HYLID FROGS OF THE GENUS *PLECTROHYLA*: SYSTEMATICS AND PHYLOGENETIC RELATIONSHIPS

BY

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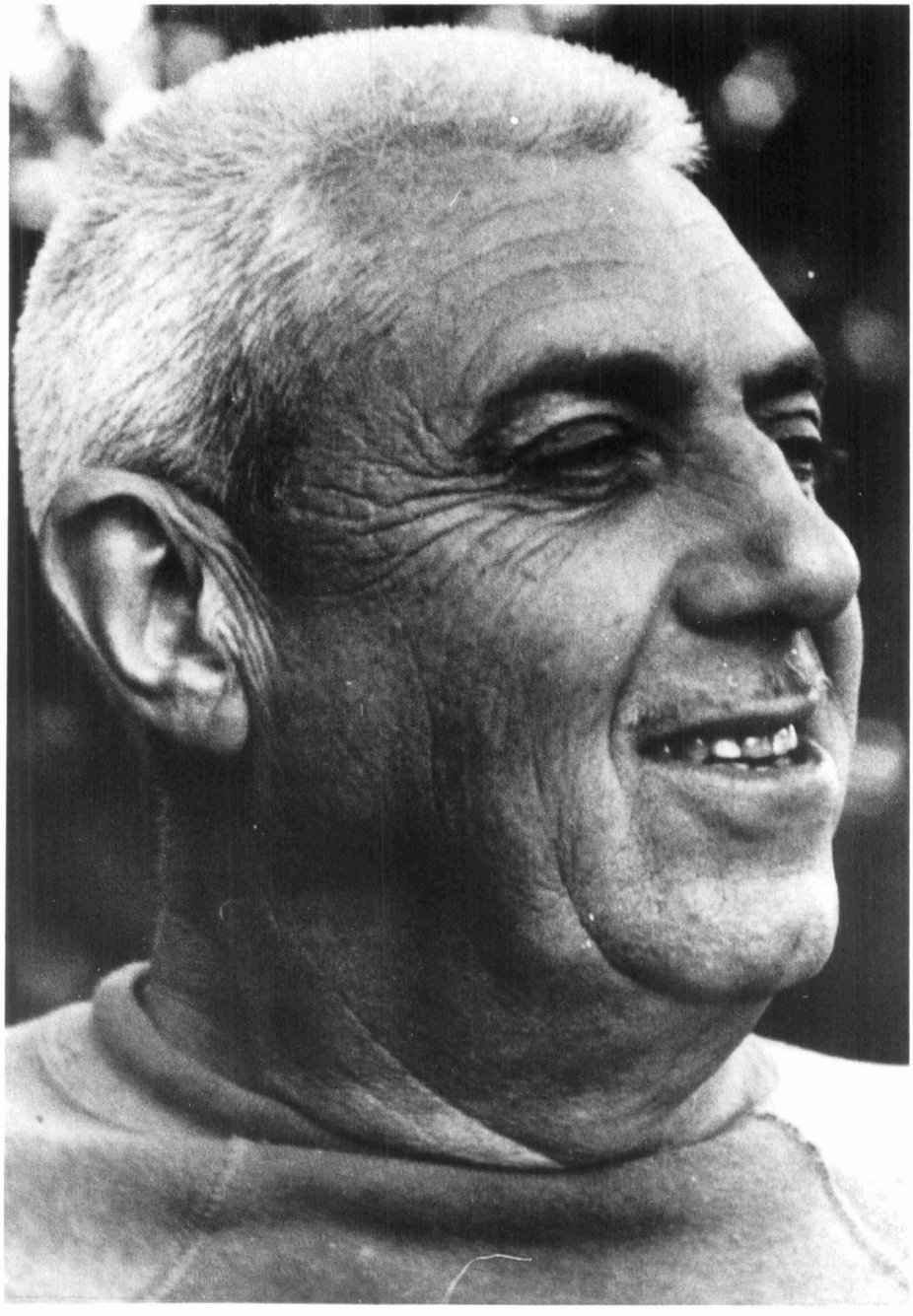

Hylid Frogs of the Genus *Plectrohyla:* Systematics and Phylogenetic Relationships

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ABSTRACT

Duellman, W.E. and J.A. Campbell. 1992. Hylid frogs of the genus Plectrohyla: *Systematics and phylogenetic relationships. Misc. Publ. Mus. Zool. Univ. Michigan, 181:1–32, 22 figs.* Fifteen species are recognized in *Plectrohyla,* including two new species: *P. acanthodes* from Chiapas, Mexico, and *P. teuchestes* from Alta Verapaz, Guatemala. *P. guatemalensis, P. hartwegi,* and *P. lacertosa* are redescribed. Keys are provided for the identification of adults and tadpoles. A phylogenetic analysis shows that the *Hyla bistincta* group is the sister-group to *Plectrohyla,* which is diagnosed by six synapomorphies. Intrageneric relationships within *Plectrohyla* have been only partially resolved. Four sets of sister species are identified: (1) *P. ixil* + *P. matudai,* (2) *P. quecchi* + *P. sagorum,* (3) *P. acanthodes* + *P. guatemalensis,* and (4) *P. hartwegi* + *P. teuchestes.* These four lineages form a polytomy with the remaining seven species. Males of at least some species of *Plectrohyla* seem to be territorial and engage in combat with other males.

Key words: *Anura, Hylidae,* Plectrohyla, Hyla bistincta *group, new species, phylogenetic relationships, biogeography, breeding behavior, reproduction.*

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INTRODUCTION

The frog family Hylidae provides a fertile field of investigation for systematists. The group is extremely speciose, with 35 recognized genera and more than 660 species (updated from Frost, 1985). Genera and species groups within the large, paraphyletic genus *Hyla* have been recognized traditionally on the basis of overall similarity. Although some of these genera probably are monophyletic, most are assemblages of species that share distinctive characters that separate them from *Hyla*.

The great number of hylid species, mostly of unknown phylogenetic relationships, hinders phylogenetic analyses because of the difficulty of determining meaningful outgroups within the family. Nevertheless, some progress has been made in phylogenetic analyses of morphological characters of some groups (e.g., *Flectonotus* and *Fritziana* by Duellman and Gray, 1983; *Ptychohyla* by Duellman and Campbell, 1982, and Campbell and Smith, 1992; and *Stefania* by Duellman and Hoogmoed, 1984). Phylogenetic analyses of other groups have been based on biochemical data (Hedges, 1986; Duellman and Hillis, 1987).

