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A NEW SPECIES OF *HYLA* (ANURA: HYLIDAE) FROM THE MIXTECA ALTA, OAXACA, MEXICO

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ABSTRACT: We describe a new species, genus *Hyla*, from the oak forests of the Mixteca Alta of northwest Oaxaca. We tentatively place this species in the phenetic *Hyla bistincta* group. The new species is similar in coloration to species of the *Hyla eximia* group, but differs from them by lacking a quadratojugal.

Key words: Amphibia; Anura; Hylidae; *Hyla ameibothalame*, new species; Mixteca Alta; Oaxaca; Mexico

IN THE last seven years, 12 new species of *Hyla* have been described from several areas of Oaxaca (Campbell and Duellman, 2000; Mendelson and Campbell, 1994, 1999; Mendelson and Toal, 1996; Toal, 1994; Toal and Mendelson, 1995; Ustach et al., 2000). Most of these species are from the northern versant of the Oaxaca

highlands, especially the Sierra de Juárez. During our recent surveys in the poorly known Mixteca Alta of northwestern Oaxaca, we collected a series of frogs of the genus *Hyla* from an oak forest of the Mixteca Alta in the District of Yosocuno, Municipality of San Pedro Nopala. Subsequent examination of comparative material revealed an additional specimen deposited in the Museo de Zoología, Facultad de Ciencias (MZFC) at Universidad Nacional Autónoma de México.

MATERIALS AND METHODS

All measurements and terminology follow that of Duellman (1970); measurements (in millimeters) were made to the nearest 0.1 mm with dial calipers. Observations were made under stereo microscope. Osteological observations were made from one cleared-and-stained paratype. Sex was determined by observation of nuptial excrescences and direct observation of the gonads. Format of the description and diagnosis follows that of Toal and Mendelson (1995). Webbing formulae follow those of Myers and Duellman (1982). Color notes from life were taken from field notes (L. Canseco-Márquez) and photographs of live specimens. Snout-vent length is abbreviated SVL throughout. Tadpoles were staged according to Gosner (1960), and terminology follows that of Altig (1970). Specimens examined for comparison are from the collections at the University of Kansas (KU); Museo de Zoología, Facultad de Ciencias, UNAM (MZFC); and Laboratorio de Herpetología, Escuela de Biología, BUAP (EBUAP).

SYSTEMATICS

During 1996–1998, we conducted herpetological surveys in various regions of northern Oaxaca. At one locality, we discovered a population of enigmatic frogs that we here describe as a new species of the genus *Hyla*. We examined a series of eight adult specimens and five tadpoles and describe them as

Hyla ameibothalame sp. nov.

Holotype.—EBUAP 1024 (original field no. LCM 918), an adult male from 1 km

S Yosocuno, Municipality of San Pedro Nopala, 2455 m (17° 51' N, 97° 34' W), Mixteca Alta, Oaxaca, México; obtained by L. Canseco-Márquez on 24 July 1998.

Paratypes.—All paratype specimens are from Oaxaca, Mexico. Males: EBUAP 1023, 1025–26, same locality as holotype; EBUAP 918, from El Polvorín, 5 km E Yosocuno (cleared and stained specimen), 15 December 1996; EBUAP 919–20, from 2 km S Yosocuno, 16 December 1996. Female: MZFC 07480, from near km 156, along new Tehuacán–Oaxaca road, 30 July 1995. A photograph of one paratype is presented in Fig. 1.

Diagnosis.—A moderate-sized frog tentatively referred to the phenetic *Hyla bistincta* group (sensu Duellman, 1970; see discussion by Toal and Mendelson, 1995) distinguished from other Middle American species of *Hyla* by the following combination of characters: (1) quadratojugal absent; (2) ossified prepollex bearing small nuptial excrescences in adult males; (3) snout truncate in lateral view, rounded in dorsal view, vertical rostral keel absent; (4) skin thin (i.e., more similar to that of *H. sabrina* than to that of *H. bistincta*); (5) flanks uniform, mottling absent; (6) vocal slits absent; (7) tarsal fold present, extending entire length of tarsus; (8) tympanum round, distinct, tympanic annulus indistinct; (9) fingers long with vestigial webbing; (10) feet with complete webbing; (11) axillary membrane present, small; (12) thoracic fold present; (13) dark face mask present, extending from corner of mouth, through eye, and converging at symphysis of upper jaw (Fig. 2).

