chaneque also on the northern versant of the Chiapas highlands, and *H. erythromma* and *P. leonhardschultzei* on the Pacific versant of the Sierra Madre de Sur).

Field work, principally by Campbell in the Sierra Juárez and the Sierra Mixes and by Janalee P. Caldwell, who spent a year (1969–70) on a transect across the mountains of Oaxaca, resulted in the discovery of additional species and provided material for the reassessment of the taxonomic status of populations of hylid frogs on the northern slopes of Oaxaca. Caldwell (1974) described *H. cyanomma* and *H. sabrina* from the Sierra Juárez and also reported the discovery of a southern population of *H. siopela* in the region; Toal and Mendelson (1995) distinguished the population assigned to *H. siopela* in the Sierra Juárez as a new species, *H. celata* and placed *H. bogertae* in the synonymy of *H. crassa*. Likewise, Mendelson and Campbell (1999) showed that the frogs in the Sierra Juárez formerly assigned to *H. chaneque* represented an undescribed species, which they named *H. nephila*. Toal (1994) described *H. calvicollina* from the Sierra Juárez, and Ustach et al. (2000) described *H. calthula* from the Sierra Mixes. The only other taxonomic changes have been the placement of *H. erythromma* in the genus *Ptychohyla* and the placement of *P. ignicolor* in the genus *Duellmanohyla* (Campbell and Smith, 1992). Campbell and Brodie (1992) reported *H. melanomma* from the lower slopes of the highlands in northern Oaxaca. Thus, 14 species of stream-breeding hylids have been reported from the northern versant of the Oaxacan highlands west of the Isthmus of Tehuantepec.

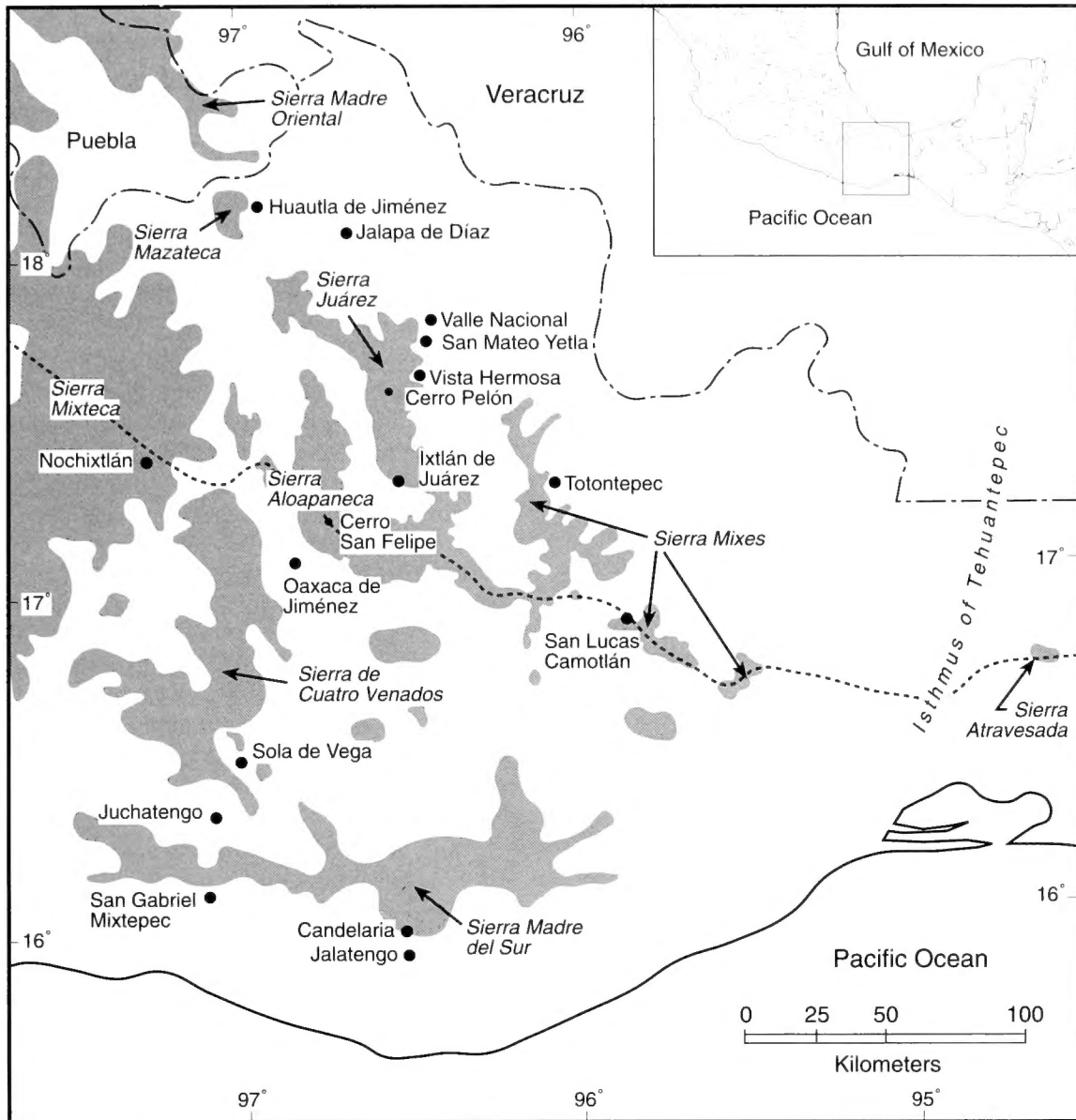


Fig. 1. Map of the highlands of Oaxaca, Mexico, showing place names mentioned in the text. Areas above 2000 m are shaded; the dotted line represents the Continental Divide.

Herein we describe one new species in the *Hyla bistincta* Group that we discovered in the Sierra Mixes. We show that the specimens assigned to *Hyla melanomma* from the lower Atlantic versant of Oaxaca by Campbell and Brodie (1992) actually represent an undescribed species in the *Hyla pinorum* Group and that specimens formerly identified as *Hyla arborescandens* from the Sierra Juárez represent an undescribed species in the *Hyla miotympanum* Group. *Ptychohyla erythromma* and *P. leonhardschultzei* were described from the Sierra Madre del Sur in Guerrero; we document that specimens that formerly were assigned to these species from the Atlantic versant of Oaxaca represent previously unrecognized species. We take this oppor-

tunity to provide comparisons of the tadpoles of some of the species that we recognize.

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

The standard terminology and measurements described by Duellman (1970) are used; measurements were made with calipers and rounded to 0.1 mm. The sex of specimens was determined by presence of secondary sexual characters (vocal slits and nuptial excrescences) or by direct observation of gonads. Webbing formulae follow the convention proposed by Savage and Heyer (1967) as modified by Myers and Duellman (1982). All measurements of specimens are given in millimeters; snout-vent length is abbreviated SVL. Original observations of colors in living individuals were taken from field notes and color transparencies on file in the Natural History Museum at The University of Kansas and at The University of Texas at Arlington. The color photographs reproduced herein were taken by us or by William W. Lamar. Tadpoles were staged according to the developmental tables provided by Gosner (1960). For purposes of habitat description, we recognize the vegetation associations proposed and chorographed by Leopold (1950). We have relied on a plethora of maps of the region, but have found the series produced by the Dirección General de Geografía del Territorio Nacional (1:250,000) and the American Geographical Society (1:1,000,000) to be particularly useful. Both of us have spent considerable time in Oaxaca; WED

conducted periodic fieldwork in the state from 1955 through 1966 and JAC surveyed its upland herpetofauna periodically from 1969 through 1984. Specimens collected by us were fixed in buffered formalin (diluted to 10% of stock solution). Adult anurans were transferred to 70% ethanol and larvae were retained in formalin for permanent storage. Most of the material from these trips is curated in the collections of our respective institutions. Data for collecting sites were converted to metric equivalents where necessary.

Specimens examined for this study (Appendix) are housed in the herpetological collections at the American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Field Museum of Natural History (FMNH), Los Angeles County Museum of Natural History (LACM), Museum of Comparative Zoology at Harvard University (MCZ), National Museum of Natural History (USNM), Texas Cooperative Wildlife Collection at Texas A&M University (TCWC), The University of California Museum of Vertebrate Zoology (MVZ), The University of Illinois Natural History Museum (UIMNH), The University of Kansas Natural History Museum, (KU), The University of Michigan Museum of Zoology (UMMZ), The University of Texas at Arlington (UTA), and the Zoologisches Museum in Berlin (ZMB).

DESCRIPTIONS OF NEW SPECIES

Hyla abdivita new species

Hyla melanomma (part)—Campbell and Brodie, 1992:190.

Holotype.—UTA A-13347 (original field no. JAC 7582), an adult male, one of a series from the Río Aloapan, 16.1 km (by road) W Jalapa de Díaz (18°01'12" N, 96°39'36" W, 405 m), Oaxaca, Mexico; collected on 5 June 1983 by Jonathan A. Campbell, David M. Hillis, and William W. Lamar.

Paratypes.—Two adult males, KU 289223 (formerly UTA A-13346) and UTA A-13348, collected with the holotype.

Diagnosis.—*Hyla abdivita* is a member of the *Hyla pinorum* Group (sensu Duellman, 1970) and has a brown dorsum with small, dark brown spots on the head, body, and limbs; the flanks are cream with diffuse brown spots and the hidden surfaces of the hind limbs are uniform pale brown. The snout is acuminate in dorsal view, and the diameter of the tympanum is less than 50% of the diameter of the eye. An abbreviated axillary membrane is present, and enlarged tubercles below the vent are absent; the feet are about three-fourths webbed. Of the other members of the *Hyla pinorum* Group, axillary membranes are present in *H. bivocata*, *juanitae*, *melanomma*, *perkinsi*, and *pinorum*;

the membrane is most extensive in the *H. pinorum*. Of these species, the snout is acuminate in dorsal view in *H. bivocata*, *melanomma*, and *perkinsi*, and in *H. perkinsi* a vertical rostral keel is present. *Hyla perkinsi* also differs from *H. abdivita* by having a dull green dorsum and a discontinuous yellow stripe on the flank. *Hyla bivocata* and *H. melanomma* differ by having a yellow or yellowish-tan dorsum with a lateral white (*H. bivocata*) or dark brown (*H. melanomma*) stripe; both species have enlarged tubercles below the vent. Furthermore, *H. melanomma* has a proportionately larger tympanum (> 50% of the eye), and *H. bivocata* has less webbing on the feet (about two-thirds webbed).

In most other hylids on the lower northern slopes of the Oaxacan highlands (*H. cyclada*, *H. miotympanum*, *H. nephila*, *Duellmanohyla ignicolor*, and *Ptychohyla acrochorda*), the dorsum is predominately green; adult male *D. ignicolor* have ventrolateral gland and those of *P. acrochorda* have a large gland on the chest. *Hyla psarosema* has a dark brown dorsum with green and gold flecks and the much larger (males > 50 mm SVL) *H. nephila* is brown with large green blotches on the dorsum and transverse bars on the limbs. Males of the predominately brown *Ptychohyla zophotes* have ventrolateral glands and spiny nuptial excrescences.

The only other hylids in the region with an extensive axillary membrane are *Hyla dendroscarta*, a bromeliad-breeder on the slopes of the Sierra Juárez, and *H. ebraccata* and *H. godmani*, both of which are pond-breeders in the lowlands. The small (males < 32 mm) *H. dendroscarta* has a pointed snout in dorsal view and a uniformly yellowish-tan dorsum. The small (males < 30 mm SVL) *H. ebraccata* is yellow with dark brown dorsal markings, usually consisting of an hourglass-shaped mark on the back. The larger *H. godmani* (males > 33 mm SVL) has a uniformly or faintly mottled pale gray or tan dorsum and a yellow venter; the hidden surfaces of the hind limbs are yellow.

Description of holotype.—Adult male; head as wide as body, slightly wider than long; head width 35.2% SVL; head length 34.5% SVL; snout short, acuminate in dorsal view, inclined posteroventrally in profile; canthus rostralis rounded, barely curved; loreal region shallowly concave; lips thin, not flared; nostrils protuberant, directed anterolaterally; internarial region slightly elevated; top of head flat; interorbital distance about 50% greater than width of upper eyelid. Supratympanic fold moderately heavy, curving posteriorly from posterior corner of orbit above tympanum to point above insertion of arm; fold covering upper edge of tympanum; tympanum round, elevated, with distinct annulus, separated from eye by distance about twice diameter of tympanum; diameter of tympanum 36.4% diameter of eye.

Upper arms slender; forearms moderately robust; axillary membrane extending about one-third length of upper arm; ulnar tubercles absent; weak transverse dermal fold on wrist; fingers moderately short, bearing moderately large, round discs; width of disc on third finger slightly greater than diameter of tympanum; narrow dermal fringe along outer edge of Finger IV. Subarticular tubercles large, rounded, nearly flat; supernumerary tubercles prominent, subconical; palmar tubercle not evident; prepollex slightly enlarged, elliptical, bearing dark, keratinized nuptial excrescence on inner edge. Fingers about one-third webbed (Fig. 2); webbing formula: $I2\frac{1}{2}-2\frac{1}{2}III^+-2\frac{1}{2}III2-1IV$. Hind limbs moderately slender; tibia length 52.9% SVL, foot length 48.3% SVL; tibiotarsal articulation extending to anterior edge of orbit; heels of adpressed limbs overlapping by about 40% length of shank; weak transverse dermal fold on heel; thin tarsal fold extending full length of tarsus; inner metatarsal tubercle elliptical, rounded in profile, visible from above; outer metatarsal tubercle round, about one-fifth size of inner tubercle. Toes moderately long, slender, bearing discs only slightly smaller than those on fingers; subarticular tubercles moderately small, round; supernumerary tubercles prominent, subconical, in irregular rows; narrow dermal fringe on inner edge of Toe I and outer edge of Toe

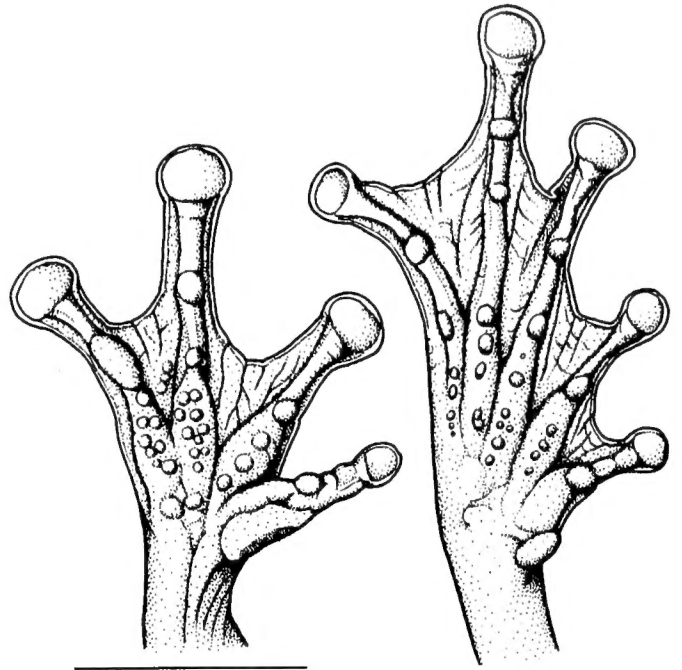


Fig. 2. Hand and foot of *Hyla abdivita*, adult male holotype, UTA A-13347. Line = 5 mm.

V; toes about three-fourths webbed (Fig. 2); webbing formula: $I1\frac{1}{2}-2III1\frac{1}{2}-2III1-2IV2-1V$.

Cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short, not expanded laterally; no enlarged tubercles below vent; skin on dorsal surfaces of head, body, and limbs, and on flanks shagreen; skin on throat, chest, belly, and ventral surfaces of thighs granular; other ventral surfaces smooth. Tongue cordiform, shallowly notched posteriorly, barely free behind. Dentigerous processes of vomers elevated, posteromedially inclined between large round choanae, widely separated medially, each bearing four teeth. Vocal slits extending from midlateral base of tongue to angles of jaws; vocal sac single, median, subgular.

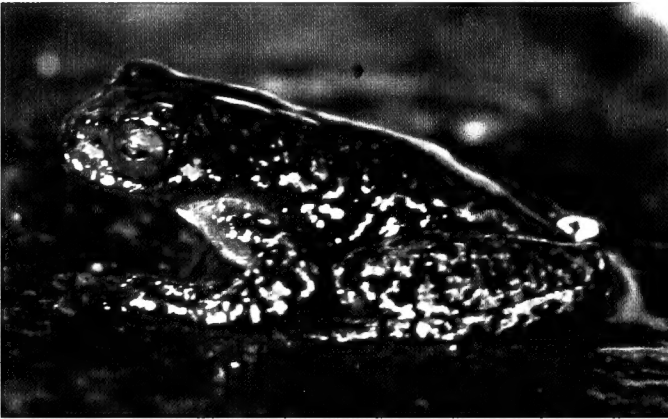
In preservative, dorsum of head, body, and limbs brown with few, small, darker brown spots on head and body and faint, irregular dark marks on limbs; lateral edge of brown dorsum on body darker brown; canthal region and supratympanic fold dark brown; broad, creamy-white labial stripe with minute brown flecks around tip of snout to tympanum; flanks cream with diffuse brown marks (3 on right, 2 on left) on anterior part of flanks; anterior and posterior surfaces of thighs uniform pale brown; dorsal surfaces of digits and webbing pale brown; dorsal surfaces of discs dark brown; all ventral surfaces pale cream; faint brown flecks on throat.