Although many external features of frogs, particularly hylids, are difficult to characterize for phylogenetic analyses, anuran systematists are slowly amassing evidence necessary for the incorporation of these characters into phylogenetic analyses. Likewise, as more is learned about larval features, characteristics of tadpoles have been found to be useful (e.g., groups of South American *Hyla* by Duellman and Trueb, 1983). Perhaps the most useful suite of characters are to be found in the skeletons, as demonstrated for African ranines by Clarke (1981) and for pipids by Cannatella and Trueb (1988).

For half a century a group of Central American hylids has been recognized as a distinctive genus, *Plectrohyla* (Hartweg, 1941; Hartweg and Orton, 1941). Additional species were described by Stuart (1942, 1948a, 1952). The genus was reviewed by Duellman (1970), who recognized ten monotypic species. Subsequently, McCranie and Wilson (1981) named *P. dasypus* from Honduras, and Duellman and Campbell (1984) named *P. pokomchi* and *P. tecunumani* from Guatemala and noted that "*P. guatemalensis*" was a composite. Frogs of the genus *Plectrohyla* are inhabitants of cold mountain streams in the uplands of nuclear Central America from extreme eastern Oaxaca, Mexico, through Guatemala to central Honduras and northern El Salvador.

During the course of our independent field studies in Central America and study of specimens of *Plectrohyla,* we became aware of suites of characters that diagnosed *Plectrohyla* and groups of species within that genus. Accordingly, herein we (1) review the taxonomy of the species of *Plectrohyla;* (2) describe two new species in the *Plectrohyla guatemalensis* group; (3) provide new data on *P. guatemalensis* and *P. hartwegi;* (4) report on life history phenomena in the genus; (5) propose a partial phylogeny of *Plectrohyla* based on morphological characters; and (6) interpret some aspects of the biogeography of the genus based on the partial phylogeny of the frogs and the history of nuclear Central America.

Frogs of the genus *Plectrohyla* greatly interested the late Laurence C. Stuart, certainly one of the most colorful biologists ever associated with the Museum of Zoology of The University of Michigan. During his extensive field work in Guatemala, Stuart gathered many important data on *Plectrohyla* and discovered three new species. "Don Pancho" Stuart was very influential in our respective development in systematic herpetology; in grateful appreciation we dedicate this publication to his memory.

ACKNOWLEDGMENTS

We are indebted to Robert F. Inger, Arnold G. Kluge, Carl S. Lieb, Jens V. Vindum, David B. Wake, and John W. Wright for the loan of critical specimens. We are especially grateful to James R. McCranie and Larry David Wilson for providing many specimens from Honduras. We thank Gretchen Bracher and Anne A. Musser for their fine illustrations, John E. Simmons for the photographic prints, Ronald Altig for alerting us to the existence of an uncatalogued collection containing specimens of *Plectrohyla,* Darrel R. Frost for assistance with the phylogenetic analysis, and Linda Trueb for many helpful suggestions. Campbell's field work in Guatemala was supported by the Watkins Fund, Museum of Natural History, The University of Kansas, and the Organized Research Fund of The University of Texas at Arlington. We also thank the late L.C. Stuart for generous support. Collecting permits were provided by officials of the Comisión Nacional del Medio Ambiente (CONAMA) and the Instituto Nacional Forestal (INAFOR) of Guatemala and the Dirección General de Flora y Fauna Silvestres of Mexico.

MATERIALS AND METHODS

The data on which this study is based were obtained from 795 preserved frogs, 28 skeletons, 3 lots of eggs, 145 lots of tadpoles, and 30 lots of young. Museum specimens are identified by the standardized symbolic codes given by Leviton et al. (1985). Measurements and other morphological data follow the definitions of Duellman (1970). Snout-vent length is abbreviated SVL. All statistical analyses were accomplished through the use of Biomedical Computer Programs (Dixon, 1981). Morphological characters were ordered into transformation series using the out-group method (Hennig, 1966) as codified by Watrous and Wheeler (1981). Phylogenetic analysis was accomplished by using the computer programs PAUP (Phylogenetic Analysis Using Parsimony, Version 2.4; Swofford [1990]) and HENNIG86 (Version 1.5; Farris, 1988). Tadpoles were staged according to Gosner (1960). The distribution maps are based on specimens reported by Duellman (1970) and specimens examined subsequently.

TAXONOMY

Genus *Plectrohyla* Brocchi

Plectrohyla Brocchi, 1877a:92.—Type species: *Plectrohyla guatemalensis* Brocchi, 1877a, by original designation.

Cauphias Brocchi, 1877b:129.—Substitute name for *Plectrohyla* Brocchi, 1877a.

Diagnosis.—(1) Medium to large hylid frogs (adults 44–90 mm in SVL) with robust bodies; (2) alary process of premaxilla bifurcate; (3) sphenethmoid ossified anteriorly so as to include the septum nasi; (4) prefrontals abutting anteri-

orly and posteriorly along midline exposing ovoid frontoparietal fontanelle; (5) medial ramus of pterygoid articulating with otic capsule; (6) prepollex enlarged and ossified in both sexes; (7) skin on dorsum of head and body thick; (8) fingers long with little or no webbing and large, round, terminal discs; (9) toes extensively webbed; (10) snout short, blunt in profile; (11) forelimbs hypertrophied in breeding males; (12) tadpole with moderately depressed body and long, muscular tail with moderately shallow fins; (13) larval oral disc completely fringed with papillae, one or more rows of large papillae medial to fringing papillae, no lateral folds, and two upper and three lower tooth rows.

The bifurcate alary processes of the premaxillae are unique among hylid frogs. The only other hylids in Middle America that might be confused with species of *Plectrohyla* are members of the *Hyla bistincta* group, males of which have enlarged, rounded prepollices (elongate, spine-like, or bifid in *Plectrohyla*). Other hylids in which the prepollex is modified into a spine-like structure are members of the *Hyla boans* group, which have relatively long snouts, broad and flat heads, and relatively short fingers with extensive webbing. The only other New World hylids that approach *Plectrohyla* in general appearance are species in the *Hyla larinopygion* group in the Andes of Colombia and Ecuador; in those species, the ossified prepollex is broad and elliptical, the vomerine odontophores are transverse and abut medially at a level behind the choanae (short and not abutting in *Plectrohyla*), and the tadpoles have huge oral discs with as many as eight upper and nine lower labial tooth rows (Duellman and Hillis, 1990).

DISTRIBUTION.—Frogs of the genus *Plectrohyla* are restricted to the uplands (615–3500 m) of Nuclear Central America. They occur from southern Mexico (Sierra Madre of extreme southeastern Oaxaca and Chiapas and the Meseta Central of Chiapas) through the highlands of Guatemala and northern El Salvador to north-central Honduras.