Hyla ameibothalame may be distinguished from all other species of the *H. bistincta* group, with the exception of *Hyla crassa*, by having complete webbing on the feet. *Hyla ameibothalame* differs from *H. crassa* by having thinner skin, by reaching a smaller adult size (maximum SVL 43.0 mm versus 56.5 mm; Caldwell, 1974), and by having the tympanum distinctly visible (partially, or almost entirely obscured by flesh in *H. crassa*). *Hyla miotympanum* bears a superficial resemblance to *H. ameibothalame* and occurs in the same general area; however, it differs from the



FIG. 1.—*Hyla ameibothalame* in life. Adult male paratype (EBUAP 1026) from the type locality; 41.4 mm SVL. Photograph by L. Canseco-Márquez.

latter species by reaching a smaller size (adult males only to 38.4 mm; Duellman, 1970), having less webbing on the feet, and a small, indistinct tympanum.

Hyla ameibothalame is most similar in superficial appearance to various species in the *Hyla eximia* group (sensu Duellman, 1970; condition described in parentheses), but differs from all of these species by having a dark face mask which both converges at the symphysis of the upper jaw and extends to the corner of the mouth (does not converge anteriorly, extends directly onto lateral surface of body, not descending to corner of the mouth); coloration of the labial area not continuous with coloration of the forelimb (coloration of labial area extends onto the forelimb); having complete webbing on the feet (webbing on feet extending only about half length of digits); anal opening directed posteroventrally at midlevel of thigh (near or at the upper lev-

el of the thigh); the quadratojugal absent (quadratojugal present). The tadpole of *H. ameibothalame* differs from those of the *H. eximia* group by having the following: a complete row of fringing papillae on the anterior margin of the oral disc (anterior row absent); body elongate with low caudal fins (body rotund, with high caudal fins); enlarged row of posterior submarginal papillae (enlarged submarginal row absent).

Description of holotype.—Adult male, body robust; width of head less than width of body; head width 33.7% SVL; head length 31% SVL; head slightly wider than long; snout truncate in profile, rounded in dorsal view, without rostral keel; canthus rostralis angular; loreal region flat; nostrils ovoid, directed laterally; internarial region flat. Top of head flat; interorbital distance 32.8% head width; diameter of eye 30.6% width of head. Supratympanic fold dis-

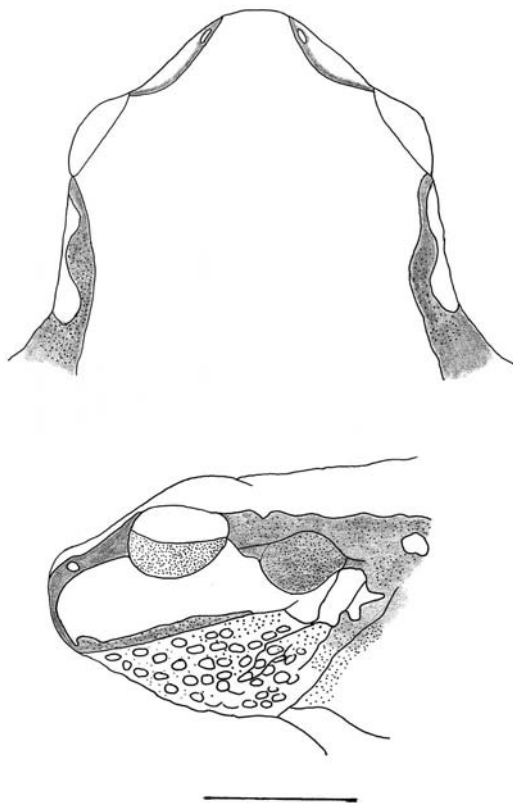


FIG. 2.—Dorsal and lateral aspects of the head of the holotype of *Hyla ameibothalame*. Stippling and shading represents color pattern; scale bar = 5 mm.

tinct, thick, extending posteroventrally from posterior corner of orbit, becoming indistinct at level of insertion of forearm; tympanum distinct, round, annulus indistinct; diameter of tympanum 59.5% diameter of eye.