Hyla abdivita, UTA A-13347, male, 26.1 mm SVL.



Hyla cyclada, KU 71216, male, 35.1 mm SVL.



Hyla psarosema, UTA A-5771, male, 31.0 mm SVL.



Ptychohyala acrochorda, UTA A-13198, male, 31.8 mm SVL.



Ptychohyala zophodes, UTA A-13463, male, 35.2 mm SVL.



Ptychohyala leonhardschultzei, UTA A-13460, male, 29.3 mm SVL.

Fig. 3. Species of stream-breeding hylid frogs from Oaxaca, Mexico.

In life, dorsum dull bronze-brown with black flecks on body and dark brown to black irregular marks on limbs; narrow brownish-black canthal, supratympanic, and lateral stripes; flanks white; venter cream; iris pale copper

with black flecks (Fig. 3).

Measurements of holotype: SVL 26.1, tibia length 13.8, foot length 12.6, head length 9.0, head width 9.2, eye length 3.3, and tympanum length 1.2

Table 1. Measurements and proportions of adult males of *Hyla abdivita*, *bivocata*, and *melanomma*. Range of variation is followed on next line by mean and one standard deviation. SVL = snout-vent length.

Measurement or proportion	<i>H. abdivita</i>	<i>H. bivocata</i>	<i>H. melanomma</i> Oaxaca	<i>H. melanomma</i> Guerrero
N	3	17	20	10
SVL	26.1–27.5 27.0 ± 0.757	24.0–28.5 25.9 ± 1.114	26.3–30.1 27.4 ± 0.852	26.7–29.7 27.2 ± 0.899
Tibia length/SVL	0.529–0.553 0.544 ± 0.013	0.519–0.604 0.559 ± 0.024	0.482–0.527 0.507 ± 0.012	0.479–0.526 0.496 ± 0.016
Foot length/SVL	0.480–0.484 0.482 ± 0.002	0.426–0.500 0.464 ± 0.021	0.410–0.454 0.435 ± 0.011	0.384–0.451 0.409 ± 0.021
Head length/SVL	0.333–0.345 0.339 ± 0.006	0.302–0.347 0.329 ± 0.011	0.300–0.341 0.328 ± 0.009	0.293–0.333 0.316 ± 0.011
Head width/SVL	0.337–0.352 0.346 ± 0.008	0.323–0.358 0.343 ± 0.008	0.316–0.345 0.329 ± 0.007	0.326–0.343 0.333 ± 0.006
Tympanum/Eye	0.364–0.387 0.379 ± 0.014	0.267–0.370 0.297 ± 0.034	0.500–0.667 0.555 ± 0.044	0.500–0.552 0.520 ± 0.017
Tympanum/SVL	0.044–0.046 0.045 ± 0.001	0.031–0.042 0.035 ± 0.003	0.058–0.065 0.060 ± 0.003	0.054–0.063 0.059 ± 0.003

Variation.—The two male paratypes have SVLs of 27.3 and 27.5 mm; see Table 1 for proportions. Structurally, all specimens in the type series are alike. There is minor variation in coloration. In UTA A-13348, there are more spots on the dorsum than in the holotype, and there is one brown spot on the right flank and none on the left flank. In KU 289223, there are fewer spots on the dorsum than in the holotype; the lateral edges of the dorsal color are darker brown and tend to form a lateral dark brown stripe. The latter individual has two brown spots on the right flank and three on the left flank.

Etymology.—The specific name is derived from the Latin *abdivitus*, which means “removed from.” The name is applied to the new species in reference to its disjunct geographical distribution in contrast to those of other species in the *Hyla pinorum* Group.

Ecology and distribution.—*Hyla abdivita* is known only from the vicinity of the type locality at an elevation of 405 m in lower montane rainforest, where it was found in sympatry with *Ptychohyla zophodes*, *Smilisca cyanosticta*, *S. baudinii*, *Hyalinobatrachium fleischmanni*, *Bufo vallericeps*, and *Rana vaillanti*.¹ The three adult males were on low vegetation along the Río Aloapan at night. The Río Aloapan was about 10–15 m wide at the time these frogs were collected, but its flow increases dramatically after heavy rains in the Sierra Mazateca; presumably during the dry season, the

size of the stream diminishes appreciably. The general weather conditions were overcast at the time of collection; apparently it had not rained for several days. Later that evening, a light rain fell for several hours. The forest bordering the Río Aloapan consisted primarily of tall, broad-leaved trees that stood in contrast to the lower secondary forest of the surrounding slopes. The type locality was reached by a treacherous, narrow road from Huautla de Jiménez, and no other vehicles were observed on this road for the three days JAC was there. The locality may be reached much more easily by entering from Jalapa de Díaz.

Tadpoles.—The tadpole of this species is unknown.

Remarks.—The *Hyla pinorum* Group, as defined by Duellman (1970), was composed of only two species—*H. pinorum* on the Pacific slopes of the Sierra Madre del Sur in Oaxaca and *H. melanomma*; in the latter, two subspecies were recognized, *H. m. melanomma* on the Pacific versant of the Sierra Madre del Sur in Guerrero and Oaxaca, and *H. m. bivocata* on the northern versant of the highlands of central Chiapas, Mexico. Subsequently, three new species were added to the group. *Hyla juanitae* was described from the Pacific versant of the Sierra Madre del Sur in Guerrero and Oaxaca (Snyder, 1972); *H. catracha* was named from the highlands of southwestern Honduras by Porras and Wilson (1987), and *H. perkinsi* was described from the northern slopes of the Sierra de los Cuchumatanes in northwestern Guatemala (Campbell and Brodie, 1992). The latter authors erroneously assigned the specimens described herein as *H. abdivita* to *H. melanomma*.

Thus, the number of species in, and breadth of distribution of, the *Hyla pinorum* Group has changed considerably since Duellman's (1970) definition of it. The tadpoles

¹Joseph R. Mendelson kindly informed us that he collected a single specimen of *Hyla abdivita* on vegetation along a small tributary of the Río Aloapan on 10 July 1992. He gave the locality as 12–15 km (by road) W Jalapa de Díaz, 400–450 m elevation. We have not examined this specimen, which bears a field tag JRM 3910 and is catalogued as Number 5235 in the Museo de Zoología Alonso Herrera in the Facultad de Ciencias at the Universidad Nacional Autónoma de México in Mexico City.

of *H. juanitae*, *melanomma*, and *pinorum* have two complete rows of marginal papillae and a tooth row formula of 2/5, whereas the tadpoles of *H. catracha* have a formula of 2/3, but also have two complete rows of marginal papillae; the tadpoles of *H. abdivita* and *H. perkinsi* are unknown. A tympanum is absent in *H. juanitae* and *H. pinorum*, and an axillary membrane is absent in *H. catracha*. The quadratojugal is in contact with the maxilla in *H. juanitae*, *perkinsi*, and *pinorum*, reduced and not in contact with the maxilla in *H. m. melanomma* and *H. m. bivocata*, and absent in *H. catracha*. Dissection of a paratype of *H. abdivita* (KU 289223) revealed a small quadratojugal not in contact with the maxilla.

Smith and Brandon (1968) noted differences in coloration and proportional size of the tympanum between *Hyla m. melanomma* and *H. m. bivocata*, and suggested that the latter taxon be recognized as separate species. Additional specimens from Chiapas and the Sierra Madre del Sur of Guerrero and Oaxaca have made it possible to undertake a morphometric analysis of these populations and *H. abdivita* (Table 1). No significant differences in SVL and proportions exist among the two populations of *H. melanomma* and *H. abdivita*. However, ANCOVA analyses revealed significant differences in tibia length/SVL, foot length/SVL, head length/SVL, and tympanum/eye between *H. m. bivocata* and both populations of *H. m. melanomma*. There are no significant differences between the populations of *H. melanomma* and between *H. abdivita* and *H. m. bivocata*, and either population of *H. m. melanomma*. Significant differences between *H. abdivita* and these other populations possibly reflect the small sample size of *H. abdivita*.

Herein, we recognize *H. bivocata* as a species distinct from *H. melanomma*, because the former has a distinctly smaller tympanum, a more acuminate snout, fewer and larger spots on the dorsum, a distinct white lateral stripe (absent in *H. melanomma*), and less webbing on the feet (two-thirds webbed, as opposed to three-fourths webbed in *H. melanomma*). Furthermore, *H. bivocata* has proportionately longer legs, feet, and head (Table 1).

Hyla cyclada new species

Hyla arborescandens (part)—Duellman, 1970:30; Caldwell, 1974:12; Toal, 1994:191; Toal and Mendelson, 1995:10; Mendelson and Toal, 1996:329.

Hyla celata (part)—Toal and Mendelson, 1995:18.

Holotype.—KU 71216 (original field no. WED 23048), an adult male from Arroyo Buena Vista, 6.5 km (by road) S Vista Hermosa (17°37'12" N, 96°22'48" W, 1625 m), Oaxaca, Mexico; obtained on 27 June 1962 by William E. Duellman.

Paratypes.—CAS 122649–52, KU 58453–55, 71217–20, 86999–7008, 87012, 137123–27, 137130–35, 137137–78, UTA A-52817–18, 39 males and 41 females from various streams 4.2–16.6 km (by road) S Vista Hermosa (1610–2020 m), Si-

erra Juárez, Oaxaca, Mexico (specific localities in Appendix).

Referred specimens.—See Appendix.

Diagnosis.—*Hyla cyclada* is a member of the *Hyla miotympanum* Group (sensu Duellman, 1970) and has a mottled green and tan dorsum and no white labial or lateral stripes. The fingers are webbed basally, and the toes are about two-thirds webbed; a distinct tympanum is present, but an axillary membrane and a tarsal fold are absent. Males have vocal slits and keratinous, nonspinous nuptial excrescences. Within the species in the *Hyla miotympanum* Group, *H. miotympanum* differs from *H. cyclada* by having white labial and lateral stripes, fingers about one-third webbed, and a weak tarsal fold. *Hyla arborescandens* differs from *H. cyclada* by having a uniformly green dorsum with a white lateral stripe and proportionally longer legs and feet.

Most other hylids on the northern slopes of the Oaxacan highlands (*Hyla miotympanum*, *H. nephila*, *Duellmanohyla ignicolor*, and *Ptychohyla acrochorda*) have a predominately green dorsum; males of *D. ignicolor* have ventrolateral glands and those of *P. acrochorda* have a large gland on the chest. The much larger (males > 50 mm SVL) *H. nephila* is brown with large green blotches on the dorsum and transverse bars on the limbs, whereas males of the predominately brown *Ptychohyla zophotes* have ventrolateral glands and spinous nuptial excrescences. At higher elevations in the Sierra Juárez, *H. cyclada* may be sympatric with four members of the *Hyla bistincta* group, all of which lack vocal slits in males. Of these, *H. celata* and *H. calvicollina* most closely resemble *H. cyclada*, but they have vertical rostral keels (present in some *H. cyclada*) and no vocal slits; the larger (males > 50 mm SVL) *H. cyanomma* has a green dorsum and blue iris and lacks a tympanum. *Hyla crassa* has a distinct tarsal fold and a heavy supratympanic fold that nearly obscures the tympanum. *Hyla hazelae*, which occurs at high elevations in the Sierra Juárez, differs from *H. cyclada* by having a pale green dorsum, yellow venter, bronze canthal stripe, and an indistinct tympanum. In the Sierra Mixes, the sympatric *H. psarosema* has a dark brown dorsum with green and gold flecks, and the larger (males > 50 mm SVL) *H. calthula* has black flanks and a tan dorsum with black spots; males of both of these species lack vocal slits.

Description of holotype.—Adult male; head as wide as body, slightly wider than long; head width 33.0% SVL; head length 32.5% SVL; snout moderately short, bluntly rounded in dorsal view, bluntly rounded (nearly truncate) in profile; canthus rostralis rounded, barely curved; loreal region shallowly concave; lips moderately thin, not flared; nostrils slightly protuberant, directed dorsolaterally; internarial region slightly depressed; top of head flat; in-

Table 2. Measurements and proportions of adults of *Hyla arborescandens*, *H. celata*, and *H. cyclada*. Range of variation is followed on next line by mean and one standard deviation. SVL = snout-vent length.

Measurement or Proportion	<i>Hyla arborescandens</i> Pan de Olla, Veracruz		<i>Hyla cyclada</i> Sierra Juárez, Oaxaca		<i>Hyla cyclada</i> Sierra Mixes, Oaxaca		<i>Hyla celata</i> Sierra Juárez, Oaxaca	
	Males	Females	Males	Females	Males	Females	Males	Females
N	18	1	41	40	14	2	23	11
Snout-vent length	31.7–37.6 34.9 ± 1.950	43.6	31.9–39.5 34.3 ± 1.737	41.2–49.9 43.7 ± 1.650	31.7–36.9 34.7 ± 1.416	42.5–45.2 43.9 ± 1.909	42.0 37.8–46.2	46.7 43.2–49.8
Tibia length/SVL	0.513–0.562 0.538 ± 0.016	0.505	0.471–0.520 0.495 ± 0.013	0.444–0.500 0.465 ± 0.011	0.501–0.538 0.520 ± 0.013	0.509–0.541 0.525 ± 0.023	0.459–0.539 0.495 ± 0.021	0.460–0.530 0.500 ± 0.023
Foot length/SVL	0.481–0.517 0.494 ± 0.012	0.477	0.432–0.497 0.463 ± 0.016	0.405–0.462 0.437 ± 0.015	0.467–0.524 0.502 ± 0.015	0.482–0.536 0.509 ± 0.038	0.401–0.467 0.443 ± 0.015	0.433–0.497 0.460 ± 0.019
Head length/SVL	0.307–0.356 0.326 ± 0.014	0.305	0.299–0.350 0.326 ± 0.010	0.281–0.340 0.312 ± 0.11	0.314–0.357 0.338 ± 0.014	0.327–0.348 0.352 ± 0.015	0.260–0.327 0.298 ± 0.019	0.273–0.331 0.302 ± 0.018
Head width/SVL	0.327–0.367 0.347 ± 0.011	0.337	0.302–0.365 0.332 ± 0.014	0.293–0.357 0.318 ± 0.010	0.317–0.358 0.342 ± 0.014	0.350–0.353 0.352 ± 0.002	0.299–0.325 0.309 ± 0.007	0.295–0.322 0.312 ± 0.008
Tympanum/Eye	0.357–0.500 0.424 ± 0.033	0.360	0.410–0.600 0.469 ± 0.038	0.457–0.574 0.491 ± 0.026	0.421–0.500 0.458 ± 0.027	0.511–0.533 0.522 ± 0.016	0.306–0.583 0.472 ± 0.075	0.386–0.758 0.546 ± 0.112
Tympanum/SVL	0.043–0.059 0.052 ± 0.004	0.041	0.045–0.058 0.051 ± 0.003	0.043–0.064 0.048 ± 0.004	0.044–0.058 0.051 ± 0.004	0.051–0.056 0.054 ± 0.004	0.035–0.055 0.044 ± 0.005	0.039–0.056 0.049 ± 0.006

terorbital distance about 25% greater than width of upper eyelid. Supratympanic fold moderately heavy, curving posteriorly from posterior corner of orbit above tympanum to point above insertion of arm; fold barely covering upper edge of tympanum; tympanum slightly higher than long, barely elevated, with distinct annulus, separated from eye by distance about 150% length of tympanum; diameter of tympanum 42.1% diameter of eye.

Forelimbs moderately slender; axillary membrane absent; row of low ulnar tubercles nearly forming low fold on ventrolateral edge of forearm; no transverse dermal fold on wrist; fingers moderately short, bearing narrow lateral fringes and moderately large discs slightly wider than long; width of disc on third finger noticeably greater than length of tympanum; dermal fringes absent on fingers. Subarticular tubercles large, rounded, nearly flat; supernumerary tubercles low, indistinct; palmar tubercle not evident; prepollex enlarged, elliptical, bearing dark, keratinized nuptial excrescence on inner edge; excrescence also on inner edge of thumb. Fingers webbed only basally; webbing formula: I2½—2½II2½—3III2½—12IV. Hind limbs moderately slender; tibia length 59.3% SVL, foot length 45.3% SVL; tibiotarsal articulation extending to middle of orbit; heels of adpressed limbs overlapping by about 25% length of shank; distinct transverse dermal fold on heel; tarsal fold absent; inner metatarsal tubercle elongately elliptical, flattened in profile, barely visible from above; outer metatarsal tubercle subconical, less than one-tenth size of inner tubercle. Toes moderately long, slender, bearing narrow lateral fringes and discs noticeably smaller than those on fingers; subarticular tubercles moderately large, rounded; supernumerary tubercles low, subconical, in single row on proximal segment of each digit; dermal

fringes absent on toes; toes about two-thirds webbed; webbing formula: I1½—2III½—2III1—2IV2—1½V.