CONTENT.—Fifteen species are recognized, two of which are named and described herein.

REMARKS.—Duellman and Campbell (1984) noted that *P. guatemalensis* seemed to be a composite of three species. Gross comparisons of specimens revealed that they could be separated into three geographic groups—Alta Verapaz, Guatemala (11 adults); central and southern highlands of Guatemala and adjacent El Salvador and Honduras (29 adults); and Meseta Central in Chiapas, Mexico, and the adjacent Sierra de los Cuchamatanes, Guatemala (19 adults). Seven measurements were recorded for these adults (Table 1) and for 45 *P. hartwegi* from Baja Verapaz, Guatemala, and eight *P. pokomchi* from Baja Verapaz, Guatemala. These represent all of the discernible populations of *Plectrohyla* having bifid prepollices.

Morphometric data from all five samples were subjected to a stepwise discriminant analysis. The results showed good separation except that the dispersion of *P. pokomchi* overlapped those for the samples of *P. guatemalensis* from (1) Central Highlands of Guatemala and (2) Meseta Central of Chiapas and the Sierra de los Cuchamatanes. The data for *P. pokomchi* were deleted from the data set, and a reanalysis provided significant discrimination in a 3-step model (Fig. 1), based on tibia length, head length, and eye diameter. In the jack-knifed classification, 98.1% of the specimens were classified into their *a priori* groups. One specimen from the Meseta Central-Cuchumatanes group (UMMZ 94432) was misclassified as belonging to the Central Highlands group. A second specimen (UTA A-5365) was placed erroneously in the Central Highlands group and was identified subsequently as *Plectrohyla pokomchi.*

This 3-step model using four groups of specimens separates *P. hartwegi* and the sample from Alta Verapaz on the basis of their having longer feet and longer heads in comparison with the other samples (Fig. 1, Canonical Axis I). A similar, but not so great, discrimination exists between the samples from the Central Highlands and the Meseta Central-Cuchumatanes. The major variation described by Canonical Axis II (Fig. 1) is a smaller eye diameter in *P. hartwegi,* as compared with specimens from Alta Verapaz.

The discriminant analysis of morphometric data supports our contention based on skin texture and coloration that specimens previously referred to *P. guatemalensis* represent three species. Only one name, *P. guatemalensis,* is available for these frogs, and it applies to the species inhabiting the Central Highlands of Guatemala. Accordingly, we provide names and descriptions for the other species.

Brief diagnoses, including numbered comparable statements, are provided for each of the 15 species, together with a statement of distribution and any pertinent remarks. Full descriptions are provided only for the two new species, for *P. guatemalensis* in its present restricted definition, *P. hartwegi* previously known from only a few specimens, and *P. lacertosa* previously known only from the holotype. For full descriptions of the other species, see Duellman (1970), McCranie and Wilson (1981), and Duellman and Campbell (1984). Campbell and Kubin (1990) provided a description of the tadpole of *P. avia.*

Plectrohyla ***acanthodes*** new species

HOLOTYPE.—KU 58824, an adult male, from a stream 6.2 km (by road) S of Rayón Mescalapa, 1690 m, Chiapas, Mexico (17°10′N, 92°58′W), one of a series collected on 5 August 1960 by William E. Duellman and John Wellman.

PARATYPES.—Nine males and five females, all from Chiapas, Mexico (see Appendix).

DIAGNOSIS.—(1) Maximum SVL 63.2 mm in males, 62.3 mm in females; (2) prepollical spine bifid; (3) tubercles present on dorsal surfaces of head and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum dull olive-green or dull gray with large, pale, olive-green spots; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

The dorsal coloration immediately distinguishes this species from other *Plectrohyla* having bifid prepollices; *P. acanthodes* is most like *P. guatemalensis* in size and structure, but the latter differs by having closely packed, round tubercles on the dorsum, as contrasted with the scattered conical tubercles in *P. acanthodes.*

DESCRIPTION.—Body moderately slender; average SVL 56.2 mm in males, 56.8 mm in females (Table 1); head slightly wider than long, slightly narrower than body; snout short, round in dorsal view, bluntly rounded in profile; nos-

Table 1. Summary of morphometric data for the *Plectrohyla guatemalensis* group. First line = mean ± 1 standard deviation; second line = range.

Character	*P. acanthodes* 12 ♂♂	7 ♀♀	*P. guatemalensis* 16 ♂♂	13 ♀♀	*P. hartwegi* 20 ♂♂	25 ♀♀	*P. pokomchi* 7 ♂♂	1 ♀	*P. teuchestes* 6 ♂♂	5 ♀♀
SVL	56.2 ± 4.52	56.8 ± 2.92	47.5 ± 4.20	48.6 ± 4.83	68.6 ± 3.82	65.2 ± 5.09	51.4 ± 2.26	49.0	73.4 ± 3.82	70.4 ± 2.03
	48.2–63.2	54.0–62.3	40.0–52.1	42.1–54.1	54.0–62.3	53.6–76.6	48.0–55.2	—	72.1–76.1	68.4–73.6
Tibia length	28.7 ± 1.55	28.9 ± 1.02	24.6 ± 1.82	23.8 ± 2.20	36.4 ± 1.79	34.7 ± 1.79	26.8 ± 2.26	25.9	41.3 ± 0.47	39.4 ± 1.74
	25.0–31.0	17.6–30.5	20.5–26.4	20.6–27.5	33.7–40.7	32.4–39.5	25.3–28.3	—	40.7–42.1	37.5–41.7
Foot length	25.5 ± 1.56	26.4 ± 0.87	24.6 ± 1.97	21.8 ± 2.53	33.1 ± 1.54	30.9 ± 1.76	24.0 ± 0.64	24.7	35.8 ± 1.08	33.7 ± 0.82
	23.5–28.7	25.3–27.6	18.2–25.1	19.0–25.8	30.0–37.4	27.9–34.2	23.3–24.9	—	34.7–37.2	32.5–34.6
Head length	16.5 ± 0.96	16.8 ± 0.51	14.1 ± 0.82	14.3 ± 1.48	22.1 ± 0.99	22.1 ± 1.26	15.9 ± 0.34	15.8	20.9 ± 0.78	20.9 ± 1.01
	15.5–17.9	16.1–17.3	12.8–14.7	12.2–16.5	19.7–24.5	19.6–23.6	15.4–16.5	—	19.9–21.7	20.0–22.4
Head width	18.1 ± 0.93	18.5 ± 0.77	15.1 ± 0.97	15.0 ± 1.40	24.2 ± 1.06	22.9 ± 1.55	17.1 ± 0.24	17.7	25.2 ± 0.77	22.3 ± 1.10
	16.3–19.9	17.7–19.9	13.1–16.8	13.4–17.3	22.6–27.2	21.0–27.0	16.8–17.5	—	24.1–25.9	21.5–23.5
Eye diameter	6.1 ± 0.78	6.3 ± 0.82	4.6 ± 0.33	4.8 ± 0.51	6.6 ± 0.19	6.6 ± 0.51	5.2 ± 0.37	5.7	7.8 ± 0.31	8.1 ± 0.30
	4.8–7.5	5.5–7.7	4.0–5.1	4.1–5.7	5.8–7.1	5.8–7.7	4.7–5.7	—	7.0–8.5	7.8–8.6
Tympanum diam.	2.4 ± 0.26	2.1 ± 0.19	1.9 ± 0.18	1.9 ± 0.22	2.7 ± 0.36	2.7 ± 0.19	2.1 ± 0.33	2.6	2.6 ± 0.36	2.7 ± 0.27
	2.0–2.8	1.9–2.4	1.6–2.2	1.7–2.4	1.8–3.1	2.4–3.0	1.7–2.5	—	2.1–2.8	2.5–3.2