Axillary membrane present, small; thoracic fold present; dermal fold on wrist present. Fingers long, slender (Fig. 3), with broad lateral fringe, bearing ovoid terminal discs; relative lengths of fingers I < II < IV < III; discs on Fingers II, III, IV equal in size, smaller than diameter of tympanum; disc on Finger I smaller than discs on other fingers. Subarticular tubercles large, diameter 75% diameter of disc on Finger I, rounded, elevated, none bifid; supernumerary tubercles smaller than subarticular tubercles, rounded, elevated; prepollical tubercle large, elliptical, about three times size of subarticular tubercles;

large palmar tubercles flat, bifid; nuptial excrescences extensive, composed of fine, brown spines, located on ossified, enlarged, blunt prepollex and inner surface of Fingers I and II; a few nuptial spines present on medial lateral fringe of Finger III, near terminal disc and lateral surface of distal subarticular tubercle on Finger IV; distinct row of ulnar tubercles present, round, subconical; webbing on hands vestigial. Heels of adpressed hindlimbs overlap; tibiotarsal articulation extending to snout; tarsal fold present, extending entire length of tarsus; tibia length 49.2% SVL; foot length 44% SVL; inner metatarsal tubercles, large, elongate, two times size of subarticular tubercles; outer metatarsal tubercle absent; distinct, large subarticular tubercles rounded, elevated, diameter about one-half width of terminal disc on same toe; small, flat supernumerary tubercles barely evident, rounded; toes long, slender, with broad lateral fringe, bearing ovoid discs same size as discs on finger; webbing on toes: **I1—1III1—2III1—2IV2—IV** (Fig. 3).

Anal opening directed posteroventrally at midlevel of thigh; cloacal sheath short. Skin on dorsum smooth; skin on throat, belly, ventral surface of thighs, medial surfaces of forelimb and hindlimb granular; skin on ventral surface of forelimb with distinct, large granules, extending to level of nuptial excrescence; tongue large, broadly cordiform, barely free posteriorly; vomerine teeth 6/5, narrowly separated medially, situated on transverse processes at midlevel of choanae; choanae ovoid, widely separated. Vocal slits absent.

Measurement (in millimeters): SVL 40.6, tibia length 20, foot length 17.9, head length 12.6, head width 13.7, diameter of tympanum 2.5, diameter of eye 4.2, interorbital distance 4.5, distance eye–tympanum 1.3.

Variation.—Variation in body measurements among seven males and one female of *Hyla ameibothalame* is summarized in Table 1; this series of *H. ameibothalame* does not exhibit marked sexual dimorphism. Webbing formula on the feet in the single female is **I1½—2½III1—2½III1½—2½IV2½—1½V**. The male paratypes close-