Cloacal opening directed posteroventrally at upper level of thighs; cloacal sheath short, not expanded laterally; no enlarged tubercles below vent; skin on dorsal surfaces of head, body, and limbs, and on flanks smooth; skin on throat smooth; skin on chest, belly, and posteroventral surfaces of thighs granular; other ventral surfaces smooth. Tongue cordiform, shallowly notched posteriorly, barely free behind. Dentigerous processes of vomers elevated, anteromedially inclined between posterior margins of large, ovoid choanae, widely separated medially, each bearing four teeth. Vocal slits extending from midlateral base of tongue to angles of jaws; vocal sac single, median, subgular.

In preservative, dorsum of head, body, and limbs reddish tan with faint darker brown reticulations; flanks tan with indistinct vertical brown marks; loreal and tympanic regions brown; anterior and posterior surfaces of thighs uniform brown; dorsal surfaces of digits (including discs) and webbing tan; all ventral surfaces creamy tan.

In life, at night, dorsum pale tan; venter creamy white, and anterior and posterior surfaces dull yellowish tan; by day, dorsum tan with dark green reticulations and greenish wash posteriorly on body; anterior and posterior surfaces of thighs dark brown. Iris deep copper (Fig. 3).

Measurements of holotype: SVL 35.1, tibia length 17.3, foot length 15.9, head length 11.4, head width 11.6, eye length 3.8, and tympanum length 1.6.

Variation.—Within the type series from the Sierra Juárez and 14 males and 2 females from the Sierra Mixes, males are significantly smaller than females (Table 2), whereas

there are no significant differences in snout-vent length between samples of the same sex from the two sierras. However, there are differences in proportions; ANCOVA analyses revealed that both males and females from the Sierra Mixes have significantly longer tibiae and feet and larger heads than specimens from the Sierra Juárez (Table 2). Two males from higher elevations (Cerro Machín and Cerro San Felipe, 2370 and 2670 m, respectively) have SVLs of 37.5 and 38.0 mm, and two females from there have SVLs of 48.8 and 49.1 mm.

Structurally, there is little variation within specimens from the Sierra Juárez and the Sierra Mixes. A vertical rostral keel is evident in some specimens, and a few individuals have a bifid distal subarticular tubercle on the Finger IV. All adult males have a brown, keratinized nuptial excrescence on the prepollex. Among 54 males, the excrescence is restricted to the prepollex in six specimens; in 48 others, the excrescence is continuous onto the median surfaces of the penultimate phalange of the thumb in 20 specimens, whereas the excrescence on the median surface of the thumb is narrowly separated from that on the prepollex in 28 specimens. Males have 3–5 teeth on each vomerine process for a total of 6–10 (\bar{x} = 8.2, n = 47) vomerine teeth, and females have 5–7 teeth on each process for a total of 10–13 (\bar{x} = 10.5, n = 40) vomerine teeth.

In preservative, the dorsal markings are variable among adults. In 81 specimens from the Sierra Juárez, the dorsum is unmarked in 13 males and 5 females; the dorsum has dark flecks in 16 males and 12 females, and dark reticulations in 12 males and 23 females. All 16 specimens from the Sierra Mixes have dark flecks on the dorsum; three of four specimens from Cerro Machín and Cerro San Felipe have dark flecks on the dorsum, and one female has dark reticulations. Dark flecks are present on the throat in most specimens; in most individuals, these flecks are diffuse and generally most evident peripherally, but three males and two females from the Sierra Juárez have distinct flecks on the entire throat. Dark flecks are present on the throat in 35 of 41 males and 35 of 40 females from the Sierra Juárez, in 10 of 14 males and in both females from the Sierra Mixes, and in all four specimens from Cerro Machín and Cerro San Felipe.

Variation in coloration in life and metachrosis in specimens from the north slope of the Sierra Juárez is evident from field notes by Duellman (WED) and Janalee P. Caldwell (JPC):

KU 54353–55.—Dorsum pale green; canthal stripe dark olive; throat and belly white; undersides of legs yellow; iris pale copper. Dorsum later changed to greenish tan with olive reticulations (WED, 12 August 1960).

KU 137125–27.—Dorsum tan with darker mottling; anterior and posterior surfaces of thighs, under surfaces

of shanks, and first three toes bright yellow, changing to pale green dorsally; venter white (JPC, 23 November 1969).

KU 137073–74.—At night, dorsum mottled dark and pale green. Later changed to dark greenish brown with faint mottling. Under surfaces of hind limbs to first three toes dark yellow; belly creamy yellow. Iris copper (JPC, 17 January 1970).

KU 137134.—Male; dorsum mottled dark and pale brown; axilla, under surfaces of arms, palms, groin, anterior surfaces of thighs, and undersurfaces of shanks bright yellow; posterior surfaces of thighs and first three toes having brown pigment mixed with yellow; iris and canthus dark brown (JPC, 25 January 1970).

KU 137128.—Dorsum mottled dark and pale brown; anterior surfaces of thighs bright yellow-orange; posterior surfaces of thighs and ventral surfaces of shanks to first three toes dull orange overlain by brown; canthus dark brown; venter greenish gray but chin iridescent white; iris dark bronze (JPC, 1 April 1970).

KU 137168–73.—Dorsum mottled dark and pale brown, becoming paler on flanks; canthus dark brown; anterior surfaces of thighs, groin, and ventral surfaces of shanks yellow-orange; posterior surfaces of thighs, tarsi, and first three toes yellow but mostly covered with brown pigment; venter, including chin, greenish white with some iridescent copper on margin of chin (JPC, 12 June 1970).

KU 137132.—Dorsum greenish brown with dark brown flecks; canthus dark brown; anterior surfaces of thighs and groin yellow-orange; posterior surfaces of thighs and shanks to first three toes same color overlain with brown pigment; venter iridescent greenish yellow; nuptial excrescences dark brown; iris copper with brown reticulations (JPC, 13 June 1970).

An adult male (KU 127119) from Cerro Machín, 2370 m was described as dorsum mottled dark and pale brown; nuptial excrescences and dorsal surfaces of digital discs dark brown; groin, anterior and posterior surfaces of thighs, and ventral surfaces of shanks to first three toes bright yellow; venter iridescent white (JPC, 23 January 1970).

Etymology.—The specific name is derived from the Greek *kyklados*, which denotes a garment with encircling borders. The name is used in reference to the tan edges of the dorsal coloration.

Tadpoles.—The presumed tadpole of this species was described and illustrated (as *Hyla arborescandens*) by Duellman (1970). Only tadpoles in Stage 25 are known. They are assigned to this species because of their similarity to the tadpoles of *H. arborescandens* from Puebla. These similarities include two rows of small marginal papillae, absence of submarginal papillae, presence of fine serra-

tions on the beaks, and a denticle formula of 2/4. The tadpoles assigned to Oaxacan "*Hyla arborescandens*" by Caldwell differ by having submarginal papillae, coarse serrations on the upper beak, and a denticle formula of 2/3; presumably these tadpoles belong to *H. sabrina*, a species in the *Hyla bistincta* Group.

Ecology and distribution.—Most specimens of *Hyla cyclada* are from cloud forests at elevations between 1600–2180 m on the northern versant of the Sierra Juárez; the species also is known from pine-oak forest at elevations of 2370 and 2670 m near the crest of the Sierra Juárez (Cerro Machín and Cerro San Felipe) and from cloud forest and oak-madroño forest at elevations of 2121–2568 m in the Sierra Mixes. At the lower elevations on the northern slopes of the Sierra Juárez, *H. cyclada* was found along the same streams as *H. nephila*, *H. sabrina*, *Duellmanohyla ignicolor*, and *Ptychohyla zophodes*.

At night, females and calling males were on low vegetation or boulders along small streams, but one male was on a branch in a spray zone of a waterfall and another was calling from beneath a rock at the edge of a small stream. By day, adults were found in arboreal bromeliads. Adults apparently are active throughout the year; they have been collected in every month except September, October, and December. Tadpoles have been found in pools in streams in January, February, April–July, and November.

Remarks.—With the exception of the color painting (Pl. 57, fig. 3), all illustrations labeled *Hyla arborescandens* in Duellman (1970) are *H. cyclada*. Moreover, the descriptions of mating call and tadpoles (Duellman, 1970:383) are of *H. cyclada*. Specimens from the Sierra Mixes referred to *H. celata* by Toal and Mendelson (1995) are *H. cyclada*.

The *Hyla miotympanum* Group, as defined by Duellman (1970), was composed of only two species. *Hyla miotympanum* is widely distributed on the eastern slopes of the Sierra Madre Oriental from central Nuevo León to central Veracruz, with disjunct populations in the Sierra de Los Tuxtlas in southern Veracruz and on the northern slopes of the central highlands of Chiapas, Mexico. As recognized by Duellman (1970), *H. arborescandens* occurred in the Sierra Madre Oriental from northern Puebla to north-central Oaxaca, Mexico. Duellman (1970) noted slight differences in size and proportions of specimens from Pan de Olla, Veracruz, as compared with those from the north slope of the Sierra Juárez in Oaxaca. Acquisition of a large series of specimens from the Sierra Juárez permits a more accurate assessment of the differences between the northern populations, to which the name *H. arborescandens* Taylor is applied, and the Oaxacan populations that we recognize as *H. cyclada*.

Specimens from near the type locality of *Hyla arborescandens* do not differ significantly in size from *H.*

cyclada; however, significant differences exist in some proportions (Table 2). ANCOVA analyses revealed that the ratios of tibia length and foot length to SVL are significantly greater in *H. arborescandens* than in *H. cyclada* from the Sierra Juárez, but not from *H. cyclada* from the Sierra Mixes. However, there are differences in coloration. The dorsum in *H. arborescandens* lacks dark flecks or reticulations. A lateral row of dark dashes that is nearly continuous in many specimens defines a pale lateral stripe in *H. arborescandens* (Duellman, 1970, Pl. 57, fig. 3).

Coloration in life of *Hyla arborescandens* is notably different from that of *H. cyclada*, as evidenced from the following field notes on living individuals of *H. arborescandens*:

KU 53818.—Dorsum dark green; canthus brown; belly white; throat lemon yellow; iris bronze (WED, 25 December 1959).

KU 64316–20.—Dorsum uniform brown; flanks green; venter pale yellow; iris silvery bronze (WED, 12 February 1961).

Tadpoles found in the same stream as calling males of *Hyla arborescandens* at the Río Octapa, 3.7 km NNE Tezuitlán, Puebla, are similar to those assigned to *H. cyclada*, except that the body is brown with greenish-yellow flecks; the denticle formula ranges from 2/4 in small individuals to 2/6 in large individuals in Stage 25.

Externally, *Hyla cyclada* is extremely similar to *H. celata*, which is restricted to elevations above 2600 m in the Sierra Juárez. The color patterns of the two species are similar, but *H. celata* is larger (Table 2) and males lack vocal slits. The ratio of head length to SVL is significantly different in males in males (Fig. 4) but not in females.

Duellman (1970) reported two specimens of "*Hyla arborescandens*" from a semiarid area 25.5 km N Nochixtlán, Oaxaca; actually, the locality is 25.5 km S Nochixtlán. Reexamination of one of these specimens (UIMNH 58548) reveals that it is a *Hyla sumichrasti*; the other specimen is no longer in the UIMNH collection.

Hyla psarosema new species

Hyla sabrina (part)—Toal and Mendelson, 1995:10.

Holotype.—UTA A-5782 (original field no. JAC 3435), an adult male from 3.6 mi (= 5.8 km) W (by road) Totontepec (17°14'24" N, 96°03'36" W, 2103 m), Sierra Mixes, Oaxaca, Mexico, one of a series collected on 5 April 1978 by Jonathan A. Campbell.

Paratypes.—Four from the type locality: UTA A-5771, 5783, and KU 289216, all adult males, and UTA A-5776, an adult female.

Diagnosis.—*Hyla psarosema* is a member of the *Hyla bistincta* Group (sensu Duellman, 1970; Duellman and

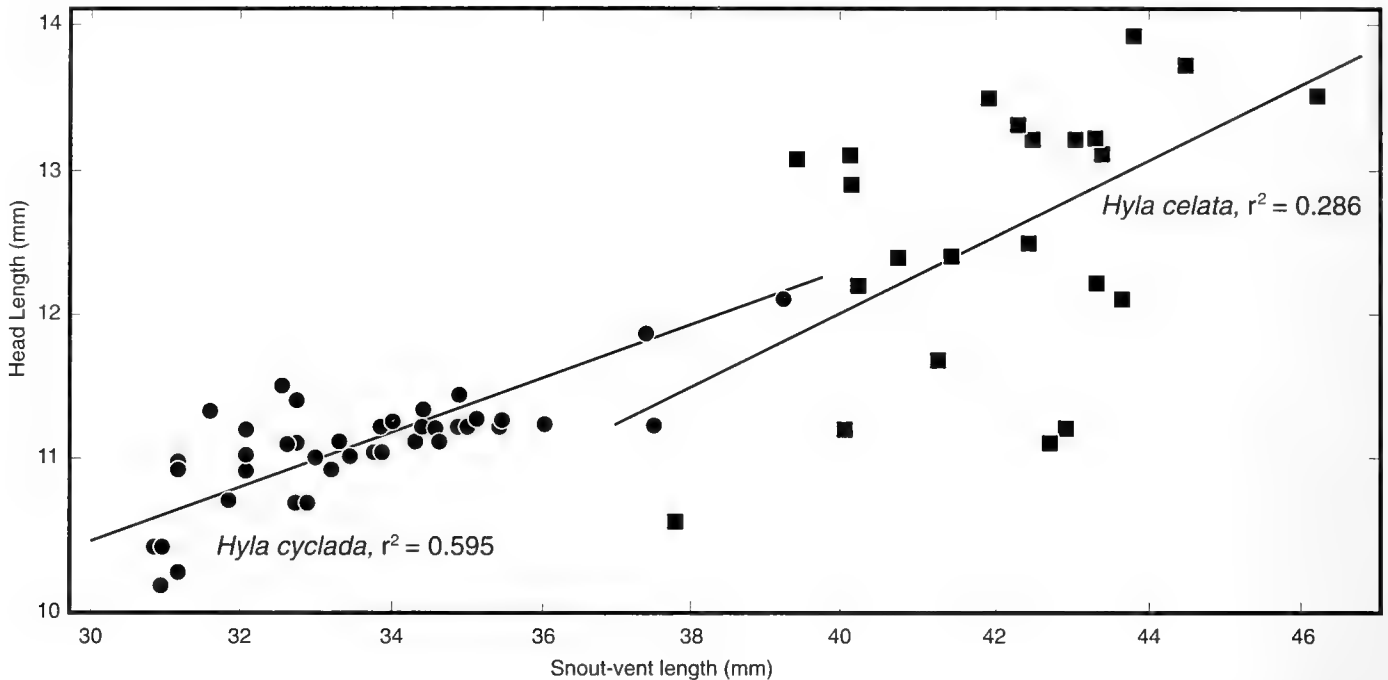


Fig. 4. Differences in snout-vent length and correlations between snout-vent length and head length in males of *Hyla celata* and *H. cyclada* in the Sierra Juárez, Oaxaca.

Campbell, 1992) and has a dark slate-brown dorsal ground color with whitish flecks and reticulations on the trunk and exposed surfaces of the limbs; these pale markings are larger and more numerous on the flanks and limbs than on the dorsum of the body. The hidden surfaces of the hind limbs are uniform brown. The tympanic annulus is not evident externally. Males in breeding condition have nuptial excrescences of minute spines covering the entire prepollex and lack vocal slits. This is the smallest species of the *H. bistincta* Group; males reach a known maximum SVL of 31.4 mm and females, 37.3 mm. A rostral keel is absent, and the skin on the dorsum is thick; an axillary membrane and tarsal fold are present; a thoracic fold and the quadratojugal are absent.

Of the other members of the *Hyla bistincta* Group, tympanic annuli are not evident externally in *H. sabrina*, *H. cyanomma*, and *H. pachyderma* (Table 3). *Hyla sabrina* can be distinguished because it lacks a tarsal fold, has thin skin on the dorsum, attains a larger SVL (47.3 and 50.4 mm in males and females, respectively), and has a dorsum that is almost uniform green or mottled with green and/or brown. Nuptial excrescences are absent in all known adult males of *H. sabrina*; it is unknown whether this species may develop these structures during certain times of the year. *Hyla cyanomma* has less of an axillary membrane (< one fourth versus > one third of length of upper arm), is a much larger frog (attaining SVLs of 47.0 and 64.5 mm in males and females, respectively), and has a distinctive olive-green dor-

sum that is uniformly colored or marked with a few small, yellow spots. Adult males of this species have been collected at different times of the year and invariably lack nuptial excrescences. *Hyla cyanomma* is known in the Sierra Juárez from a single stream that is at a higher elevation than the type locality for *H. psarosema* (2670 vs. 2103 m). *Hyla pachyderma* lacks an axillary membrane, has a thoracic fold, attains a SVL of 39.9 mm in males and 55.7 mm in females, and has a dorsum with indistinct, scattered, dark flecks.