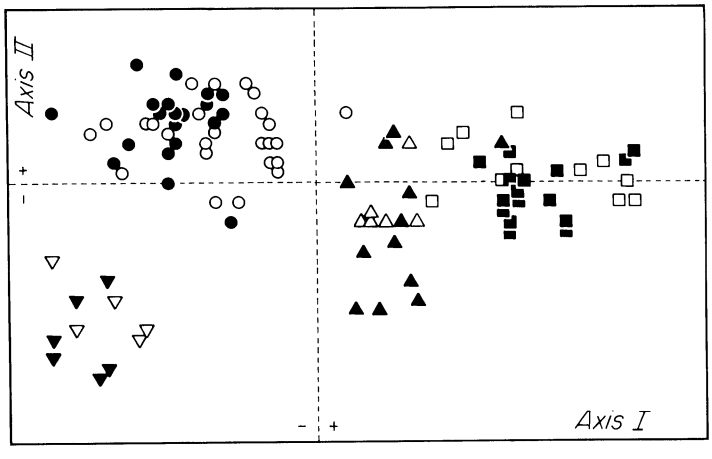

FIG. 1. Stepwise discriminant analysis of morphometric data for four samples of *Plectrohyla*. Squares = *P. acanthodes*, triangles = *P. guatemalensis*, circles = *P. hartwegi*, inverted triangles = *P. teuchestes*. Solid symbols are males; open symbols are females.

tril somewhat closer to tip of snout than to eye; eye-nostril distance about three-fourths diameter of eye; canthus rostralis angular, slightly curved; loreal region moderately concave; lips rounded in both sexes; interorbital and internarial areas flat; nostril barely protuberant anterolaterally; eye large; supratympanic fold heavy, extending from posterior corner of orbit to insertion of forelimb; tympanum and tympanic annulus barely evident; upper one-fourth of tympanum covered by supratympanic fold.

Upper arm and forearm slender in females, moderately robust in males; axillary membrane absent; row of small tubercles along ventrolateral edge of forearm; hand moderately large; fingers relatively short, bearing thick dermal fringes laterally and round discs terminally; diameter of disc on third finger equal to about 60% of diameter of eye; relative lengths of fingers 1<2<4<3; subarticular tubercles large, subconical; supernumerary tubercles small, conical, present only proximally; palmar tubercle low, flat, bifid; prepollex massive, bifid, lacking nuptial excrescences; webbing absent between first and second fingers; outer fingers about one-fourth webbed; webbing formula for outer fingers **II**2—3**III**3—2**V**. Hind limbs moderately long, robust; tibia length about 51% of SVL; foot length about 45% of SVL; outer tarsal fold absent; inner tarsal fold slightly curved, present only on distal one-half of tarsus; outer metatarsal tubercle small, conical; inner metatarsal tubercle large, flat, elliptical, visible in dorsal view; toes moderately long, slender, bearing discs slightly smaller than those on fingers; relative lengths of toes 1<2<3=5<4; subarticular tubercles large, round; supernumerary tubercles large, subconical; toes about three-fourths webbed; webbing formula **I**1—2**II**1—2**III**1—2**IV**2—1**V**.

Skin on all dorsal surfaces smooth with uniformly distributed conical tubercles; skin on throat, belly, and ventral surfaces of thighs granular; skin on ventral surfaces of arms and shanks smooth. Anal opening directed posteroventrally at midlevel of thighs, bordered laterally by dermal folds; anal tube short, bordered above by transverse dermal fold. Dentigerous processes of vomers strongly protuberant, narrowly separated medially, posteromedially inclined at posterior border of small, ovoid choanae, each bearing 3 or 4 teeth. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind; vocal slits and vocal sac absent.

Coloration in preservative: Dorsum dull dark brown with or without large, faint, pale spots; posterior surfaces of

thighs, flanks, and webbing brown; venter dull creamy tan; males with brownish suffusion on chest and dark brown on throat.

Coloration in life: Dorsum dull olive-green or dull gray with large olive-green spots; venter and webbing grayish white; iris pale bronze with greenish tint (Fig. 2). The juveniles are paler than the adults. In life, the dorsum was pale olive-green with or without paler green spots; the posterior surfaces of the thighs were yellow, and the throat and chest were silvery green.

Measurements: Morphometric data are summarized in Table 1. Measurements (in mm) for the holotype are: SVL 58.3, tibia length 29.2, foot length 25.8, head length 16.2, head width 18.3, diameter of eye 6.0, diameter of tympanum 2.0.

TADPOLES.—A series of 13 tadpoles (KU 60031–33) is available from the vicinity of the type locality (Table 2).