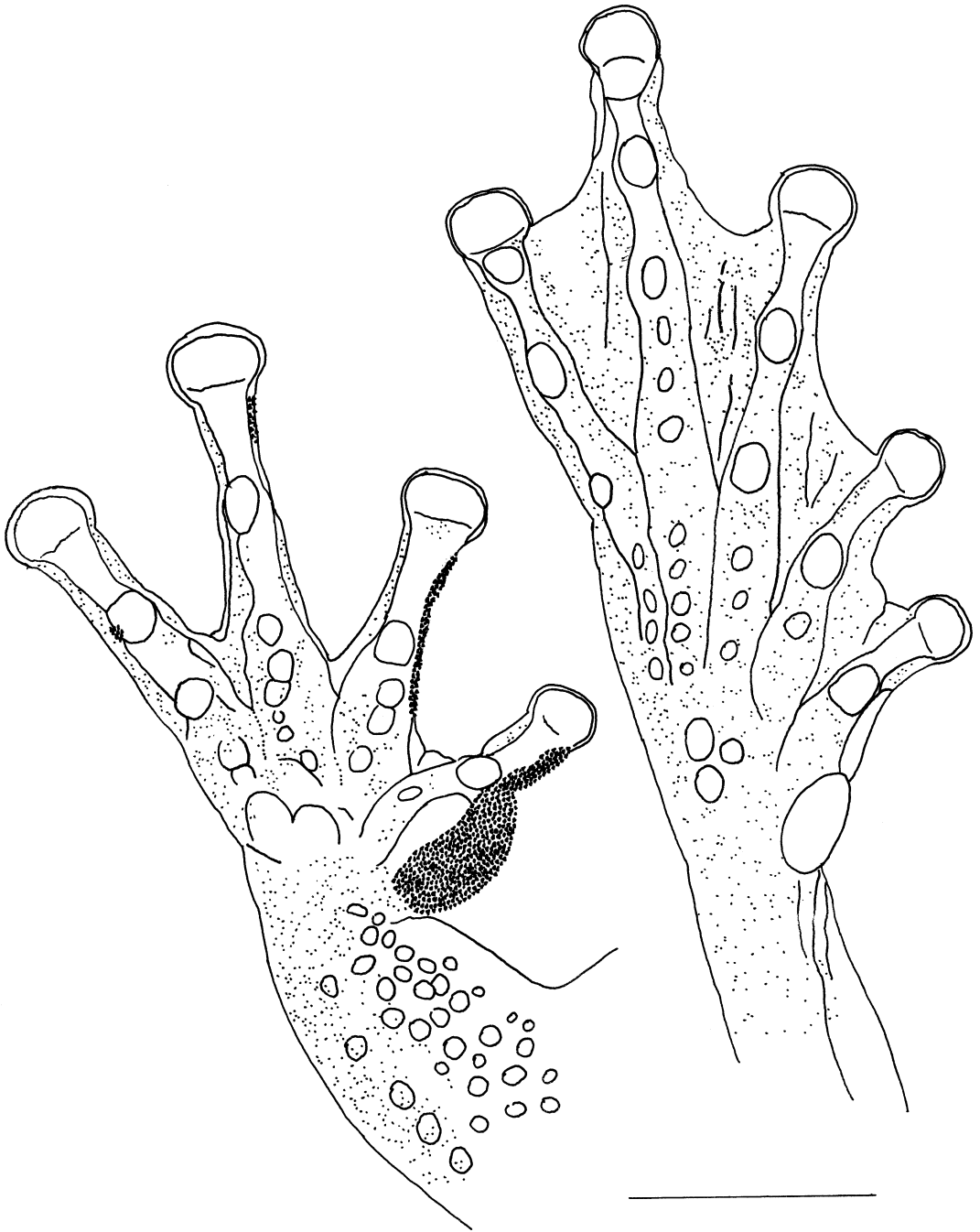


FIG. 3.—Ventral aspects of the hand and foot of the holotype of *Hyla ameibothalame*. Stippling represents distribution of dark pigments on the ventral surfaces of hand and foot; scale bar = 5 mm.

TABLE 1.—Morphometric variation in *Hyla ameibothalame*; range, followed by mean in parentheses.

Measurement	Males (n = 7)	Female (n = 1)
SVL	39.5–43.1 (41.3)	43.1
Head width	13.4–15.3 (14.1)	15.1
Head length	11.9–13.2 (12.6)	11.9
Foot length	17.3–18.4 (17.8)	19.0
Tibia length	20.0–21.7 (20.9)	22.1
Diameter of tympanum	2.1–2.6 (2.3)	2.6
Diameter of eye	4.2–4.4 (4.2)	4.4

ly resemble the holotype in all aspects except that the webbing on the foot of one male (EBUAP 1025) is as follows: **I**½—**2III**½—**2½III**½—**2IV**2—**2½V**; Two males (EBUAP 1025, 1026) lack distinct row of ulnar tubercles.