Hyla psarosema occurs in sympatry, or near sympatry, with *H. crassa*, *H. calthula*, *H. nephila*, *H. cyclada*, and perhaps *Ptychohyla zophodes*. *Hyla crassa*, a member of the *H. bistincta* Group, can be distinguished from *H. psarosema* by its large size (56.5 and 63.1 mm SVL in males and females, respectively), almost fully webbed feet, presence of a thoracic fold and externally visible tympanic annulus, lack of an axillary membrane, and somewhat variable dorsal pattern in adults of darker spots or blotches on a paler background. *Hyla calthula* is also a member of the *H. bistincta* Group; it is large (56.1 and 61.3 mm SVL in males and females, respectively), has an externally evident tympanic ring, lacks an axillary membrane, and has distinct black stripes extending along the flanks from the anterior margin of the upper lip through the orbital region to the insertion of the hind limbs. *Hyla nephila* is a member of the *H. taeniopus* Group and has vocal slits, smooth thin skin, externally visible tympanic annulus, reaches a greater SVL

Table 3. Characteristics of members of the *Hyla bistincta* group lacking external tympanic annuli.

Character	<i>Hyla cyanomma</i>	<i>Hyla pachyderma</i>	<i>Hyla psarosema</i>	<i>Hyla sabrina</i>
Maximum SVL ♂♂ (mm)	47.0	39.9	31.4	47.3
Maximum SVL ♀♀ (mm)	64.5	55.7	37.3	50.4
Skin on dorsum	Thick	Thick	Thick	Thin
Axillary membrane	Abbreviated	Absent	Present	Present
Webbing on foot	Three-fourths	Three-fourths	Two-thirds	Two-thirds
Thoracic fold	Absent	Present	Absent	Absent
Tarsal fold	Present	Present	Present	Absent
Nuptial excrescences	Absent	Present	Present	Absent
Dorsal color pattern	Olive green with or without yellow spots	Grayish brown with darker flecks*	Dark gray with pale flecks or vermiculations	Mottled green or brown
Distribution	Sierra Juárez	Sierra Madre Oriental	Sierra Mixes	Sierra Juárez
Elevation (m)	2650–2670	1600	2103	1650–2020

* In preservative.

(> 60 mm in males and females), and has a dorsal pattern of distinct, large blotches. *Hyla cyclada* is a member of the *H. miotympanum* Group; it is characterized by a green dorsum mottled with tan or gold, presence of an externally evident tympanic annulus, and absence of an axillary membrane and tarsal fold. *Ptychohyla zophodes* may occur in the Sierra Mixes. (See Remarks for this species.) Nonetheless, the species of *Ptychohyla* occurring in the Sierra Mixes can be distinguished from *H. psarosema* by the presence of an externally visible tympanum, a dorsal color pattern not consisting of pale flecks and reticulations, large ventrolateral glands, nuptial excrescences with relatively large spines, and vocal slits in breeding males.

Description of holotype.—Adult male; head as wide as body, slightly longer than wide; head width 31.1% SVL; head length 32.8% SVL; snout short, rounded in dorsal view, truncate in profile; canthus rostralis moderately sharp, barely curved; loreal region shallowly concave, lips thick, not flared; nostrils protuberant, slitlike, directed anterolaterally; internarial region slightly concave; top of head flat; interorbital distance about 1.2 times width of upper eyelid. Supratympanic fold not well developed, curving posteriorly downward from corner of orbit to level well above insertion of arm; tympanic annulus covered with skin, not visible externally.

Upper arms moderately robust; forearms extremely hypertrophied; axillary membrane present; series of three small, flat, pale ulnar tubercles; weak transverse dermal fold on lateral side of wrist; fingers long and slender, bearing moderately large, round discs; width of disc on third finger slightly greater than tympanic annulus (when exposed); dermal fringes along outer edge of fingers inconspicuous to absent. Subarticular tubercles moderate in size,

rounded in profile, nearly flat in section; supernumerary tubercles relatively few, subconical, inconspicuous; palmar tubercle small, flat, partially bisected; prepollex greatly enlarged, elliptical, bearing a large, mostly pale nuptial excrescence over nearly entire surface; nuptial excrescence with minute spines, some with black tips. Fingers with only a trace of webbing (Fig. 5); webbing formula: I2½—3III—3½III¾—3IV. Hind limbs moderately slender; tibia length 54.8% SVL, foot length 48.5% SVL; tibiotarsal articulation extending to tip of snout; heels of adpressed limbs overlapping by about 25% length of shank; no transverse dermal fold on heel; thin tarsal fold extending almost full length of tarsus; inner metatarsal tubercle ovoid, almost round, flat in profile, not visible from above; outer metatarsal tubercle round, flat, about one-fourth size of inner tubercle. Toes slender, bearing discs only barely smaller than those on fingers; subarticular tubercles moderately small, round; supernumerary tubercles inconspicuous, small, rounded or flat; dermal fringes present on unwebbed portion of toes, inner edge of Toe I, and outer edge of Toe V; toes about two-thirds webbed (Fig. 5); webbing formula: I1—2III—1 3/4III¾—2IV2—1V.

Cloacal opening directed ventrally at midlevel of thighs; cloacal sheath short, not expanded laterally; no enlarged tubercles below vent; skin on dorsal surfaces of head, body, and limbs, and on flanks shagreen; skin on throat, chest, belly, and ventral surfaces of upper arms and thighs granular; other ventral surfaces smooth. Tongue cordiform, shallowly notched posteriorly, barely free behind. Dentigerous processes of vomers elevated, bearing 5/4 teeth, teeth arranged in crescent-shaped series along medial and posterior edges, separated medially by distance about 0.75 the width of a dentigerous process.

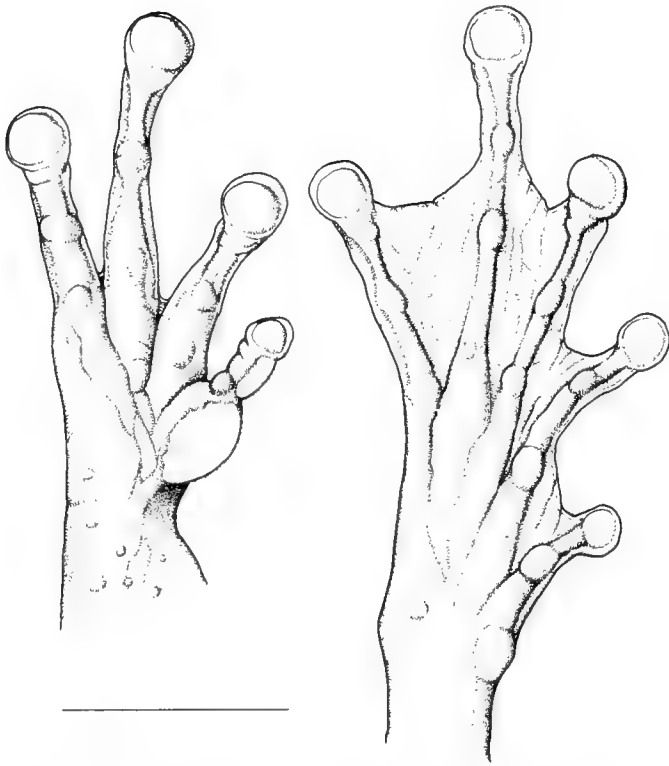


Fig. 5. Hand and foot of *Hyla psarosema*, adult male holotype, UTA A-5782. Line = 5 mm.

In preservative, dorsum of head and limbs grayish brown with a faint indication of paler mottling; flanks pale gray with indistinct whitish mottling; dorsal surfaces of limbs gray-brown, somewhat paler than dorsum; a broad canthal stripe only slightly darker than surrounding region; side of head uniform gray-brown; Fingers I–III cream-colored with scattered melanophores; Finger IV and toes also cream, but with more concentrated brown melanophores; throat, chest, and belly cream with indistinct dark mottling; hidden surfaces of limbs with heavy concentration of brown melanophores; ulnar tubercles white; a poorly defined whitish stripe above vent; palpebral membrane without pigment except along dorsal edge which is brown.

In life, ground color of dorsum dark slate-brown with whitish flecks and reticulations on body and dorsal surfaces of limbs; irregular bright green spots on top and sides of head, a few green spots on dorsal surfaces of limbs and flanks; venter whitish with dark gray mottling; iris copper with black reticulations (Fig. 3).

Measurements of holotype: SVL 29.9, tibia length 16.4, foot length 14.5, head length 9.8, head width 9.3, and eye length 3.5.

Variation.—In the series of three adult male paratypes plus the holotype, the SVL is 29.4–31.4 (\bar{x} = 30.7), the tibia

length/SVL is 0.522–0.551 (\bar{x} = 0.540), the foot length/SVL is 0.481–0.539 (\bar{x} = 0.504), the head length/SVL is 0.315–0.333 (\bar{x} = 0.324), and the head width/SVL is 0.311–0.332 (\bar{x} = 0.321). In the single female, the SVL length is 37.3, the tibia length/SVL is 0.552, the foot length/SVL is 0.509, the head length/SVL is 0.314, and the head width/SVL is 0.314. The external morphology for individuals in the type series is similar in most respects. Only minor variation exists in coloration. In UTA A-5771, the dorsal ground color is reddish brown, and UTA A-5783 and KU 289216 have less dark mottling on the venter. A narrow white stripe is present above the vent in UTA A-5776, 5782, and KU 289216; it is present as an indistinct dash in UTA A-5783 and absent in UTA A-5771.

Notable variation is present in the nuptial excrescences of the four males, all collected on 4–8 April 1978 near the end of the dry season. The holotype (UTA A-5782, 29.9 mm SVL) has nuptial excrescences composed of minute spines and the tips of many of these spines are dark brown or black. In KU 289216 (29.4 mm SVL), the nuptial excrescences are composed of entirely of white, minute spines even smaller than those of the holotype. The nuptial excrescences of UTA A-5783 (31.4 mm SVL) form a thick, white pad with minute, rounded papillae; those of UTA A-5771 (31.0 mm SVL) are thin, milky white, translucent pads that are completely smooth. Differences in nuptial excrescences suggest that these structures develop seasonally and that various stages of development are represented in the type series. Whether the nuptial excrescences are in the process of being formed or lost is open to speculation. Based on their SVLs and the extreme hypertrophy of the antibranchium, all males seem to be mature adults. Seasonal variation in nuptial excrescences is known in *H. chryses*. Adult males collected in June and July lacked these structures, but individuals collected in September have excrescences (Mendelson and Toal, 1996).

The vomerine teeth in all paratypes are arranged in a more-or-less straight transverse series along the posterior edge of the process, in contrast to the holotype in which a few teeth are also present on the medial edge. The number of vomerine teeth in males ranges from 3–5; there are five teeth on each of the dentigerous processes of the single female. The dentigerous processes are separated by 25–75% (\bar{x} = 50%) of the width of a dentigerous process in males, and a distance of less than 25% in the female, which has relatively larger dentigerous processes that are only slightly smaller than the choanae.

Etymology.—The specific name is derived from the Greek *psaros*, which means “speckled” or “dappled,” and *sema*, which means a “mark.” The name is applied to the new species in allusion to its distinctive color pattern, which immediately distinguishes it from all other hylids in Mexico.

Ecology and distribution.—*Hyla psarosema* is known only from the type locality at an elevation of 2103 m in cloud forest, where it was found in microsympatry with *H. nephila* and *H. cyclada*. Three adult males were in crevices between large boulders in splash zones of waterfalls on a small stream that is a tributary of Río La Lana. One male and the female were on leaves of vegetation along the same stream. All specimens were found late at night. At the end of the dry season, this stream was less than 1.5 m wide in most places, but some of the plunge pools at the base of waterfalls were up to 1 m deep, and some of the waterfalls were up to about 10 m high. In some places the stream ran underneath or between huge boulders making access along the stream difficult. In 1978, the area was pristine cloud forest, but by 1983, the area had been totally cleared and burned. The stream was badly silted and littered with burned logs.

Tadpoles.—The larvae of this species are unknown.

Remarks.—The *Hyla bistincta* Group, as defined by Duellman (1970), was composed of nine species occurring in the Mexican highlands west of the Isthmus of Tehuantepec. Among other things, this group is characterized by a clear palpebral membrane, long fingers with little webbing, toes at least two-thirds webbed, a broad, flat, ossified prepollex that does not project as a spine, relatively thick and glandular skin in most species, a quadratojugal that is reduced or absent and that does not articulate with the maxilla. Sexual dimorphism in size is present, but less pronounced than in some other groups of hylids. Except for one species (*H. bistincta*), all members of the group lack vocal slits. (See Table 3 for additional characters.)

Subsequent to Duellman (1970), a number of new species in this group was described, as follow: *H. mykter* Adler and Dennis (1972), *H. cembra* Caldwell (1974), *H. cyanomma* Caldwell (1974), *H. sabrina* Caldwell (1974), *H. calvicollina* Toal (1994), *H. celata* Toal and Mendelson (1995), *H. labedactyla* Mendelson and Toal (1996), and *H. calthula* Ustach et al. (2000). *Hyla bogertae* Straughan and Wright (1969) was synonymized with *H. crassa* by Toal and Mendelson (1995). With these taxonomic changes and the recognition of *H. psarosema*, the number of species in the *Hyla bistincta* Group has grown to 17. The greatest radiation of these frogs occurs on the Atlantic versant in the states of Puebla, Veracruz, and Oaxaca (12 species). Ten species in this group are endemic to Oaxaca, and six of these species occur on the Atlantic versant of the state.

Ptychohyla acrochorda new species

Hyla erythromma (part)—Duellman, 1970:391.

Ptychohyla erythromma (part)—Campbell and Smith, 1992:165.

Holotype.—UTA A-13197 (original field no. JAC 8940),

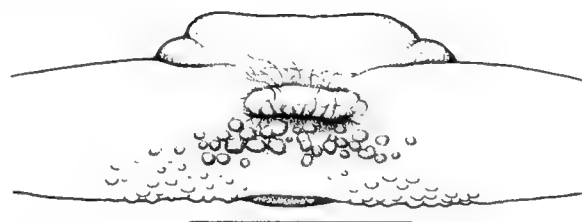


Fig. 6. Posterior view of cloacal region of *Ptychohyla acrochorda*, UTA A-13222, showing enlarged tubercles below vent. Line = 5 mm.

an adult male from 11.6 km S Valle Nacional (Puente Dañado), Sierra Juárez, Oaxaca, Mexico, 750 m (17°43'12" N, 96°18'36" W), on 24 July 1983, obtained by Jonathan A. Campbell.

Paratypes.—KU 87082–96, 87103, 87106–09, 100902–14, 200890–99, UTA A-13198–22, 34145–46, 71 adults from streams at elevations of 594–900 m in the vicinity of San Mateo Yetla (south of Valle Nacional) on the northern versant of the Sierra Juárez, Oaxaca, Mexico (specific localities in Appendix).

Referred specimens.—See Appendix.

Diagnosis.—A member of the genus *Ptychohyla* (sensu Campbell and Smith, 1992) in which the ground color of the dorsum is lime-green, the iris is whitish or silver with reddish-brown reticulations, and a tarsal fold is present. There are 10–20 enlarged white tubercles below the vent, extending along the proximal one half to three fourths of the ventrolateral surface of the thigh (Fig. 6). There is marked sexual dimorphism in size, with males reaching a maximum SVL length of 36.3 mm and females, 57.6 mm. Breeding males have a distinctive chest gland (Fig. 7), dark nuptial excrescences consisting of several hundred tiny spines, and a call consisting of a long, moderately low-pitched, slowly pulsed note. Tadpoles have 4/6 rows of labial denticles; males possess dark nuptial excrescences consisting of several hundred tiny spines, a call that is emitted as a long, single note.

Several other hylids in the Sierra Juárez might be confused with *P. acrochorda*. Breeding males of *Ptychohyla zophodes* (following species description) have well-developed ventrolateral glands; the dorsum is brown, gray-brown, or reddish brown, and the nuptial excrescence consists of fewer than 100 spines. Breeding males of *Duellmanohyla ignicolor* have pronounced ventrolateral glands and lack a tarsal fold; the venter is flecked with black, and nuptial excrescences are absent.

Some of the various species of *Hyla* found at low to intermediate elevations in the cloud forest of the Sierra Juárez can be distinguished from *P. acrochorda*, as follow. *Hyla cyclada* lacks well-developed fringes along the forearm and foot; the tibiotarsal articulation extends to the middle of the eye, and there are no enlarged tubercles below the vent.

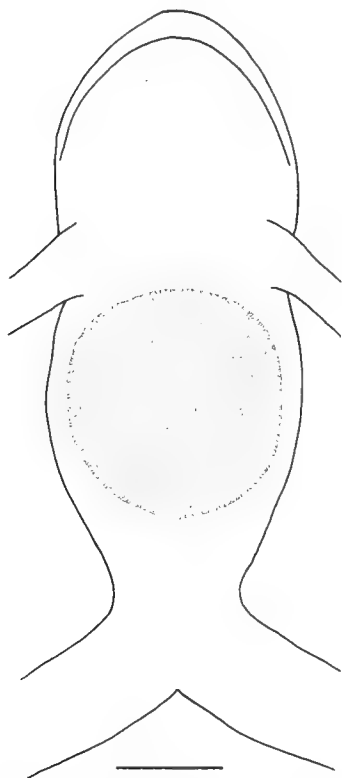


Fig. 7. Chest gland (stippled) of male *Ptychohyla acrochorda*, UTA A-13222. Line = 5 mm.