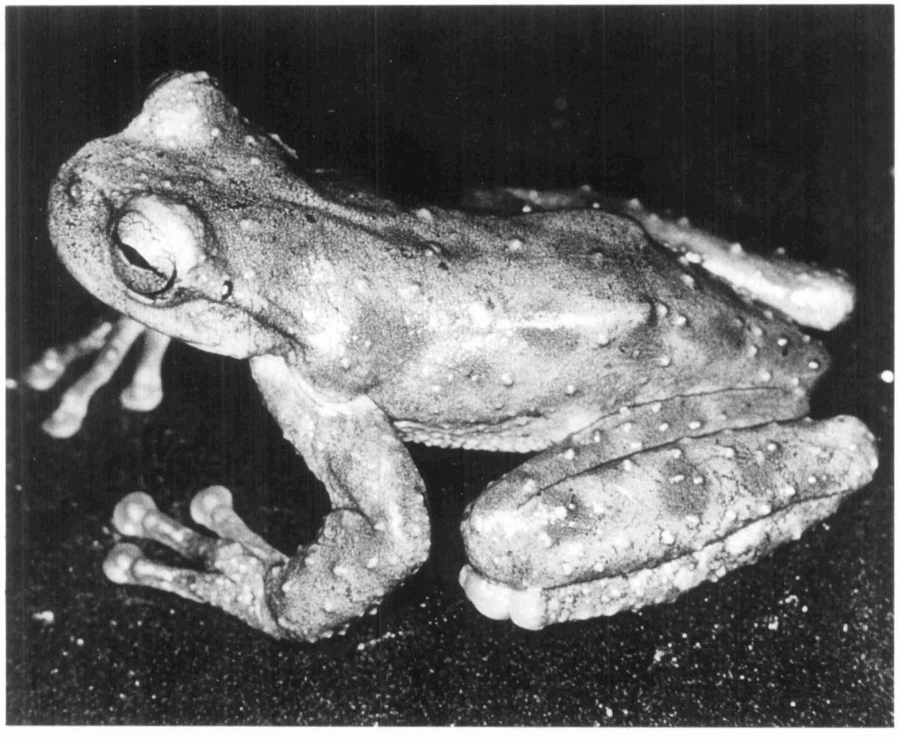

FIG. 2. *Plectrohyla acanthodes*, KU 58822, male, 55.4 mm SVL.

Table 2. Measurements of tadpoles of *Plectrohyla acanthodes*. Means in parentheses.

Stage	N	Body length (mm)	Total length (mm)
25	6	11.9–16.4 (14.3)	30.8–40.4 (35.8)
28–29	2	16.0–17.5 (16.8)	41.2–46.8 (44.0)
37–39	2	18.2–18.4 (18.3)	48.0–48.4 (48.2)
40–42	3	18.8–19.0 (18.9)	50.0–52.7 (51.1)

Body slightly depressed, wider than deep; snout in dorsal view bluntly rounded, nearly truncate; snout in profile bluntly rounded; posterior edge of body gradually rounded in dorsal view; eyes moderately small, widely separated, directed laterally; nostrils directed anterolaterally at point midway between eyes and tip of snout. Opening of sinistral spiracle directed posterodorsally on midline at about midlength of body; anal tube short, dextral. Caudal musculature moderately robust, not extending to tip of bluntly rounded tail; depth of caudal fins equal to depth of caudal musculature at midlength of tail; dorsal fin originating on posterior part of body; gut arranged in spiral coils.

In preservative, body brown dorsally and laterally; belly gray with minute white flecks; caudal musculature brown with small, irregular, dark brown spots; caudal fins translucent with small brown spots (Fig. 3).

Oral disc moderately large, lacking lateral folds; two rows of small labial papillae fringing disc, except only one row midventrally; a few large, discrete papillae between fringing papillae on lower lip and third lower tooth row; numerous large and small papillae laterally. Jaw sheaths robust with short, blunt serrations; upper jaw sheath broadly arched with short lateral processes; lower jaw sheath broadly V-shaped. Two upper and three lower labial tooth rows; lower rows slightly shorter than upper rows, third shortest; second upper row narrowly interrupted medially (Fig. 3).

DISTRIBUTION AND ECOLOGY.—This species is known from several localities in cloud forest at elevations of 1540–1700 m on the northern slopes of the Meseta Central de Chiapas; all frogs are from streams in the Río Teapa drainage. The various localities on the northern slopes of the Meseta Central de Chiapas are along the road from the Pan-American Highway to Teapa, Tabasco, and all of the streams are between the villages of Pueblo Nuevo Solistahuacán and Rayón Mescalapa (Fig. 4). The species also is known from

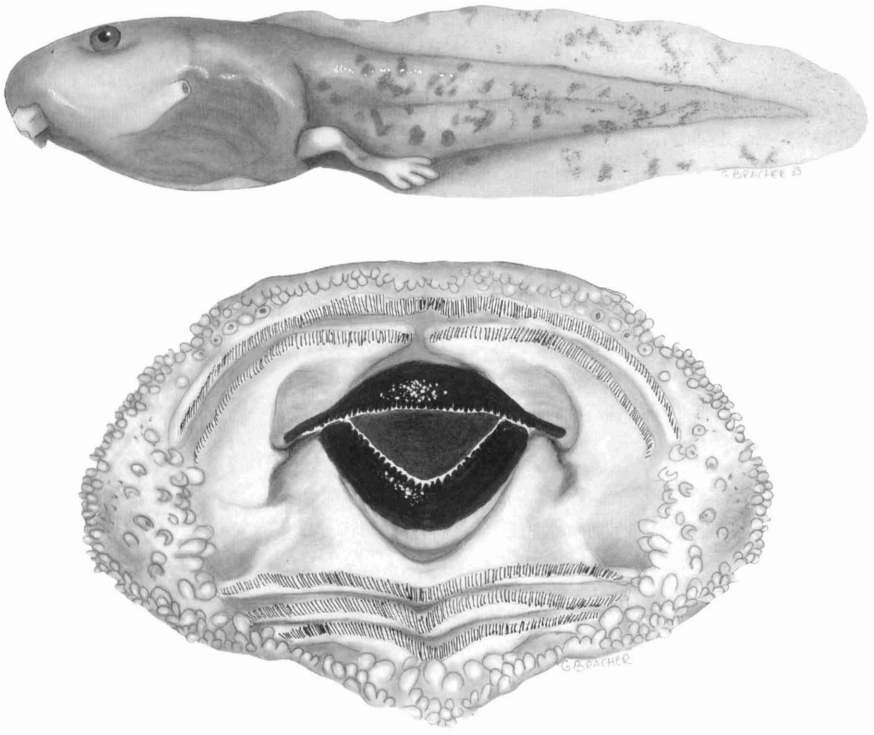

FIG. 3. Tadpole of *Plectrohyla acanthodes,* KU 60031, 48.0 mm total length.