Coloration in life.—The coloration of all dorsal surfaces bright green; dorsal coloration of forelimbs not continuous with coloration of dorsum of body, separated by dark brown lateral stripe; dark brown lateral stripe extending from the snout, through the eye, tympanum, and supratympanic fold onto the flanks; lateral stripes converge on the snout, extend ventrally to the lip, continuous with narrow dark brown labial stripe; dark brown stripe is present on the anterior and posterior surface of thighs. A faint white anal stripe is present and a narrow white labial stripe is present above a dark brown labial stripe; terminal discs on the digits greenish yellow. Ventral surfaces of body cream; throat cream with peripheral areas gray. Inguinal areas and webbing on feet greenish yellow; iris gold. One paratype (EBUAP 1026) has fine cream lines extending along the ventral surfaces of the arms.

Coloration in preservative.—All dorsal surfaces dull bluish gray; lateral surfaces including flanks, tympanum, anterior and posterior surfaces of the thighs, fingers, and webbing dull gray; other colors similar to animals in life.

Cranial osteology.—The following description is based on the examination of a single cleared and stained specimen male (EBUAP 918). Frontoparietals widely separated medially throughout their length; frontoparietal fontanelle present, large, ovoid. Nasals long, slender, separated me-

dially, not overlapping or touching sphenethmoid; quadratojugal absent; anterior arm of squamosal not extending more than one-half the distance to maxillary; teeth present on maxillary, premaxillary and prevomer; prevomerine teeth spatulate, small; maxillary and premaxillary teeth long, some slightly recurved.

Tadpole.—From a stream at the type locality, we collected a series of hylid tadpoles referable to the *H. bistincta* group because they have a continuous row of fringing papillae on the upper lip and submarginal papillae medial to the fringing row. We refer these tadpoles to *H. ameibothalame* because they are the only hylid tadpoles that we found at the type locality; both the adults and tadpoles appear to be referable to the *H. bistincta* group. The following description is based on a series of five tadpoles collected on 17 December 1996 (EBUAP 1174) in Gosner Stage 27 (Gosner, 1960); format follows that of Ustach et al. (2000). Measurements (mm): total length 46.8–50.6 (\bar{x} = 49.1); body length 15.1–16.2 (\bar{x} = 15.6); tail length 31.6–34.5 (\bar{x} = 33.5); interorbital distance 3.1–3.4 (\bar{x} = 3.2); internarial distance 3.4–3.7 (\bar{x} = 3.5); oral disc diameter 5.1–6 (\bar{x} = 5.4). Tadpole is illustrated in Fig. 4 and mouthparts are illustrated in Fig. 5.

Body ovoid in dorsal view; in lateral view higher posteriorly than anteriorly; snout rounded in dorsal and lateral views; eyes moderate in size, directed dorsolaterally; interorbital distance slightly less than internarial distance; nostrils small, rounded, directed dorsolaterally. Spiracle sinistral, short, opening near midbody, slightly below midline. Vent tube dextral. Caudal musculature robust, highest at junction with body, pointed at tip; dorsal fin slightly higher than ventral fin; tip of caudal fin rounded.

Oral disc large, ventral in position, not emarginate, with complete single row of marginal papillae; single row of submarginal papillae present above A_1 , obscured by overhanging row of marginal papillae; two rows of submarginal papillae present below P_3 , one large and one small. Numerous papillae present laterally. Labial tooth row formula 2(2)/3, A_2 gap present,