The tadpoles of *H. cyclada* have 2/4 rows of denticles. *Hyla celata* has a vertical keel on the rostrum and lacks vocal slits, tarsal folds, and axillary membranes; the dorsum usually is brown with scattered black flecks, and the tadpoles have 2/3 rows of denticles. *Hyla mixe* has distinct bars on the dorsal surfaces on the limbs, lacks a tympanum, and has a tadpole with 7/10–11 rows of denticles. *Hyla nephila* has a greenish- or reddish-brown dorsum marked with large dark blotches and males and females both attain SVLs exceeding 60 mm; tadpoles have 2/4 rows of denticles. *Hyla sabrina* lacks nuptial excrescences and vocal slits in breeding males, has a tan venter with dark brown mottling, and lacks a tympanum and webbing on the hands.

Ptychohyla acrochorda has been confused previously with *P. erythromma* of the Pacific slope of Guerrero. *Ptychohyla erythromma* is known from only a few specimens, including the holotype (a small [subadult?] female with a SVL of 26.2 mm), a small series of juveniles (14.1–18.5 mm in SVL), and several samples of tadpoles. The absence of adequate material of *P. erythromma* precludes a detailed comparison between the two species, but the large series of adults and tadpoles of *P. acrochorda* permits assessment of variation in that species and differentiation between *P. erythromma*

and *P. acrochorda*. Among the differences between *Ptychohyla erythromma* and *P. acrochorda* are the following. *Ptychohyla erythromma* has a bright blood-red iris, a more acute snout in dorsal view, proportionally smaller finger and toe discs, and low and inconspicuous dermal fringes on the forearm and foot. It lacks enlarged tubercles along the forearm and on the heel, and the webbing on hand is slightly more extensive, with a webbing formula of $I2\frac{1}{2}-2\frac{1}{2}III\frac{1}{2}-2\frac{1}{2}III2\frac{1}{4}-2IV$. There is slightly less webbing on foot, with webbing formula of $I1\frac{1}{2}-2III\frac{1}{4}-2III1\frac{1}{2}-2IV2-1V$. There are only two enlarged tubercles below vent and no enlarged tubercles extending along the proximal ventrolateral surface of thigh. The pale lip stripe is expanded to form a large pale spot below the eye, and the gular region has pale brown blotches.

Ptychohyla sanctaecrucis, a similar species in eastern Guatemala, differs from *P. acrochorda* in the following characters. *Ptychohyla sanctaecrucis* has a well-defined, conspicuous white upper lip margin. The discs on fingers and toes are slightly smaller, and dark pigment is restricted to the immediate area around the vent. Enlarged white tubercles are restricted to the area below the vent; they do not grade out onto the proximal portion of the ventrolateral surface of the thighs. The tadpoles have 5/7 rows of denticles.

Description of holotype.—Adult male; head slightly wider than body, about as wide as long; head width 36% SVL; head length 36% SVL; snout rounded in dorsal view, truncate in profile; canthus angular, distinctly curved; loreal region slightly concave; lips moderately thick and slightly flared; nostrils protuberant; internarial region depressed, top of head flat. Supratympanic fold thin, extending from eye across top of tympanum, obscuring the upper edge of tympanic annulus, then downward to about insertion of forelimb; tympanum round, its diameter about 107% distance from eye and 44% of eye length.

Arm moderately robust (especially forearm); axillary membrane short, extending about one-fourth length of upper arm; ventrolateral edge of forearm fringed with distinctly raised dermal ridge punctuated with enlarged tubercles; weak transverse fold on the wrist. Fingers moderately long, bearing large discs; width of the disc on third finger about equal to diameter of tympanum. Subarticular tubercles moderately large and subconical, distal tubercle on Finger IV bifid. Supernumerary tubercles small, rounded to subconical; palmar tubercle low, flat; prepollex moderately enlarged, bearing dark keratinized nuptial excrescence of several hundred tiny spines. Fingers less than one-fourth webbed; webbing formula $I2\frac{1}{2}-2\frac{1}{2}II2-3III2\frac{3}{4}-2IV$. Hind limbs moderately long and slender; tibiotarsal articulation extending to snout; tibia length 56% SVL; foot length 42% SVL; transverse dermal fold and sev-

eral conical tubercles on heel; tarsal fold narrow, low, extending full length of tarsus; inner metatarsal tubercle elongate, flat, barely visible from above; outer metatarsal tubercle small, round, less than one-sixth size of inner tubercle; toes moderately long, slender, bearing discs only slightly smaller than those on fingers; subarticular tubercles moderately small, round to subconical; supernumerary tubercles distinct, round. Toes about two-thirds webbed; webbing formula $\text{II}-2\text{III}-2\text{III}-2\text{IV}2-1\text{V}$.

Cloacal opening directed posteriorly at upper level of thighs; broad sheath above vent; about 10 enlarged tubercles below and lateral to vent (below white vent stripe). Skin on throat, chest, belly, and proximal fourfifths of ventral surface of thighs areolate, with a distinctive ovoid gland on the chest; skin on dorsal surfaces of body smooth. Tongue cordiform, not free behind. Dentigerous processes of vomers small, widely separated, transverse ridges between moderately large, ovoid choanae each bearing five teeth; vocal slits extending from midlateral base of tongue to angles of jaws; vocal sac single, median, subgular, and moderately distensible.

The color in preservative is rather uniformly lavender on the top and sides of the head, the dorsum of the body, and dorsal surfaces of the limbs. The dorsal surfaces of the discs and digits are mostly yellow; the fringe along the forearm and foot is white and the upper lip is narrowly bordered with white. The upper flanks have a white band mottled with pale brown; the groin is pale yellow and the posterior surface of the thighs is yellow brown. The gular area is white; the chest is yellowish, and the belly is cream. The stripe above the vent and the large tubercles below the vent and on the ventrolateral surface of the thighs are white. The subarticular and supernumerary tubercles on the hand are yellow, whereas the tubercles on the foot are mostly pale gray.

In life, the ground color of the holotype was lime-green. The dorsum was uniformly colored except for a small amount of indistinct pale brown mottling, which extended onto the exposed surfaces of the limbs. The green of the dorsum graded into yellow-green on the sides of the body, where the narrow interstices between the areolae were brown, thereby forming a fine reticulate pattern. The top and sides of the head, including the tympanum were green, except for the area immediately around the external nares, which was bordered with brown and the margin of the upper lip which was cream, but did not form a conspicuous lip stripe. The dorsal surfaces of the finger and toe discs were bright orange, and the webbing was orange-gray. The lower portion of the flanks between limb insertions was narrowly bordered with white and scant gray mottling. The groin was mostly a pale gray suffused over a pale purplish background. The upper portion of the tu-

bercular fringes along the ventrolateral surface of the forearm and Finger IV, and the foot and Toe V were creamy white with a slight suffusion of tiny brown melanophores. The pale foot fringe continued past the heel. Ventrally, these fringes were bordered by brown, which covered the ventrolateral surface of the forearm and foot. The throat and belly were immaculate white; the chest was pale yellow and most of the hidden surfaces of the limbs were pale pinkish purple. The posterior surface of the thighs was orange-brown. A horizontal cream stripe was present above the vent, and the area below this stripe and surrounding the vent was dark brown. Just below the vent, about 10 large white tubercles were present. Additional white tubercles extended along the ventrolateral surface of the proximal twothirds of the thighs and diminished in size distally. The iris was pale tan but had dense reddish-brown reticulations, thereby giving the eye an overall mahogany appearance.

Measurements of holotype: SVL 30.3, tibia length 17.0, foot length 13.1, head length 10.9, head width 10.8, eye length 3.6, tympanum length 1.6.

Variation.—In 57 adult males, the SVL length is 30.1–36.6 mm ($\bar{x} = 32.7$), the tibia length/SVL is 0.52–0.58 ($\bar{x} = 0.55$), the foot length/SVL is 0.37–0.47 ($\bar{x} = 0.42$), the head length/SVL is 0.33–0.40 ($\bar{x} = 0.35$), the head width/SVL is 0.33–0.37 ($\bar{x} = 0.35$), and the tympanum/eye is 0.40–0.56 ($\bar{x} = 0.49$). In six females, the SVL length is 45.0–57.6 mm ($\bar{x} = 50.9$), the tibia length/SVL is 0.52–0.56 ($\bar{x} = 0.54$), the foot length/SVL is 0.39–0.41 ($\bar{x} = 0.41$), the head length/SVL is 0.34–0.37 ($\bar{x} = 0.34$), the head width/SVL is 0.34–0.37 ($\bar{x} = 0.35$), and the tympanum/eye is 0.44–0.52 ($\bar{x} = 0.49$).

The tarsal fold is barely discernible or absent in some individuals, but the condition of this structure seems to be largely an artifact of preservation. Males have 4–7 ($\bar{x} = 5.1$) and females have 7–9 ($\bar{x} = 8.1$) teeth on each dentigerous process of the vomers.

In contrast to the holotype, other males in life may have more conspicuous gray (e.g., UTA A-34145) to almost maroon (e.g., UTA A-13198) mottling on the dorsum (Fig. 3). In some individuals, the nares are edged with black, and the dorsal surfaces of the digital discs are yellowish, but heavily suffused with smoky gray. The number of enlarged white tubercles below the vent varies from about 10–20, and white tubercles may be present from about one half to three fourths of the ventrolateral surface of the proximal portion of the thigh. The eye color varies somewhat because of variations in the amount and color of iris reticulation that varies from dark brown, gray-brown, to reddish brown. The palpebral membrane is flecked with greenish gold. Specimens sleeping on leaves by day had a somewhat subdued turquoise-green dorsum. In preserva-

Table 4. Measurements of tadpoles of *Ptychohyala acrochorda* at various stages of development. Range of variation is followed on next line by mean and one standard deviation. Tadpoles collected on 7 June and 24 July 1983.

Stage	N	Body length	Total length
25	7	7.8–9.4	18.8–28.3
		8.9 ± 0.54	25.3 ± 3.17
26	6	8.5–10.6	23.1–31.4
		9.7 ± 0.93	27.1 ± 3.02
27	10	9.0–11.7	24.8–38.0
		10.4 ± 0.83	30.3 ± 3.98
28	5	10.1–12.5	29.9–36.6
		11.3 ± 0.94	33.3 ± 3.07
31	1	12.2	36.7
32	1	12.4	36.6
34	1	12.6	38.4
36	2	11.7–12.2	37.5–37.6
		12.0 ± 0.35	37.6 ± 0.07
37	3	11.6–12.5	36.1–37.9
		12.2 ± 0.52	37.2 ± 0.95

tive, some individuals have inconspicuous darker mottling on the dorsum of the body and dorsal surfaces of the limbs.

Tadpoles.—Thirty-six tadpoles in various stages of development were collected at the type locality on 7 June and 24 July 1983 (Table 4). Individuals in this sample are in Stages 25–37. The maximum total lengths of tadpoles ranged from 18.8 mm (Stage 25) to 37.9 mm (Stage 37), and the maximum body length ranged from 7.8 mm (Stage 25) to 12.5 mm (Stage 37).

In a series of 10 tadpoles in Stage 27, the total length is 24.8–38.0 (\bar{x} = 30.3) mm, and the body is 9.0–11.7 (\bar{x} = 10.4) mm. The mouth is ventral; the eyes are moderately small and directed dorsolaterally, and the nostrils are situated about two fifths of the distance from the eyes to the tip of the snout. The spiracle is sinistral and posteroventral to the eyes; the cloacal tube is dextral. The caudal musculature is robust and terminates at a point just anterior to the tip of the tail. The dorsal fin does not extend onto the body and reaches its greatest height in the posterior half of the tail. The ventral fin is about uniform in height throughout most of the length of the tail, but is slightly higher posteriorly. At the midlength of the tail, the height of the dorsal fin is equal to about two thirds that of the caudal musculature, and the height of the ventral fin only slightly less.

The mouth is moderately large, and the lips have deep lateral folds. One or two rows of small papillae border the periphery of the mouth; the upper (anterior) lip usually has a single row of papillae, but these are arranged in two irregular rows in some specimens; the oral disc is bordered by two rows of papillae laterally and posteriorly. The lateral fold contains 15–18 relatively large papillae. The lower

beak bears short, blunt serrations; the serrations on the upper beak are relatively smaller and more pointed. There are four upper and six lower rows of labial denticles. The first upper row is not well developed; it is fragmented into short series of denticles and is shorter than the other upper rows of denticles. The second and third upper rows are complete; the second row is slightly longer than the third. The fourth upper row is about equal to or slightly longer than the third row and widely interrupted medially. The first four lower rows are about equal in length, but slightly shorter than the upper rows; the fifth and sixth rows of denticles are shorter than the first four lower rows. The first lower row is not interrupted medially. The denticles on the first to third lower rows are well developed; rows four to six are successively less developed, and the sixth row is fragmented into short series of denticles.

In preservative, the body is medium brown with a few small, indistinct blotches. The venter is milky white and translucent. The tip of the snout varies from whitish to colored similarly to the dorsum. The caudal musculature is creamy tan, and the caudal fins are almost transparent. In some specimens, an area devoid of brown pigment demarcates the posterior edge of the body. The caudal musculature is marked by dense brown melanophores; these are most dense anteriorly and become relatively sparse posteriorly. The dorsal fin is marked with brown spots and flecks; the ventral fin may also have a few dark markings, but these are relatively few in number. Small white flecks, presumably guanophores, cover nearly the entire body and tail, but are most conspicuous on the caudal fins.

In life, the dorsum and sides of the body of tadpoles in Stage 28 are dark brown with whitish, lichenose markings and a few coppery flecks (Fig. 8). The posterior edge of the body from the insertion of the hind limb to the dorsolateral area is unpigmented or not, and the venter of the body is grayish white. The caudal musculature is tan with dark brown stippling. The fins are pale yellow-gray and translucent with scattered dark brown flecks or small blotches, more on the dorsal fin than the ventral fin. The iris is bright copper.

Ptychohyala acrochorda is sympatric with *P. zophodes* in the Sierra Juárez. The tadpoles of *P. zophodes* can be distinguished from those of *P. acrochorda* by the following characters. In the larvae of *P. zophodes*, the fourth upper tooth row has a narrow gap and the first lower row of denticles has a narrow median gap. The lateral processes of the upper beak are comparatively slender. Almost invariably there is at least a fragmented seventh (if not also an eighth) lower row of denticles. There are 12–15 papillae in the lateral fold (vs. 15–18), two rows of fringing papillae along the anterior lip of the oral disc, and the caudal fins are slightly higher.

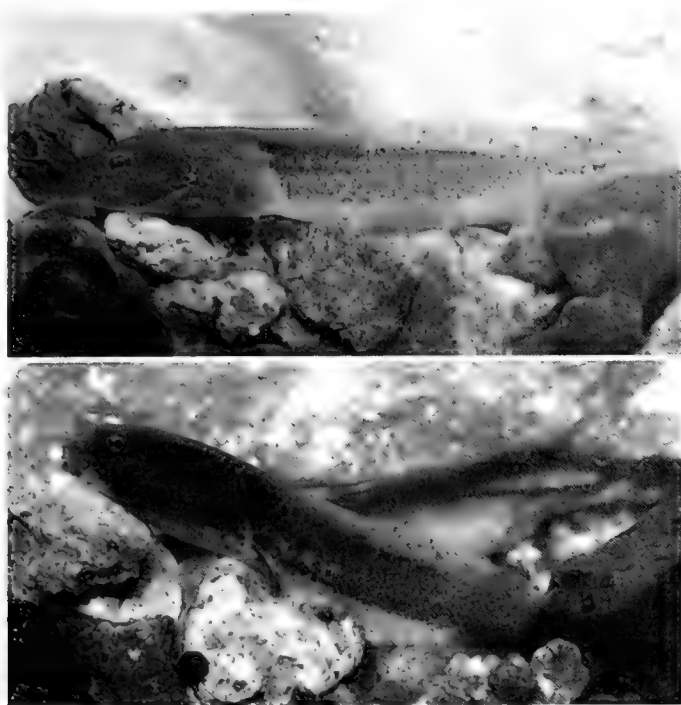


Fig. 8. Tadpoles of *Ptychohyla*. Upper.—*P. acrochorda*, UTA A-27910, Stage 28, 36.6 mm total length. Lower.—*P. zophodes*, UTA A-27900, Stage 39, 38.1 mm total length.

The tadpoles of *Ptychohyla erythromma* differ from those of *P. acrochorda* in that the sixth lower tooth row is fragmented into series of teeth, especially laterally, and these series are usually not arranged in linear fashion. The fringing oral papillae of the oral disc are relatively shorter. There are two or three rows of papillae along the anterior margin of the oral disc, and, other than the marginal and sub-marginal papillae, there are only about half a dozen or fewer papillae in the lateral fold (e.g., KU 87616).

The tadpole of *Ptychohyla acrochorda* (as *Hyla erythromma*) from the Sierra Juárez was illustrated by Duellman (1970: figs. 260D and 261B).

Etymology.—The specific epithet is derived from the Greek *akrochordon*, which means “wart,” in allusion to the distinctive white warts on the posterior surface of the thigh in this species.