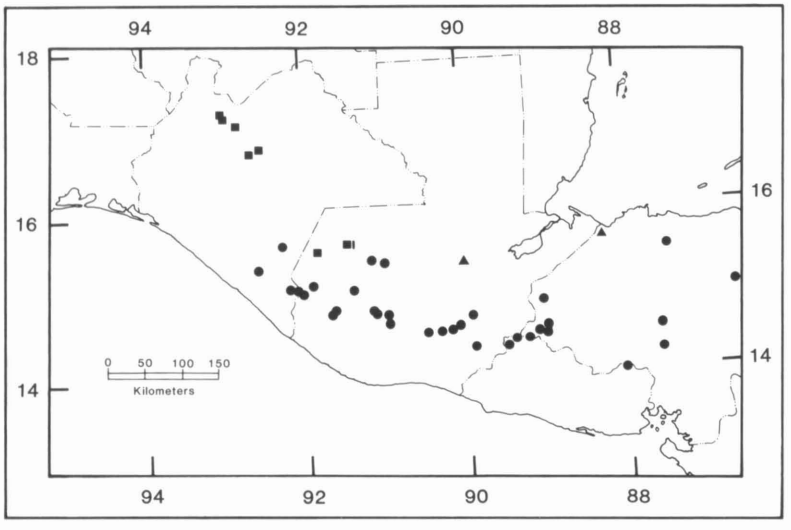

FIG. 4. Distribution of *Plectrohyla acanthodes* (squares), *P. guatemalensis* (circles), and *P. teuchestes* (triangles). In instances where several localities are in close proximity, a single symbol is used.

elevations of 2200 and 2250 m in cloud forest on the northern slopes of the Sierra de los Cuchumatanes in Guatemala. This highland mass is continuous via a narrow ridge at an elevation of about 1500 m with the Meseta Central de Chiapas, where the species is known from pine-oak forest at elevations of more than 2000 m.

On the northern slopes of the Meseta Central de Chiapas, adults were found at night in June and August. One was on a rock in a stream; one was in a hole behind a waterfall, and the others were on branches of bushes and trees 1–1.5 m above streams. At San Juan Ixcoy, one male was on the bank of a cascading stream by day. Tadpoles were found in rocky streams, where they adhered to rocks in flowing water. Metamorphosing young were found on bushes at night in June.

ETYMOLOGY.—The specific name is from the Greek *akanthodes* meaning thorny and is used in reference to the conical tubercles on the dorsum.

REMARKS.—On the northern slopes of the Meseta Central de Chiapas, *P. acanthodes* occurs in the same streams with one other large hylid, *Hyla chaneque,* and three smaller species—*Plectrohyla ixil, Ptychohyla macrotympanum,* and *Hyla melanomma.*

Plectrohyla avia Stuart

Plectrohyla avia Stuart, 1952:6.—Holotype: UMMZ 102280, from Granja Lorena, 10 km [airline] northwest of Colomba, Departamento Quezaltenango, Guatemala.

DIAGNOSIS.—(1) Maximum SVL 90.4 mm in males, 74.4 mm in females; (2) prepollical spine long, pointed; (3) small tubercles present on dorsal surfaces of head and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum uniformly green becoming paler on flanks; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla avia can be distinguished from all other *Plectrohyla* with long, pointed, prepollical spines by its much larger size, uniformly green dorsum (Fig. 5), and absence of vocal slits. The only other species of *Plectrohyla* that approach *P. avia* in size have bifid prepollical spines.

DISTRIBUTION.—All individuals have been found in cloud forest at elevations of 1685–2200 m on the Pacific slopes of the Sierra Madre from southeastern Chiapas, Mexico, to the volcanos of southwestern Guatemala (Fig. 6).

Plectrohyla dasypus McCranie and Wilson

Plectrohyla dasypus McCranie and Wilson, 1981:1.—Holotype: KU 186025, from Quebrada Cusuco at El Cusuco, 1580 m, 5.6 km west-northwest of Buenos Aires, Sierra de Omoa, Departamento Cortés, Honduras (15°30′N, 88°13′W).

DIAGNOSIS.—(1) Maximum SVL 44.0 mm in both sexes; (2) prepollical spine blunt, with nuptial excrescences in males; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits present; (6) dorsum bronze with small black spots bordered by lime-green; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla dasypus can be distinguished from all other *Plectrohyla* having short, blunt, prepollical spines by the presence of vocal slits. Furthermore, it is the only species (other than some *P. matudai*) having black spots bordered by lime-green on a bronze dorsum.

DISTRIBUTION.—This species is known from a single stream in cloud forest at elevations of 1530–1690 m in the Sierra de Omoa in northwestern Honduras (Fig. 6).

Plectrohyla glandulosa (Boulenger)

Hyla glandulosa Boulenger, 1883:164.—Syntypes: BMNH 1947.2.20.40–41 from "Guatemala."

Plectrohyla cotzicensis Stuart, 1948a:17.—Holotype: UMMZ 95902 from the source of the Río Cuilco, on the slopes of Cerro Cotzic, 2 km northwest of Ixchiguán, Departamento San Marcos, Guatemala.

Plectrohyla glandulosa—Duellman, 1964:455.

DIAGNOSIS.—(1) Maximum SVL 49.1 mm in males, 49.7 mm in females; (2) prepollical spine blunt; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum uniform dull olive-green in females; olive-green with irregular olive-brown or dark brown marks in males; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla glandulosa differs from other *Plectrohyla* having short, blunt, prepollical spines and lacking vocal slits by having few, weak tubercles on a greenish-gray dorsum. The dorsum is strongly tuberculate in *P. pychnochila* and *P. tecunumani,* of which the latter has bold, irregular dark markings; the dorsum is smooth in *P. lacertosa,* which has a uniformly brown dorsum. Furthermore, *P. glandulosa* is unique in the genus by having an outer tarsal fold.

DISTRIBUTION.—This species is widely distributed in fir forest, pine-cypress forest, and montane grasslands at elevations of 2400–3500 m in the Sierra de los Cuchumatanes and the central and southern highlands of Guatemala, and the highlands of northwestern El Salvador and adjacent Honduras (Fig. 6).

Plectrohyla guatemalensis Brocchi

Plectrohyla guatemalensis Brocchi, 1877a.—Syntypes: MNHN 6332 (2 specimens) from "Pacicilla" (= Patzicia), Departamento Chimaltenango, Guatemala.

DIAGNOSIS.—(1) Maximum SVL 52.1 mm in males, 54.0 mm in females; (2) prepollical spine bifid; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum dull olive-brown to dull green with reddish brown markings, with bright green flecks in some individuals; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla guatemalensis differs from all other *Plectrohyla* with bifid prepollices by having closely packed, round tubercles on the dorsum. In size and structure it is most like *P. acanthodes* and *P. pokomchi;* the former has scattered conical tubercles and pale green spots on the dorsum, and the latter has scattered round tubercles on a green dorsum and red webbing on the feet.