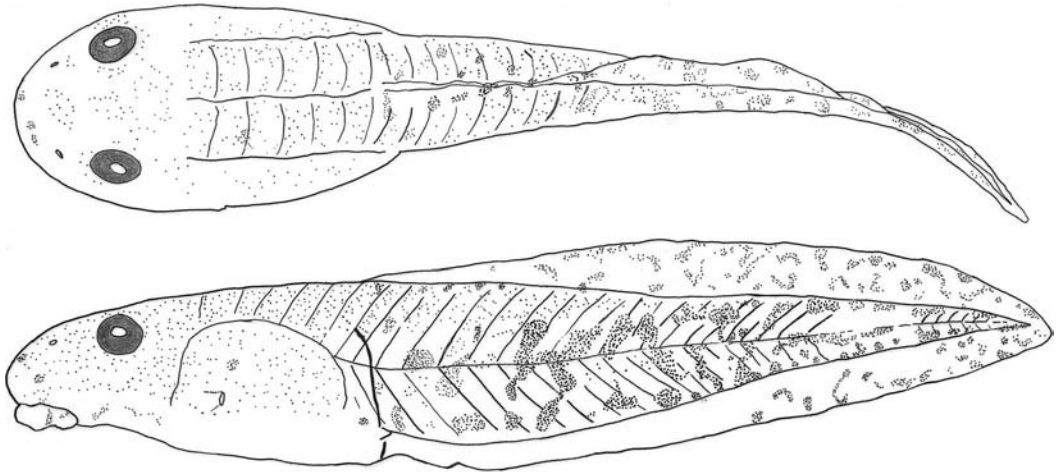


FIG. 4.—Dorsal and lateral views of the tadpole of *Hyla ameibothalame* (EBUAP 1174; Gosner Stage 27); scale bar = 5 mm.

narrow. Teeth in P_2 slightly longer than teeth in P_1 and P_3 . Upper jaw moderately wide, lateral processes taper abruptly posterolaterally; lower jaw shallowly V-shaped; both jaws finely serrate.

In preservative dorsum pale gray; venter transparent, gut visible; caudal musculature cream with irregular golden spots; caudal fins opaque with irregular golden flecks.

Distribution and ecology.—*Hyla ameibothalame* is known only from two localities in northwestern Oaxaca: Yosocuno and near Nativitas. This region is known as the Mixteca Alta, and is covered by oak and pine-oak forests; the specific localities

where *Hyla ameibothalame* has been found are pure oak forests (Fig. 6). Known elevational range is 2455–2670 m. Oak trees at the type locality are covered with pendant lichens and arboreal bromeliads. Clouds usually cover the area in the afternoon during the rainy season and are usually absent during the dry season. During the dry season (December 1996), we found three specimens (EBUAP 918–20) by day taking refuge on leaves or in the central axes of arboreal bromeliads about 2–3 m above the ground. However, during the rainy season (July 1998), no specimens were seen in the bromeliads, but rather were found taking refuge among leaves of agaves (EBUAP 1023–26). Perhaps the frogs shift microhabitat in the rainy season because, at this time, the bromeliads are full of water. In contrast to what we have typically seen in this species, the female specimen (MZFC 7480) was found in an arboreal bromeliad near Nativitas in the rainy season (July 1995). We also found individuals of the anigid lizard *Abronia mixteca* in some bromeliads with *H. ameibothalame*. The tadpoles that we refer to *H. ameibothalame* were taken from a small stream near Yosocuno in December; in this stream, we also collected tadpoles of *Bufo occidentalis* (the only other amphib-

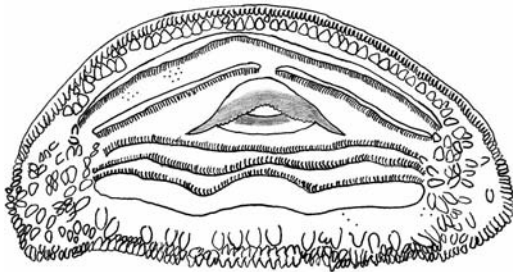


FIG. 5.—Mouthparts of the tadpole of *Hyla ameibothalame* (EBUAP 1174; Gosner Stage 27); scale bar = 1 mm.



FIG. 6.—Habitat of the type locality, showing the *Agave* used by *Hyla aneibothalame* for refuge during the rainy season. The oaks in the background are laden with pendant lichens and abundant arboreal bromeliads, the latter of which are used by these frogs as refuges during the dry season.

ian that we encountered at the type locality).

Males collected in July 1998 have well developed nuptial excrescences and appear to be in breeding condition. However, we heard no advertisement calls produced by this species. The eggs and breeding behavior are unknown.

Etymology.—The specific epithet is formed from the Greek *ameibo*, meaning to change, and *thalame*, meaning den or resting-place, and refers to this frog's habit of switching between bromeliads and agaves during the dry and wet season, respectively.