Ecology and distribution.—*Ptychohyla acrochorda* is known only from mesic forest on the Atlantic slopes of the Sierra Juárez. This species occurs at elevations between 594 and 900 m along small streams flowing through montane rainforest. Adults are most frequently encountered at night sitting on streamside vegetation. Most adults and tadpoles have been collected from June through August, a period corresponding to the early rainy season. However, calling males have been found in February, March, May,

November, and December. Tadpoles are present in streams practically throughout the year.

The soft call of breeding males is difficult to hear at long distances; it has been our experience that one has to practically be in the bushes with these frogs to hear them. Duellman (1970) described the call of this species (as *Hyla erythromma*) as consisting “of a single note, and call groups are repeated at intervals of about 30 to 50 seconds.” In one recording (KU Tape 350), the duration of a note was 0.62 sec. There were 26 pulses per second; the fundamental frequency was 87 at Hz, and the dominant frequency at 2266 Hz.

Remarks.—*Ptychohyla acrochorda* previously was confused with *P. erythromma* (Campbell and Smith, 1992; Duellman, 1970), a species occurring on the Pacific slopes of Guerrero some 300–350 km west of localities for *P. acrochorda*. The environments inhabited by these two species are distinctly different—*P. acrochorda* occurs in extremely mesic, dense cloud forest, whereas *P. erythromma* lives in relatively dry, open forest that lies within the ecotone between tropical deciduous forest and pine-oak forest.

Taylor (1937) described *Hyla erythromma* from a single individual collected at Agua del Obispo, Guerrero, Mexico. This small species is unique among Mexican hylids in having a horizontal pupil, bright red eyes, and a faintly reticulated palpebral membrane. Despite the considerable collective efforts of herpetological field investigations in the Mexican state of Guerrero (resulting by our estimate in more than 6000 specimens of amphibians and reptiles), scant additional material of this species has been found.

We have visited Agua del Obispo, the type locality of *P. erythromma*, on several occasions from the mid-1950’s to the early 1980’s and found the species difficult to collect. The type locality is situated at 17°19’44” N and 99°28’23” W at 1000 m elevation in an area of scattered, small pines and brush that appears to be ecotonal between tropical deciduous forest, which is found slightly below, and pine-oak forest, which is present in the mountains above. The hillsides flanking the small stream were severely cut over and most of the water was exposed to direct sunlight. We suspect that *P. erythromma* may be now extirpated from the region around Agua del Obispo, but it may exist in suitable habitat elsewhere in the Sierra Madre del Sur.

The well-developed ventrolateral glands that characterize some species of *Ptychohyla* (Duellman, 1970), as well as the mental glands found in *Duellmanohyla ignicolor*, are absent in this species. Campbell and Smith (1992) stated that *P. acrochorda* (reported by them as *P. erythromma*) appeared “to have glandular skin in the ventrolateral region, but lacked hypertrophied glands,” and for that reason, they considered this species to lack ventrolateral glands for purposes of phylogenetic analysis. However, adult male

P. acrochorda do have well-developed chest glands that are evident externally and extend over most of the chest from the posterior level of insertion of the forelimbs (Fig. 7). These glands somehow seem to have been overlooked previously.

The overall habitus of *P. acrochorda* is more similar to that of *P. sanctaerucis* of eastern Guatemala than it is to any other known species; indeed, these two species possibly are closely related. Similarities include a marked sexual dimorphism in size with females exceeding 50 mm SVL, nuptial excrescences of breeding males made up of numerous tiny spines, a relatively pale rather than blood-red iris, a lime-green dorsal coloration that is often marked with darker mottling, a lack of hypertrophied ventrolateral glands in breeding males, and general morphology of the larvae. Examination of *P. sanctaerucis* reveals that this species also has a well-developed chest gland in adult males. No adult male *P. erythromma* is available; thus the presence or absence of the chest gland in this species remains unknown. *Ptychohyla acrochorda* and *P. sanctaerucis* inhabit a similar cloud forest habitat at comparable elevations on either side of the lowlands of the Isthmus of Tehuantepec.

Ptychohyla zophodes new species

Ptychohyla leonhard-schultzei (part)—Duellman, 1960:191.

Ptychohyla leonhardschultzei (part)—Duellman, 1963:323; Duellman, 1970:541; Campbell and Smith, 1992:165.

Holotype.—UTA A-13465 (original field no. JAC 7580), an adult male from 16.1 km W Jalapa de Díaz at Río Aloapan (18°01'12" N, 96°39'36" W, 405 m), Oaxaca, Mexico, one of a series collected by Jonathan A. Campbell on 5 June 1983.

Paratypes.—KU 289217–18, UTA A-13461, and 13463 collected with the holotype.

Referred specimens.—See Appendix.

Diagnosis.—A member of the genus *Ptychohyla* (sensu Campbell and Smith, 1992), in which breeding males have well-developed ventrolateral glands, dark nuptial excrescences consisting of more than 50 small spines, and a call that is a single note emitted as a long, moderately low-pitched "wraack." In this species, males attain a SVL of 37.4 mm and females, 43.6 mm. The ground color of the dorsum is brown or brownish gray, and the iris is copper-colored with fine black reticulations; a tarsal fold is present. Tadpoles have 4/6 rows of denticles.

The only other species of hylid that possesses ventrolateral glands and is known to occur on the northern versant of the highlands of Oaxaca is *Duellmanohyla ignicolor*. The latter is easily distinguished from *P. zophodes*, because *D. ignicolor* has a green dorsal coloration and less webbing on the hand, and lacks a tarsal fold and nuptial excrescences in breeding males. The tadpoles of *D. ignicolor* are

strikingly different from those of *P. zophodes* in having a large funnel-shaped oral disc and 3/3 short rows of denticles.

Ptychohyla acrochorda differs from *P. zophodes* in having a greenish dorsum, a whitish iris with reddish-brown reticulations, and conspicuous, large, white tubercles below the vent. Breeding males of *P. acrochorda* have nuptial excrescences composed of several hundred minute spines and a chest gland, and lack ventrolateral glands.

Ptychohyla zophodes differs from *P. leonhardschultzei* in the following features. *Ptychohyla zophodes* has a darker dorsal coloration (dark brown or gray-brown versus pale tan, yellowish brown, or pale reddish brown). The throat, chest, and belly are distinctly spotted or mottled with dark brown (vs. immaculate or with indistinct, small spots only on throat); the ventral surfaces of the thighs are suffused or speckled with dark brown (vs. immaculate orange). The discs on the hands and feet are proportionally larger (disc on Finger III larger than tympanum vs. about equal or slightly smaller). The hand and foot webbing is dark gray or brown (vs. cream, yellow, or tan) and the margin of the upper lip is darkly pigmented (vs. pale); a pale subocular spot is absent (present in *P. leonhardschultzei*) (Fig. 3). The webbing on the hind feet is more extensive, usually most obviously between the first two digits ($< 1\frac{1}{2}$ –2 in *P. zophodes*, $> 1\frac{1}{2}$ –2 in *P. leonhardschultzei*); the nuptial excrescences in males of *P. zophodes* have more than 50 small spines, whereas those of *P. leonhardschultzei* have fewer than 35 spines.

Description of holotype.—Adult male; head about as wide as body, slightly longer than wide; head width 33% SVL; head length 35% SVL; in dorsal view, snout rounded with vertical keel on rostrum, truncate in profile; canthus angular and slightly curved; loreal region concave; lips moderately thick and slightly flared; nostrils are protuberant, internarial region slightly depressed, top of head flat. Supratympanic fold well developed, extending from eye across top of tympanum, obscuring upper edge of tympanic annulus, then downward to point above insertion of forelimb and just above level of center of tympanum; tympanum round, diameter approximately 50% diameter of eye, separated from eye by a distance of about 1.1 times diameter of tympanum.

Arm moderately robust (especially forearm); short axillary membrane extending about one-fourth length of upper arm; ventrolateral edge of forearm fringed with distinctly raised dermal ridge punctuated with enlarged tubercles; weak transverse fold weak on wrist, present only laterally; fingers moderately long, bearing large discs; width of disc on Finger III greater than diameter of tympanum; subarticular tubercles moderately large, subconical; distal tubercle on Finger IV wider than long,

not distinctly bifid; supernumerary tubercles small, mostly rounded; palmar tubercle low, flat; prepollex moderately enlarged, bearing dark, keratinized nuptial excrescence composed of more than 50 tiny spines; fingers about one-third webbed; webbing formula: $I2^{3/4}-2^{3/4}III1^{1/2}-2^{1/4}III2-2IV$; webbing on distal portions of digits continuous with well-developed lateral fringes, making digits broad and flat. Hind limbs moderately long, slender; tibiotarsal articulation extending to snout; tibia length 51% SVL, foot length 43% SVL; transverse dermal fold and three large, rounded tubercles on heel; tarsal fold wide, low, extending about three-fourths length of tarsus; inner metatarsal tubercle elongate, flat, barely visible from above; outer metatarsal tubercle small, round, and less than one-fourth size of inner metatarsal tubercle; toes moderately long, slender, bearing discs only slightly smaller than those on fingers; subarticular tubercles moderately large, round to subconical; supernumerary tubercles distinct, round; toes about three-fourths webbed; webbing formula: $I1^{1/4}-2III1-2III1-2IV2-1V$.

Cloacal opening directed posteriorly at upper level of thighs; broad sheath above vent; region below vent coarsely areolate. Skin on throat, chest, belly, and proximal four fifths of ventral surfaces of thighs areolate; skin on dorsal surfaces of body finely rugose. Tongue cordiform, not free behind. Dentigerous processes of vomers consisting of moderately large elevations slightly inclined posteromedially, separated from each other by less than width of a single process, between ovoid choanae (slightly larger than dentigerous processes), each bearing five teeth. Vocal slits extending from posterolateral base of tongue to angles of jaws; vocal sac single, median, subgular, moderately distensible.

The color in preservative is dark brown on the top of the head and dorsum of the body, with large, dark, gray-brown mottling on the latter. The dorsal surfaces of the limbs are dark brown with irregular, wide, gray-brown bars or spots. The dorsal surfaces of the discs and digits are pale gray-brown; the large tubercles on fringe along the forearm are white, and the low ridge along the outer tarsus and Toe V is slightly paler than the surrounding area, but does not form a continuous pale line. The upper lip is not bordered with white. The flanks, especially in the axillary and groin regions, are whitish with distinct, dark brown mottling, and the posterior surfaces of the thighs are reddish brown. The gular area is cream, and the chest and belly are whitish, but the venter has an overall dusky appearance owing to the heavy suffusion of dark brown pigment on the throat and dark gray-brown markings on the chest and belly. A crescent-shaped white stripe is present above the vent; the stripe curves downward on either side of the vent. The region around the vent is dark brown. The subarticular and supernumerary tubercles on

the hand and foot are pale gray. The palmar and plantar surfaces are dark gray-brown.

In life, the ground color of the dorsum of the holotype was deep brown. Irregular black mottling was present on the top and sides of the head, the dorsum of the trunk, and the exposed surfaces of the limbs. The shank had two irregular black transverse bars. The brown of the dorsum graded into a purplish brown on the sides of the body, which were heavily mottled with dark brown. Conspicuous white patches, mottled with black, were present in the axillary and inguinal regions. The tympanum was uniformly brown, and the area below the eye was paler than the rest of the head, but no conspicuous suborbital spot was present. Irregular dark brown pigment extended to the margin of the upper lip. The dorsal surfaces of the finger and toe discs were brown to gray, and the webbing was dark gray-brown. The larger tubercles on the fringes along the ventrolateral surface of the forearm and Finger IV and on the foot and Toe V were creamy white; these formed broken cream lines. The cream fringe on the foot continued onto the heel. The venter was whitish but darkly suffused with brown to almost black mottling, spots, and blotches. The posterior surfaces of the thighs were dark orange-brown. A horizontal cream stripe was present above the vent, and the area below this stripe and surrounding the vent was dark brown. Just below the vent about 10 large white tubercles were present. The iris was copper colored with fine black reticulations.

Measurements of holotype: SVL 37.4, tibia length 19.1, foot length 15.9, head length 13.0, head width 12.2, eye length 4.0, and tympanum length 2.0.

Variation.—In three adult males from the type locality, the SVL is 35.2–37.4 mm ($\bar{x} = 36.0$), the tibia length/SVL is 0.47–0.51 ($\bar{x} = 0.50$), the foot length/SVL is 0.42–0.45 ($\bar{x} = 0.44$), the head length/SVL is 0.34–0.35 ($\bar{x} = 0.35$), the head width/SVL is 0.32–0.34 ($\bar{x} = 0.33$), and the tympanum/eye is 0.45–0.55 ($\bar{x} = 0.50$). In of two females from the type locality, the SVL is 41.5–43.6 mm ($\bar{x} = 42.6$), the tibia length/SVL is 0.50–0.52 ($\bar{x} = 0.51$), the foot length/SVL is 0.42–0.44 ($\bar{x} = 0.43$), the head length/SVL is 0.33, the head width/SVL is 0.31–0.32 ($\bar{x} = 0.32$), and the tympanum/eye is 0.46–0.48 ($\bar{x} = 0.47$).

The tarsal fold is a relatively broad, obtuse fold that extends from about two-thirds to practically the entire tarsus. *Ptychohyla zophodes* has well-developed ventrolateral glands, but lacks a mental or chest gland. Males have 3–5 ($\bar{x} = 3.8$) and females have 4–6 ($\bar{x} = 4.8$) teeth on each dentigerous process of the vomers.

In contrast to the holotype, other males (e.g., KU 289217–18, UTA A-13463) have less conspicuous marking on the dorsum; the dorsal blotches amount to little more than a slight smudging (Fig. 3). Also, the venter is heavily



Fig. 9. Metamorphosing young of *Ptychohyla*. Upper.—*P. zophodes*, UTA A-13176, 16.6 mm SVL, 9.8 mm tail length. Lower.—*P. leonhardschultzei*, UTA A-28002, 20.7 mm SVL, 11.7 mm tail length.

pigmented in all frogs, but the dark pigment is arranged in numerous discrete spots in some individuals, rather than a network of mottling. Females are similar in coloration to males in most respects, but females have a slightly paler dorsal ground color and commonly a more contrasting mottled pattern. The flanks of the body between limb insertions are white with dark brown mottling, whereas the white usually is restricted to the axillary and inguinal regions in males.

Metamorphosing *Ptychohyla zophodes* have a brown dorsum mottled with dark brown; the upper lip has a large and rather diffuse whitish marking below the eye. The limbs have narrow, well-defined, dark brown bars (Fig. 9); the tail is black with pale flecks, and the iris is metallic brown. At a comparable stage of development, *P. leonhardschultzei* has a paler dorsum with more distinctive mottling (Fig. 9), a smaller but more distinct white marking below the eye, limbs that are mottled rather than barred, a brownish tail with darker markings, and a copper iris.

Tadpoles.—Fifty-nine tadpoles in various stages of development were collected at the type locality on 5 April 1983 (Table 5). Individuals in this sample range from Stage

Table 5. Measurements of tadpoles of *Ptychohyla zophodes* at various stages of development. Range of variation is followed on next line by mean and one standard deviation. Tadpoles all collected on 5 June 1983 at the type locality.

Stage	N	Body length	Total length
25	7	7.6–10.3	22.2–30.3
		9.3 ± 0.94	27.2 ± 2.80
26	3	10.4–10.7	28.6–30.5
		10.5 ± 0.17	29.7 ± 0.97
27	2	10.3–10.8	29.9 ± 30.4
		10.6 ± 0.35	30.2 ± 0.35
28	4	11.5–12.1	29.2–32.8
		11.9 ± 0.26	32.3 ± 2.22
29	1	11.9	32.5
32	3	11.3–12.1	32.3–35.0
		11.6 ± 0.44	33.6 ± 1.35
33	4	11.2–12.2	26.8–32.1
		11.7 ± 0.42	30.6 ± 2.56
34	1	13.4	35.1
36	4	12.3–13.1	33.7–37.7
		12.7 ± 0.43	36.4 ± 1.81
37	10	11.9–13.6	33.4–39.1
		12.7 ± 0.59	35.7 ± 2.10
38	5	12.5–13.7	35.2–39.1
		12.9 ± 0.48	37.3 ± 1.43
39	2	12.7	34.6–35.6
40	9	13.0–14.5	36.0–44.2
		13.6 ± 0.40	38.5 ± 2.65
41	4	12.4–13.7	35.5–39.6
		13.1 ± 0.57	37.8 ± 1.93

25 to 41. The maximum total length of tadpoles is 22.2 (Stage 25) to 44.2 mm (Stage 40), and the maximum body length is 7.6 (Stage 25) to 14.5 mm (Stage 40).

In a series of 10 tadpoles in Stage 37, the total length is 33.4–39.1 (\bar{x} = 35.7) mm, and the body length is 11.9–13.6 (\bar{x} = 12.7) mm. The mouth is ventral; the eyes are small and directed dorsolaterally, and the nostrils are situated about two fifths of the distance from the eyes to the tip of the snout. The spiracle is sinistral and posteroventral to the eyes; the cloacal tube is dextral. The caudal musculature is moderately robust and terminates just short of the tip of the tail. The dorsal fin does not extend onto the body and reaches its greatest depth at about midlength of the tail, whereas the ventral fin is uniform in height throughout most of the length of the tail. At midlength of the tail, the height of the dorsal fin is subequal to, or slightly greater than, the caudal musculature, whereas the height of the ventral fin is less (one half to two thirds) than the caudal musculature.