DESCRIPTION.—Body moderately robust; average SVL

FIG. 5. *Plectrohyla avia*, UTA A–24646, male, 79.5 mm SVL. Photo by D. G. Barker.

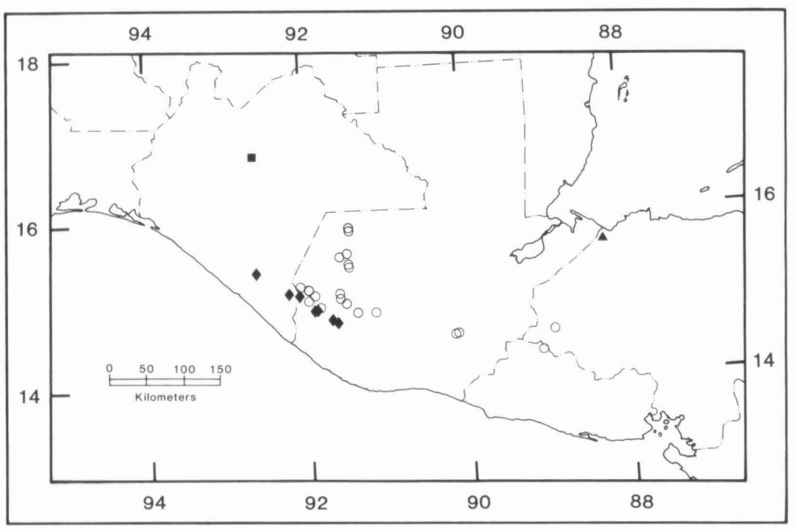

FIG. 6. Distribution of *Plectrohyla avia* (diamonds), *P. dasypus* (triangle), *P. glandulosa* (open circles), and *P. pychnochila* (square). In instances where several localities are in close proximity, a single symbol is used. The putative type locality of *P. pychnochila* in the Mexican state of Veracruz is not shown.

47.5 mm in males, 48.6 mm in females (Table 1); head slightly wider than long, as wide as body; snout short, in dorsal view pointed above and bluntly rounded below, in profile bluntly rounded; nostril much closer to eye than to snout; eye-nostril distance equal to about 80% of diameter of eye; canthus rostralis angular, nearly straight; loreal region concave; lips rounded in both sexes, swollen in breeding males; interorbital and internarial areas flat; nostril slightly protuberant dorsolaterally; eyes large; supratympanic fold heavy, extending from posterior corner of eye to point above insertion of arm; tympanum and tympanic annulus indistinct; upper one third of tympanum covered by supratympanic fold.

Upper arm and forearm slender in females, robust in

males; axillary membrane absent; row of tubercles along ventrolateral edge of forearm; hand moderately large; fingers slender, bearing narrow lateral fringes and large round discs; diameter of disc on third finger much greater than diameter of eye; relative lengths of fingers 1<2<4<3; subarticular tubercles moderately large, subconical; supernumerary tubercles large, round, present only on proximal segments; palmar tubercle low, flat, bifid; prepollex massive, bifid, lacking nuptial excrescences; webbing absent between first and second fingers; outer fingers about one-fourth webbed; webbing formula for outer fingers **II**2—3½**III**3—2**IV.** Hind limbs moderately short, robust; tibia length about 50% of SVL; foot length about 48% of SVL; outer tarsal fold absent; inner tarsal fold distinct on distal three-fourths of tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle elliptical, flat, visible from above; distinct dermal fringe extending from inner metatarsal tubercle to disc of first toe; toes slender, bearing discs only slightly smaller than those on fingers; relative lengths of toes 1<2<3<4<5; subarticular tubercles moderately large, round; supernumerary tubercles small, present only on proximal segments; toes about four-fifths webbed; webbing formula **I**1—2**II**1—2**III**1—2**IV**2—1**V.**

Skin on all dorsal surfaces with numerous, closely approximated, round tubercles; skin on throat, belly, posterior, and posteroventral surfaces of thighs granular; skin on ventral surfaces of forelimbs, thighs and shanks smooth. Anal opening directed posteroventrally at midlevel of thighs, bordered laterally by vertical dermal folds; anal tube short, bordered above by transverse dermal fold. Dentigerous processes of vomers small, strongly protuberant, each bearing 2–4 teeth, narrowly separated medially, situated posterior to level of posterior margins of small, ovoid choanae. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind; vocal slits and vocal sac absent.

Coloration in preservative: Dorsum dull dark brown or paler brown with scattered, irregular, dark brown spots; flanks and posterior surfaces of thighs brown or gray; venter dull cream.

Coloration in life: Dorsum dark green with or without reddish brown spots, to reddish brown with or without dark brown spots and green flecks; posterior surfaces of thighs and webbing tan to dull gray; venter dirty white; iris deep bronze (Fig. 7).

Measurements: Morphometric data are summarized in Table 1. Males and females are about equal in size.

TADPOLES.—Three tadpoles are available from Panajachel, Departamento Sololá, Guatemala. Tadpoles in Stages 29, 30, and 33 have body lengths of 17.9, 17.2 and 18.0 mm and total lengths of 44.5, 45.1, and 48.8 mm, respectively.

Body barely depressed, as wide as deep; snout in dorsal view bluntly rounded, in profile bluntly rounded; posterior edge of body gradually rounded in dorsal view; eyes small, widely separated, directed dorsolaterally; nostrils directed dorsolaterally at point midway between eyes and tip of snout. Opening of sinistral spiracle directed posterodorsally on midline at about midlength of body; anal tube short, dextral. Caudal musculature robust, gradually tapering to pointed tip just short of tip of acutely rounded tail; at midlength of tail, depth of dorsal fin equal to depth of caudal musculature; ventral fin shallower; dorsal fin not extending onto body; gut arranged in spiral coils.

In preservative body brown above, pale gray below; caudal musculature brown with small pale flecks; caudal fins translucent (Fig. 8).

Oral disc moderately large, lacking lateral folds; one row of small labial papillae anteriorly and laterally, two rows midventrally; one row of large, discrete papillae medial to fringing papillae on upper and lower lips; numerous large papillae laterally. Jaw sheaths moderately robust with short, blunt serrations; upper jaw sheath broadly arched with moderately short lateral processes; lower jaw sheath broadly V-shaped. Two upper and three lower labial tooth rows of about equal length; ridges supporting second upper row discontinuous, but abutting, medially (Fig. 8).