Remarks.—The Mixteca Alta covers an area of 12,900 km² in the northwestern part of the state of Oaxaca and includes the political districts of Silacayoapan, Huajuapán, Coixtlahuaca, Juxtlahuaca, Teposcolula, Nochixtlán, and part of Tlaxiaco (Fig. 7). In this area, the Sierra Madre del Sur and the Sierra de Oaxaca converge and become known as the Nudo Mixteco.

The Valle de Nochixtlán is the largest in the region and constitutes the heart of the region. Some peaks in the area reach elevations of 3000 m, and the area is generally characterized by steep escarpments, broad valleys, and deep canyons. Many streams drain the area as tributaries of the Río Verde (this river is locally known as Río Atoyac, Blanco, Nochixtlán, Yanhui-tlán, Sinaxtla, Etlatongo, and Yodocono). The southeastern area of the District of Teposcolula is dominated by forests of stunted oaks.

The amphibian fauna of the Mixteca Alta is poorly known. Campbell and Duellman (2000) reported specimens of *Hyla sumichrasti* from 25.5 km south of Nochixtlán. At San Miguel Huautla, we also found *H. euphorbiacea* and tadpoles possibly referable to *H. bistrincta*. We found *H. miotympanum* along creeks at relatively low elevations in an oak forest at San Miguel Huautla (1980 m) and Santiago Apoala (2035 m). At a locality 7.5 km SE of

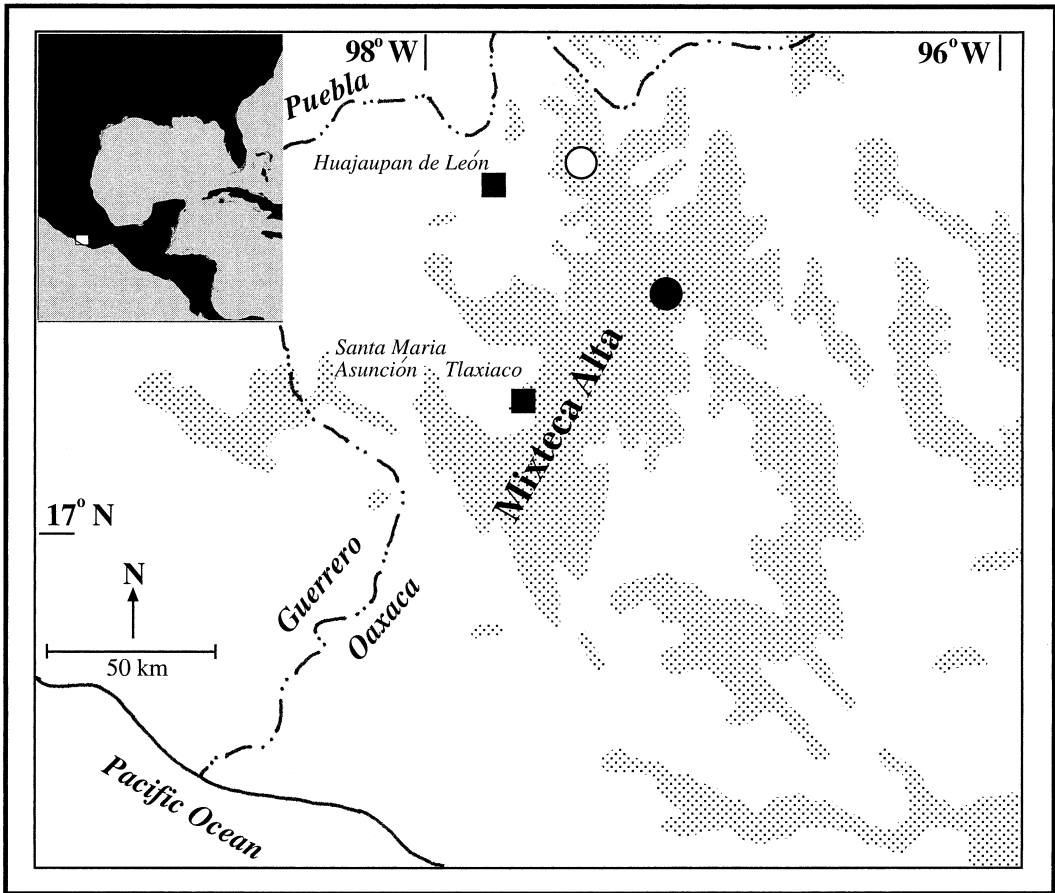


FIG. 7.—Generalized map of northwestern Oaxaca, showing the Mixteca Alta. The circles indicate the known localities for *Hyla ameibothalame*; the type locality is indicated in white. Gray pattern indicates elevations above 2000 m.