The mouth is large and the lips have deep lateral folds. One row of small papillae usually borders the lips around the anterior periphery of the mouth, but in many individu-

als, these are staggered (i.e., not in a completely linear series), and two rows are present in some individuals. Two rows of marginal papillae are present along the lateral and posterior edge of the oral disc. About 12–15 relatively large papillae are present in the lateral fold. The beaks bear short, blunt serrations. Usually there are four upper and six lower rows of denticles. The first three upper rows are complete and about equal in length, whereas the fourth upper row is slightly shorter and narrowly interrupted medially. The lower rows are about equal in length but shorter than the upper rows; the first lower row is narrowly interrupted medially. The denticles on the first to third lower rows are well developed; from tooth row four posteriorly, the rows of labial denticles are successively less well developed. In a few specimens, a fragmentary fifth upper row and a seventh and even an eighth lower row are present.

In preservative, the body is medium brown above and on the sides. The venter is creamy gray with a few indistinct darker spots. The tip of the snout is pale brown or tan. The caudal musculature is creamy tan, and the caudal fin is milky white and translucent. The posterior edge of the body is marked by a creamy white, crescent-shaped mark. The caudal musculature bears dense brown melanophores, which are grouped into small blotches or coarse mottling on the anterior part of the tail and form a finer mottling on the distal two thirds of the tail. A few, scattered, small brown flecks or spots are present on the caudal fins; these markings are more numerous on the dorsal fin than on the ventral fin and are more numerous anteriorly than posteriorly. The eyes appear to be nearly black, but under very bright light are reddish brown to deep burgundy.

In life, the dorsum and sides of the body of tadpoles at Stage 39 were dark coffee brown with whitish, lichenose markings (Fig. 8). The posterior edge of the body from the insertion of the hind limb to the dorsolateral area was unpigmented, and the venter of the body was cream with a few dark brown spots. The caudal musculature was pinkish tan with dark brown markings arranged as large spots or coarse mottling on about the proximal third of the tail and as fine stippling or mottling on the distal two thirds of the tail. The fins were pale yellowish gray and translucent with scattered dark brown flecks or small blotches and with more flecks on the dorsal fin than on the ventral fin. The dorsal surfaces of the emerging hind limbs were grayish brown and the ventral surfaces were cream. The iris was a bright copper color.

Slight differences exist between the tadpoles of *Ptychohyala zophodes* from the Sierra Mazateca and the Sierra Juárez. In comparison with tadpoles from the Sierra Mazateca, tadpoles from the Sierra Juárez have dorsal caudal fins that just barely reach the body; in many individu-

als, the upper beak lacks serrations and the overall coloration is paler, usually with a pattern of dark brown mottling on the dorsum of the body.

The tadpole of *Ptychohyala leonhardschultzei* differs from that of *P. zophodes* in having more expanded lateral processes of the upper beak, shorter serrations on the upper beak, considerably longer fringing oral papillae, and slightly shallower caudal fins. The dorsum of the body of *P. leonhardschultzei* (Stages 25–36) is pale tan or yellow with dense brown or purplish brown stippling; the caudal musculature is whitish and translucent, except for inconspicuous pale brown mottling. The iris is yellow in life, sometimes with a hint of orange. Tadpoles in later stages (40–42) are tan or pale brown with dark brown mottling on the body and tail; they have a burnished copper-colored iris in life.

The tadpole of *Ptychohyala zophodes* from the Sierra Juárez was illustrated by Duellman (1970:figs. 260D and 261B) as *P. leonhardschultzei*.

Etymology.—The specific epithet is derived from the Greek *zophodes*, which means “dusky” or “gloomy” in allusion to the distinctive dark coloration of this species, as well as its cloud-enshrouded habitat.

Ecology and distribution.—*Ptychohyala zophodes* apparently is restricted to the mesic forest of the Atlantic slopes of northern Oaxaca. This species inhabits parts of the Sierra Mazateca, the Sierra Juárez, and perhaps the Sierra Mixes at elevations of about 400–1500 m. It is found along small streams flowing through cloud forest and upper rainforest. Adults most frequently are encountered at night sitting on streamside vegetation. Most adults and tadpoles were collected in June–August, a period corresponding to the early rainy season. However, we encountered a few calling males as early as February, and as late as November and December in the dry season. Tadpoles are present in streams practically year round.

The call of *Ptychohyala zophodes* consists of a single note that sounds like a deep “wraack”; the call is similar to those of *P. leonhardschultzei*, *hypomykter*, and *euthysanota*.

Remarks.—We allocate a large series of frogs from the Sierra Juárez and a single specimen from near Totontepec in the Sierra Mixes to *P. zophodes*. The populations in these mountain ranges seem to be isolated and slightly differentiated from topotypic *Ptychohyala zophodes*. In contrast to material from the Río Aloapan, frogs from the Sierra Juárez tend to have dark spotting on the gular area, chest, and belly, but the pigment is arranged in fewer (but sometimes larger) spots. The ventrolateral surface of the trunk tends to be pale with bold, dark brown mottling in both males and females. In females, the ventral spotting is commonly confined to the gular area and chest, and the belly is immaculate. Males are smaller; in four adult males from the

Sierra Juárez, the SVL is 30.9–32.7 (\bar{x} = 31.8) mm, the tibia length/SVL is 0.48–0.52 (\bar{x} = 0.51), the foot length/SVL is 0.39–0.44 (\bar{x} = 0.41), the head length/SVL is 0.36–0.37 (\bar{x} = 0.36), the head width/SVL is 0.33–0.35 (\bar{x} = 0.34), and the tympanum/eye is 0.43–0.47 (\bar{x} = 0.45). In four females, the SVL is 33.5–43.5 (\bar{x} = 37.6) mm, the tibia length/SVL is 0.48–0.53 (\bar{x} = 0.49), the foot length/SVL is 0.35–0.43 (\bar{x} = 0.38), the head length/SVL is 0.32–0.35 (\bar{x} = 0.33), the head width/SVL is 0.31–0.34 (\bar{x} = 0.33), and the tympanum/eye is 0.39–0.51 (\bar{x} = 0.45).

A specimen from near Totontepec (UTA A-51669) was not seen in life by either of us and is tentatively allocated to *Ptychohyala zophodes*. It is a male with vocal slits; the presence of nuptial excrescences composed of low, white spines suggests that the specimen is either a subadult or in non-breeding condition. In preservative, the dorsum is pale brown with large, dark grayish-brown blotches. The side of the head is evenly pigmented to the margin of the upper lip. The ventrolateral glands are well developed and heavily mottled. The throat, chest, and belly are marked with numerous dark spots. The webbing formula between the first two toes is I1–2II. The measurements for this frog are: SVL 30.9 mm, head length 10.8 mm, head width 10.2 mm, eye 3.2 mm, tympanum 1.6 mm, tibia length 16.0 mm, and foot length 12.0 mm. This individual is unusual in having numerous glands concentrated in the gular area to form a mental gland. The only Oaxacan hyliid heretofore known to have a mental gland is *Duellmanohyla ignicolor*. The presence of nuptial excrescences and a tarsal fold in the specimen from Totontepec seems to preclude its placement with that species.

Ptychohyala zophodes was confused previously with *P. leonhardschultzei* (Campbell and Smith, 1992; Duellman, 1970), which occurs on the Pacific slopes of Guerrero and Oaxaca. These two species are separated through most of their distributions by the dry uplands of the Mesa del Sur of Oaxaca. However, in eastern Oaxaca, their distributions

converge, but apparently are restricted to different sides of the Continental Divide. *Ptychohyala zophodes* occurs in extremely mesic, dense cloud forest, whereas *P. leonhardschultzei* is more wide-ranging and occurs in relatively dry, open forest that lies within the ecotone between tropical deciduous forest and pine-oak forest. *Ptychohyala leonhardschultzei* also ranges up into cloud forest habitats on the Pacific versant, but these forests are considerably drier than cloud forests on the Atlantic versant.

We have examined the holotype of *Hyla milleri* Shannon (1951), USNM 123700, from San Lucas Camotlán, Oaxaca. This specimen is a male, perhaps subadult, 30.3 mm in SVL, and has vocal slits but lacks nuptial excrescences. It agrees in all respects with *P. leonhardschultzei*. This specimen was part of a collection made by Walter Miller, a linguist and longtime resident of Mitla, during one of his numerous forays into the hinterlands of Oaxaca. The specimen reportedly was collected "on stones projecting from the river in the village ... on the night of May 7, 1946, at 9:10 p.m." This small village lies very near the Continental Divide, and material in Miller's collections may have come from either versant. The actual village of San Lucas Camotlán can be found on different maps either on the Atlantic or Pacific versant (Río Tehuantepec Drainage). However, on the most detailed map we have for this region (Carta Topográfica 1:250,000 Minatitlán E15–7, Dirección General de Geografía del Territorio Nacional, Secretaría de Programación y Presupuesto), the village is shown at about 800 m along a small tributary of the Río Jaltepec, which flows into the Río Coatzacoalcos of the Gulf coastal plain. Regardless of drainage, the type locality of *Hyla milleri* appears to be located in a protected east-west trending valley with high ridges to the north and south. One of us (JAC) passed through the village many years ago; his impression was that the largely cut over area originally must have supported temperate evergreen forest and was much drier than the cloud forest on the north and northeast-facing slopes of Oaxaca.

DISCUSSION

The steep, wet, temperate slopes on which cloud forests flourish in the American tropics present unique opportunities for the radiation of amphibians, but simultaneously pose severe impediments to the reproductive modes found in many groups. On the one hand, the mild and moist environment prevalent in cloud forests seems to be a perfect venue for the evolution of amphibians in general, but conversely, the precipitous slopes practically preclude the presence of lentic bodies of water required by many species of amphibians to breed.

Whereas the reproductive modes of anurans are especially varied in the New World tropics (Duellman, 1992), successful reproduction on montane slopes is character-

ized by two predominant modes of reproduction—terrestrial eggs with direct development and larvae adapted for living in periodically torrential steams. A few other reproductive modes (e.g., deposition of eggs in bromeliads or tree-holes, or on leaves overhanging water) occur among cloud forest-inhabiting species of frogs in Middle America, but these seem to be exceptional and are restricted to a relatively few species of frogs. Two of the most dramatic radiations of amphibians in the New World tropics are certain groups of plethodontid salamanders (e.g., *Bolitoglossa*, *Pseudoeurycea*) and leptodactylid frogs (*Eleutherodactylus*). These groups reach their greatest diversities at moderate-to-high and low-to-moderate eleva-

tions, respectively, of mountain slopes, and both groups lay eggs that undergo direct development.

The development of steam-adapted larvae in northern Middle America has been most prevalent among hylid frogs and, to a lesser extent, the centrolenids and ranids. Although the relationships among the presumptive major lineages of Middle American hylids are not well understood, there is some evidence that many of the groups of stream-breeding hylids are closely related to other stream-breeding groups (*Hyla*, in part, with *Plectrohyla*; *Duellmanohyla* with *Ptychohyla*) and perhaps most of these lineages form a single, large monophyletic group (Campbell and Smith, 1992; Duellman, 1970).

As far as we are aware, nowhere in Middle America is the diversity of hylids greater than on the northern versant of the highlands in Oaxaca, Mexico. Inclusive of the species described herein, a total of 15 steam-breeding species is now known from the wet forests covering these slopes. This total includes 12 species of *Hyla* placed in six groups, two species of *Ptychohyla*, and one of *Duellmanohyla*. Several species of hylids (e.g., *Smilisca cyanosticta* and *S. baudinii*) that normally breed in ponds are also present up to about 1500 m in the Sierra Juárez (Vista Hermosa); in these cloud forests, these species utilize the slow-moving backwaters of certain plunge-pools, but more frequently, breed in small bodies of standing water, such as ruts in the road. Other species of hylids occurring in the region include two tree-hole breeders (*Anotheca spinosa* and *Hyla echinata*) and a species that deposits eggs on vegetation above water (*Agalychnis moreletii*). The diversity of hylids in northern Oaxaca is indicative of general species richness across many taxa (Casas-Andreu et al., 1996) and we consider the region worthy of Herculean conservation efforts by the Mexican government.

The plight of montane tropical forests in Middle America has been emphasized many times, and need not be addressed here; see Alvarez del Toro (1985) for a revealing history of habitat destruction in Mexico. A substantial portion of the cloud forests covering much of northern Oaxaca has already fallen to the relentless ping of machetes and buzz of chainsaws, and most of the upland forests of Oaxaca now have been reduced to degraded secondary growth. The previously pristine streams are polluted and severely silted. Practically all of our collecting sites along streams on the northern versant of Oaxaca have been altered within the last 20 years, either through direct

clearing, forest fires, or logging. Given the localized nature of the distributions and specialized habits of many species of stream-breeding hylids, these frogs have been severely affected as a group.

However, species of highland amphibians in Oaxaca are under a dual threat. Not only are suitable habitats vanishing, but also the general decline of amphibians worldwide is now recognized as a major ecological catastrophe. Identifying the reasons for this decline has been elusive (Stebbins and Cohen, 1995), but one recent promising lead involves a pathogenic chytrid fungus that attacks the skin of adult amphibians and the keratinized mouthparts of anuran larvae (Berger et al., 1998; Longcore et al., 1999).

Many Oaxacan stream-breeding species of hylids, once locally abundant, apparently are now extinct. For example, one of us (JAC) observed hundreds of *Hyla cyanomma* basking on large boulders by day along a short stretch of stream at the type locality of this species in 1978 and 1979. A thorough search of the area on about a dozen occasions since 1983 has not produced a single adult; furthermore, the larvae—previously so abundant and conspicuous in all of the plunge-pools—are absent. Unlike most of the Oaxacan highlands, the type locality of *H. cyanomma* to this day remains relatively undisturbed, although it has become a favorite parking place for tourists, which has resulted in the accumulation of trash; moreover, a forest fire burned much of the crest about 0.5 km above the type locality in the early 1980's. Similarly, *H. calthula* was abundant around the springs and along streams in the vicinity of Totontepec up until at least 1984, but has not been seen since. The area around Totontepec was already cleared at the time of our first visit in 1978. However, recent canalization of many of the local spring-fed streams and deforestation of the headwaters of several streams flowing through this village seems to have taken its toll on *H. calthula*. The stream near Totontepec that is the type locality for *H. psarosema* has been so drastically altered—from a pristine creek flowing through virgin cloud forest to a muddy ribbon of water running through a cornfield—that we find it hard to believe that any of the species of amphibians that we first encountered in 1978 have survived.

Sadly, we suspect that history will confirm our notions that the last several decades, and perhaps the first decade of the new millennium, will stand out as the period when the highlands of Oaxaca, as well as many other places around the planet, lost their greatest wealth of amphibian biodiversity.



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APPENDIX

SPECIMENS EXAMINED

In the following list, paratypes of species described herein are noted with an asterisk (*). All specimens are preserved in alcohol unless designated by one of the following abbreviations: C&S = cleared and stained skeletal preparation; E = eggs, L = larvae, M = metamorphs, S = dried skeleton. Unless noted otherwise, all specimens are from Mexico.

Duellmanohyla ignicolor

Oaxaca: Vista Hermosa, 1500-1600 m, KU 71334, 71716, 87149-50; 2.8 km S Vista Hermosa, 1570 m, KU 137214-17, UTA A-52775; 3.0 km S Vista Hermosa, KU 87151; 4.0 km S Vista Hermosa, 1580 m, KU 137218-22; 4.2 km S Vista Hermosa, 1580-1800 m, KU 87152-66, 87637-38, 101030-48, 103034, 104197, 137223-37; 6.5 km S Vista Hermosa, 1625 m, KU 71335-

43; 10.5 km S Valle Nacional, KU 139889 (L); 12.7 km S Valle Nacional, KU 139890-92; 34.1 km S Valle Nacional, UTA A-2897.

Hyla abdivita

Oaxaca: Río Aloapan, 16.1 km W Jalapa de Díaz, 405 m, KU 289223*, UTA A-13347 (holotype), A-13348*.

Hyla arborescandens

Puebla: 14.4 km W Huachinango, 2280 m, KU 53912; Parajo Verde, USNH 114396-402; 1.1 km W Puerto del Aire (Mexico Hwy 150 on Puebla-Veracruz border), MVZ 138992-93; Río Octapa, 3.7 km NNE Tezuitlán, 1800 m, KU 53818, 55695 (S), 58467-68, 64316-20, 68379-80 (L). Tlaxcala: Apizaco, USNM 108671; Veracruz: 3 km SW Acultzingo, UIMNH 25045 (holotype), 25048 (holotype of *Hyla forbesi*); Coscomatepec, 1543 m, KU 26848; Cumbres de Acultzingo, USNM 108672-04, 114404-05; Huatusco, 1543 m, KU 26847, 26849-50; Pan de Olla, USNM 114406-30; 2 km N Paraje Nuevo, 1700 m, KU 23955; Teocelo, 1390 m, KU 26746.