Llano de Guadalupe, we found a single specimen of *Hyla cembra* (Mendelson and Canseco-Marquez, in press).

The key presented by Duellman (2001) does not contain *H. ameibothalame*. If a specimen of *H. ameibothalame* is in hand, Duellman's key will lead to Couplet 64. At this couplet, the investigator will be faced with the choice of referring the specimen to *H. chryses* or *H. calthula*. *Hyla ameibothalame* differs markedly from both of these species by having a uniform green dorsum in life (bluish gray in preservative) and a distinctive dark brown face mask (Figs. 1, 2). Duellman (2001) presented a review of the *H. bistincta* group and a hypothesis of phylogenetic relationships among the species. We were unable to du-

PLICATE Duellman's (2001) analysis using his published data matrix (Duellman, 2001:table 80), but our preliminary analyses using that matrix suggest that *H. ameibothalame* may be closely related to several other thin-skinned species presently referred to that group (viz., *H. sabrina*, *H. chryses*, and *H. charadricola*); Duellman's (2001:fig. 400) hypothesis showed these three species forming a monophyletic group. However, we note that attempts to recover the phylogeny of the *H. bistincta* group are hampered at this point because, as Duellman (2001) pointed out, of a real lack of sources of data (e.g., tadpoles and/or skeletal specimens of several species, material for DNA analyses). Finally, although the close relationship of the *H. bis-*

tincta group with *Plectrohyla* seems well supported (Duellman, 2001; Duellman and Campbell, 1992), we note that the monophyly of the *H. bistincta* group (sensu Duellman, 2001) itself has yet to be rigorously tested.

RESUMEN

Una nueva especie del género *Hyla* es descrita para los bosques de encino de la Mixteca Alta al noroeste de Oaxaca, esta es ubicada tentativamente dentro del grupo fenético *Hyla bistincta*. La nueva especie es similar en el patrón de coloración a aquellas del grupo *Hyla eximia*, pero se pueden distinguir en que *Hyla ameibothalame* carece de cuadratoyugal.

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APPENDIX I

Specimens Examined

- Hyla arborescandens*.—MEXICO: Puebla: Zoquitlán, Sierra Negra (EBUAP 668–80).
- Hyla bistincta*.—MEXICO: Puebla: Zoquitlán, Sierra Negra [EBUAP 664–66, 667 (skeleton)].
- Hyla euphorbiacea*.—MEXICO: Oaxaca: Llano de las Flores, 3150 m (KU 71189, 71207–215); Llano de las Flores, 2800 m (KU 129164–68); Mixteca Alta, Laguna El Chicle (EBUAP 1189–97). Puebla: Zoquitlán, Sierra Negra (EBUAP 656–57, 659–60, 662–63); Chapulco (EBUAP 658).
- Hyla miotympanum*.—MEXICO: Oaxaca: Mixteca Alta: 500 m E San Miguel Huautla (EBUAP 1910–14); 4 km N San Pedro Jocotipac (EBUAP 1915–16); Santiago Apoala (EBUAP 1909).
- Hyla ameibothalame*.—MEXICO: Oaxaca: Mixteca Alta: 1 km S Yosocuno, Municipality of San Pedro Nopala (EBUAP 1024 [holotype], 1023, 1025–26); El Polvorin, 5 km E Yosocuno (EBUAP 918, cleared and stained skeletal specimen); 2 km SE Yosocuno (EBUAP 919–20); Yosocuno (EBUAP 1174, 5 tadpoles); about km 156, road new Tehuacán–Oaxaca (MZFC 7480).
- Hyla plicata*.—MEXICO: Puebla: 9 km NE Acazingo (KU 37839).