Hyla bivocata

Chiapas: 25 km S Ixhuatlán, UIMNH 78831–36, 78930; 32 km N Jitotol, UIMNH 56999–701; 18 km N Pueblo Nuevo Solistahuacán, UMMZ 123974 (4); 3.2 km E Rayón Mescalapa, 1433 m, UTA 13390–91; 6.2 km S Rayón Mescalapa, 1690 m, KU 58446, 58447–50.

Hyla calthula

Oaxaca: Totontepec, UTA A-5885 (holotype), A-5788, A-5876–86, A-5888 (L), A-6168 (L), A-6929–32, A-7636, A-7951, A-8508–09, A-13369, A-27804–34 (L), A-44999–5000 (L).

Hyla calvicollina

Oaxaca: 1.1 km N Cerro Pelón, 2712 m, UTA A-5059; 4.0 km N Cerro Pelón, 2518 m, KU 186356 (holotype).

Hyla celata

Oaxaca: 0.9–1.3 km N Cerro Pelón, 2640–2670 m, KU 59998 (L), 104125 (L), 137089 (C&S), 137090–102, 137103 (holotype), 137104–10, 137111 (C&S), 137112–18, 139812–15 (L), 139837–48 (L), 139851–53 (L), UTA A-5060, A-5742–44, 13380.

Hyla crassa

Oaxaca: 14.5 km NE Oaxaca, KU 125354; 1.9 km S El Estudiante, ca. 1850 m, KU 148696–700; tributary of Río Atoyac below Vivero El Tapanal, 1.6 km S La Cofradía, 2652 m, KU 152338–39, 152340 (L); 6.3 km SE Ixtlán de Juárez, 1910 m, KU 139850 (L); 2.3 km E and 11.6 km NE Oaxaca, 1720 m, KU 139854 (L); 5.8 km W (by road) Totontepec, UTA A-5786, A-5842–43, A-5894.

Hyla cyanomma

Oaxaca: 1.1 km N Cerro Pelón, UTA A-5054–58, A-5712–41; 1.2 km (by road) N Cerro Pelón, 2650 m, KU 136997–7007, 137009–13, 137014 (holotype), 137015–34.

Hyla cyclada

Oaxaca: 3.5 km W Cerro Machín, 2370 m, KU 137119; 52 km NNE Guelatao, MVZ 112344; 6 km W La Cumbre, Cerro San Felipe, 2670 m, KU 137120–22; 21.8 km W Tamazulapan, 2475 m, UTA A-5761–62, A-5891–92; 32 km E Teotitlán on road to Huautla, 2243 m, UTA A-13151; 5.0 km W Totontepec, 2185 m, UTA A-6843–46, A-6933, A-6936; 5.6 km W Totontepec, 2121 m, UTA A-13196, A-13345; 5.8 km W Totontepec, headwaters of Río de la Lana, 2129 m, UTA A-5763–67, A-5774–75, A-5477–79, A-5780–81, A-5838–39; 18.2 km W Totontepec, 2568 m, UTA A-5801–06; 3.9 km S Vista Hermosa, KU 86994; 4.2 km S Vista Hermosa, 1800 m, CAS 122649–52*, KU 86999–87007*, 87605 (L), 103029 (C&S), 104136 (L); 6 km S Vista Hermosa, KU 58453–55*, 59904 (C&S) 6.5 km S Vista Hermosa (Arroyo Buena Vista), KU 71216 (holotype), 71217–20*, 87008, 137123*, 139722 (E) 7.5 km S Vista Hermosa, 1900 m, KU 87606; 7.8 km S Vista Hermosa, 1650 m, KU 137124*; 9.1 km S Vista Hermosa, 1750 m, KU 137125–27*, UTA A-52817–18*; 9.3 km S Vista Hermosa, 1700 m, KU 137130–31*; 11.1 km S Vista Hermosa, 1840 m, KU 87012*, 137132–35*; 11.6 km S Vista Hermosa, 1870 m, KU 137136 (C&S); 11.9 km S Vista Hermosa, 1920 m, KU 137137–42*; 12.3 km S Vista Hermosa 1920 m, KU 137143–45*; 14.3 km S Vista Hermosa, 1970 m, KU 137146*; 15 km S Vista Hermosa, 1980 m, KU 137147–51*, 104126 (L); 15.8 km S Vista Hermosa, 1990 m, KU 137152–76*; 16 km S Vista Hermosa, MVZ 131472–74; 16.6 km S Vista Hermosa, 2180 m, KU 137177–78*, 139836 (L).

Hyla hazelae

Guerrero: Puerto del Gallo, 2530 m, CAS 143106–08. Oaxaca: Cañon Tlalixtac, 6 km SE, 17 km NE Oaxaca, 2420 m, KU 100967; 2 km S El Punto, KU 100968–69; 7.4 km W La Cumbre, 2864 m, USNM 224499; between Tlahuitoltepec and Tamazulapan, 2200 m.

Hyla melanomma

Guerrero: Agua del Obispo 980 m, AMNH 59261–63, KU 87116, 87607 (L); 11 km E Chilpancingo, FMNH 100074 (holotype); 14 km E Mazatlán, MVZ 106286–87, 106289, 106292, 106294, 106296–97, 106301, 106202; 2 km E Río Santiago, 25 km NE Atoyac, MVZ 106340–43, 106356–57. Oaxaca: 6.4 km N El Candelaria, UIMNH 9121–52; El Soledad, UIMNH 9253–54; 0.2 km N Jalatengo, 1280 m, KU 136813–15; 17.2 km S Juchatengo, UIMNH 78826–30; 29 km SSE Juchatengo, 1980 m, KU 86955; 6 km NNW San Gabriel Mixtepec, 910 m, KU 87608 (L), 87609; 12 km NNW San Gabriel

Mixtepec, 1040 m, KU 86937–52, 86953–54 (C&S), 25.8 km N San Gabriel Mixtepec, 1230 m, 136744–91, 136810, 136795–96 (C&S), UTA A-52814–16; 27.8 km N San Gabriel Mixtepec, 1320 m, KU 136797–804, 28.8 km N San Gabriel Mixtepec, 1370 m, KU 136805–09; 35.9 km N San Gabriel Mixtepec, KU 136811–12.

Hyla miotympanum

Oaxaca: 61.0 km E Teotitlán on road to Huautla, Puente de Hierro at Río Eloxochitlán, 1219 m, UTAA-13152–59 (M), A-13172–75 (M), A-13367–68, A-27932–73 (L)

Hyla mixe

Oaxaca: 33.9 km S Valle Nacional, UTA A-4342; 4.2 km S Vista Hermosa, KU 87110–11, 104183, 152374 (L).

Hyla nephila

Oaxaca: 15.4 km N Cerro Pelón, 2256 m, UTA A-4770; 16.1 km N Cerro Pelón, UTA A-4769; 40.1 km E Teotitlán, on road to Huautla, 2106 m, UTA A-13194–95; 5.0 km W Totontepec, 2158 m, UTA A-6934–35, A-6841–42; 5.8 km W Totontepec, 2103 m, UTA A-5769 (holotype), A-5768, A-5784; 10.5 km S Valle Nacional, 680 m, KU 136651; 12.7 km S Valle Nacional, 790 m, KU 136655; 4.0 km S Vista Hermosa, 1829 m, UTA A-6836; 4.1 km S Vista Hermosa, 1580 m, KU 136656; 4.2 km S Vista Hermosa, 1580 m, KU 136657–60; 7.8 km S Vista Hermosa, 1650 m, KU 136661; 8.0 km S Vista Hermosa, CAS 122627–29; 9.1–9.4 km S Vista Hermosa, 1710–1750 m, KU 136662–65; 11.1–11.9 km S Vista Hermosa, 1840–1920 m, KU 136666–85; 12.3 km S Vista Hermosa, 1920 m, KU 136686–88; 15.8 km S Vista Hermosa, 1990 m, KU 136689–91; 16.6 km S Vista Hermosa, 2020 m, KU 136692–93.

Hyla pachyderma

Veracruz: Pan de Olla, S Tezuatlán (Puebla), USNM 115026–28, 115029 (holotype).

Hyla pentheter

Guerrero: 11–13 km W Mazatlán, LACM 92416; 5.6 km N Yerbabuena, 2000 m, KU 140424–26. Oaxaca: 0.1 km N Jalatengo, 1280 m, KU 136863–71, 139782–83 (L); 3.9 km N Jalatengo, 1490 m, KU 139784 (L); 0.2–0.8 km S Jalatengo, 1280–1290 m, KU 139778–81 (L); 5.1 km S Jalatengo, 1390 m, KU 136872–77, 139775–77 (L); 29 km SSE Juchatengo, 1980 m, KU 86936; 25.3 km N San Gabriel Mixtepec, UTA A-17165; 25.8 km N San Gabriel Mixtepec, 1230 m, KU 139785–88 (L); 27.8 km N San Gabriel Mixtepec, 1320 m, KU 136887–89, 139789–91 (L); 31 km N San Gabriel Mixtepec, 1860 m, KU 104142 (L); 32.9 km N San Gabriel Mixtepec, 1530 m, KU 136879–83, 136884 (C&S), 136885–86, 139799 (L); 33.1 km N San Gabriel Mixtepec, 1530 m, KU 139793 (L), 139796 (L); 36.7 km N San Gabriel Mixtepec, 1690 m, KU 136878; 37.0 km N San Gabriel Mixtepec, 1860 m, KU 100931–33, 117426 (S), UMMZ 125377–80, 125381 (holotype); 9.3 km S Sola de Vega, UTA A-3653 (L).

Hyla psarosema

Oaxaca: 5.8 km W (by road) Totontepec, Sierra Mixes, Oaxaca, Mexico, 2103 m, KU 289216*, UTA A-5771*, A-5777*, A-5782 (holotype), A-5783*.

Hyla sabrina

Oaxaca: 7.7 km S La Esperanza, 2006 m, USNM 224503; 4.2 km S Vista Hermosa, 1580 m, KU 139816 (L); 7.8 km S Vista Hermosa, 1650 m, KU 137038–40, 137817–19 (L); 9.4 km S Vista Hermosa, 1710 m, KU 139820–21 (L); 11.0–11.6 km S Vista Hermosa, 1840–1910 m, KU 87011, 137041–43, 137045–53, 139822 (L), 139815–32 (L), UTA A-52810; 11.9 km S Vista Hermosa, 1920 m, KU 137054–62, 137063 (C&S), 137064–72;; 12.3 km S Vista Hermosa, 1920 m, KU 137073–77, 139834 (L); 13.5 km S Vista Hermosa, 1920 m, KU 137078–79; 15.8 km S Vista Hermosa, 1990 m, KU 137080–85, 137086 (holotype), 139835 (L); 16.6 km S Vista Hermosa, 2020 m, KU 137087–88, 139836 (L).

Hyla sumichrasti

Oaxaca: 25.3 km S Nochixtlán, UIMNH 53648.

Ptychohyla acrochorda

Oaxaca: Between Metates and Vista Hermosa, 900–1500 m, UTA A-34145–46*, 8.8 km S Valle Nacional, 594 m, UTA A-13222*; 9.1 km S Valle Nacional, 610 m, KU 139723; 9.2 km S Valle Nacional, 610 m, KU 136703–04, 139723–24 (L); 10.5 km S Valle Nacional, 680 m, KU 136705–06, 139725

(L); 11.5 km S Valle Nacional, 750 m, KU 200890-99; 11.6 km S Valle Nacional, 750 m, KU 100890-99*, UTA A-13197 (holotype, UTA A-13198-221*); 12.7 km S Valle Nacional, 790 m, KU 136709-26, 139755-60 (L); 13.4 km S Valle Nacional, 725 m, UTA A-27922-24 (L); 16.9 km N Vista Hermosa, 692 m, UTA A-27910-21 (L); 5.0 km S Yetla, KU 87104-09*; 6.9 km S Yetla, 800 m, KU 87103*; 7.5 km S Yetla, 700 m, KU 65128; 8.0 km S Yetla, 800 m, KU 64524-25, 68292, 87082-96*, 87618-19 (E), 87620-33 (L), 87782-83 (C&S), 100902-14.

Ptychohyla erythromma

Guerrero: Acahuitzotla, TCWC 8245; Agua del Obispo, 980 m, FMNH 100083 (holotype), KU 87615-16 (L), 87617, 10119; 1.6 km E San Andrés de la Cruz, 700 m, KU 87613; 3.3 km N San Vicente, 920 m, KU 87614

Ptychohyla leonhardschultzei

Guerrero: Agua del Obispo, 980 m, FMNH 106300, 123489-90, 126651, MCZ 29639, UIMNH 25047 (holotype of *Ptychohyla adipiventris*), 25049, 27305, USNM 114551, UTA A-13460, UTA A-28001-13 (L); Malinaltepec, ZMB 34351, 34353 (holotype of *Hyla leonhardschultzei*). Oaxaca: 10.5 km N El Candelaria, 930 m, KU 139907 (L) 2.2 km S El Candelaria, 350 m, KU 137251, 139906 (L); Grutas de San Sebastián, 1820 m, MVZ 176673-74; 1.5 km N La Soledad, 1640 m, KU 58061; 0.2 km S La Soledad, 1340 m, KU 139908 (L); 0.2 km N Jalatengo, 1280 m, KU 137257-69, 139912-14 (L); 0.4 km N Jalatengo, 1290 m, KU 137270, 139915 (L); 3.9 km N Jalatengo, 1490 m, KU 137271-72, 139916-18 (L); 4.4 km N Jalatengo, KU 1510 m, KU 139919-20 (L); 5.1 km S Jalatengo, KU 137252-55, 139909-10 (L); Río Jalatengo, 0.8 km S Jalatengo, 1280 m, KU 137256, 139911 (L); 6.0 km S Putla, CAS 135703-05; 4.3 km N San Gabriel Mixtepec, 620 m, KU 137279-85; 8.6 km N San Gabriel Mixtepec, 740 m, KU 137286-87; 14.8 km N San Gabriel Mixtepec, KU 137288-95; 25.8 km N San Gabriel Mixtepec, 1230 m, KU 137296-99, 139926-28 (L); 27.8 km N San Gabriel Mixtepec, KU 137300, 139929 (L); 30 km N San Gabriel Mixtepec, 1530 m, CAS 122681-84, 101087-94, 104173 (L); 33 km N San Gabriel Mixtepec, 1675 m, KU 101063-82, 137301, 139930-31 (L), 139932; 35.9 km N San Gabriel Mixtepec,

1680 m, KU 137302-12, 139933 (L); 37 km N San Gabriel Mixtepec, 1860 m, KU 101056-62, 104170 (L), 104172 (L); San Lucas Camotlán, USNM 123700 (holotype of *Hyla milleri*); 18.1 km N San Pedro Mixtepec, 720 m, KU 137173-78, 131921-25 (L); 9.3 km SW Sola de Vega, UTA A-2589, 3653, 7954 (L), 51840-42; 32 km S Sola de Vega, KU 148671-72; Yuatepec, Juquila Mixes, 1219 m, AMNH 83610.

Ptychohyla sanctaerucis

GUATEMALA: Izabal: near Chinamococh, Finca Semuc, 640 m, UTA A-30170 (holotype), A-30171-79; S side Chinamococh, 650 m, UTA A-30180; near Finca Semuc headquarters, 600 m, UTA A-30181; 1-3 km S Finca Semuc headquarters, 420 m, KU 217288-90, UTA A-33538-47, A-33690-91; 4.5 km S Finca Semuc, 366 m, UTA A-24954-55, 8 km W Finca Semuc, 640 m, UTA A-24956; S side Semococh, 580 m, UTA A-33537; Seshán, 700-900 m, UTA A-26486-91; Xiaccám, 880-900 m, UTA A-30182-88.

Ptychohyla zophodes

Oaxaca: 16.1 km W Jalapa de Díaz, 405 m, KU 289217-18*, UTA A-13160 (M), A-13164 (M), A-13176-93 (M), A-13461*, A-13463*, A-13465 (holotype), A-27883-909 (L); Metates, 902 m, UTA A-13466-68, A-34121-24; midway between Tlahuitoltepec and Tamazulapan, KU 139905 (L); 9.1 km S Valle Nacional, 610 m, KU 137240-45, 139893-96 (L); 8.8 km S Valle Nacional (Puente Dañado), 594 m, UTA A-28014-24 (L); 10.5 km S Valle Nacional, 680 m, KU 137246, 139897-99 (L); 12.7 km S Valle Nacional, 790 m, KU 139900-02 (L); 22 km S Valle Nacional, MVZ 137078; 34.1 km S Valle Nacional, UTA A-2896, A-3070-73, A-3077-78, A-4343-44; Vista Hermosa, 1500 m, KU 64119, 68560 (L), 71344, 71714 (L), 71717 (L), 71718, 87167-70; 4.6 km N Vista Hermosa, 1290 m, KU 137249-50, 139903 (L); 4.8 km N Vista Hermosa, 1240 m, KU 137247-48, 139904 (L); 5 km S Yetla, 540 m, KU 60045; 7.5 km S Yetla, 700 m, KU 64118, 68556-57 (L), 68559 (L), 68561, 68630 (C&S); 8 km S Yetla, 830 m, KU 87171, 101049-55, 103035 (C&S), 104198 (L); 9 km S Yetla, 800 m, KU 68558 (L); Totontepec, UTA A-51669.

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