DISTRIBUTION.—This species is widely distributed in cloud forest and humid pine-oak forest at elevations of 990–2500 m. It occurs in the highlands of the Sierra Madre from southeastern Chiapas, Mexico, eastward through the central and southwestern highlands of Guatemala to northwestern El Salvador, adjacent Honduras, and the Sierra de Nombre de Dios in north-central Honduras (Fig. 4).

REMARKS.—This species is poorly represented by series from given localities throughout the range. Considerable variation in color and dorsal skin texture has been noted. Possibly these specimens represent more than one species. This species has been found in the axils of bromeliads and in crevices along banks of streams by day and on limbs overhanging, and boulders in, streams at night. Across much of the Guatemalan Plateau, *P. guatemalensis* is sympatric with *Ptychohyla euthysanota.*

Plectrohyla hartwegi Duellman

Plectrohyla hartwegi Duellman, 1968:576.—Holotype: UMMZ 94428, from Barrejonel, 1000 m, 19 km west of Chicomuselo, Chiapas, Mexico.

DIAGNOSIS.—Maximum SVL 75.8 mm in males, 76.7 mm in females; (2) prepollical spine bifid; (3) tubercles present on dorsal surfaces of head and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum bronze tan (with green flanks) or olive-green with or without large bronze-tan blotches; (7) tadpole with greatly enlarged oral disc and jaw sheaths with short blunt serrations and no lateral processes.

The anterior and posterior surfaces of thighs in *P. hartwegi* are black or dark green with large cream (usually vertical) marks; this pattern immediately distinguishes this species from all other *Plectrohyla.*

DESCRIPTION.—Body robust; SVL 68.6 mm in males, 65.2 mm in females; head slightly wider than long, as wide as body; snout short, bluntly rounded in dorsal view, inclined anteroventrally in profile; nostril much closer to tip of snout than to eye; eye-nostril distance about 70% of diameter of eye; canthus rostralis angular, nearly straight; loreal region shallowly concave; lips rounded in both sexes, swollen in breeding males; interorbital and internarial areas flat; nostril slightly protuberant anterolaterally; eye large; supratympanic fold heavy, extending from posterior corner of orbit to point above insertion of arm; tympanum and tympanic

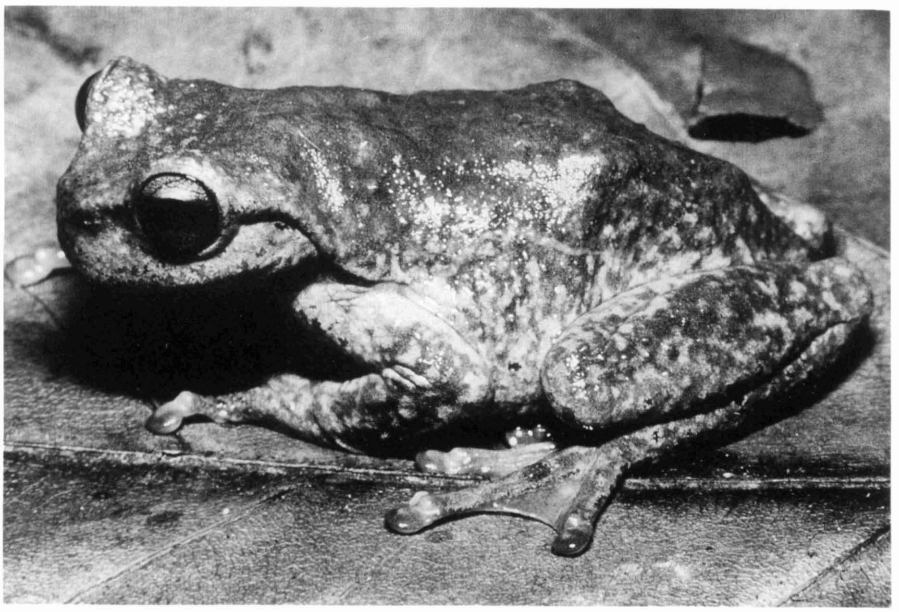

FIG. 7. *Plectrohyla guatemalensis,* UTA A–25387, female, 54.4 mm SVL. Photo by W. W. Lamar.

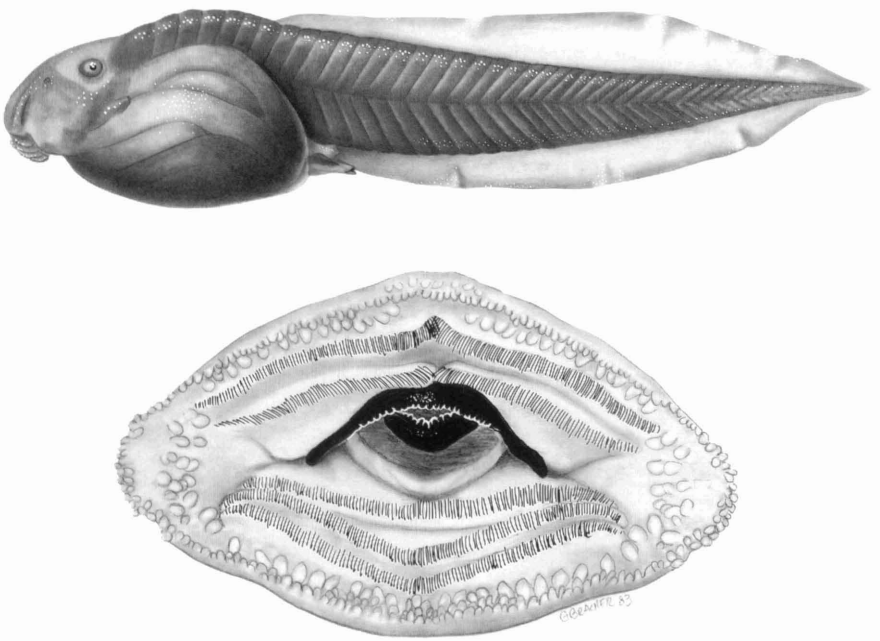

FIG. 8. Tadpole of *Plectrohyla guatemalensis,* UMMZ 98337, 48.8 mm total length.

annulus distinct; upper edge of tympanum covered by supratympanic fold.

Upper arm and forearm moderately slender in females, robust in males; axillary membrane absent; row of indistinct tubercles along ventrolateral edge of forearm; hand large; fingers moderately robust, lacking dermal fringes, bearing moderately large, round discs; diameter of disc on third finger greater than diameter of tympanum; relative lengths of fingers 1<2<4<3; subarticular tubercles large, subconical; supernumerary tubercles large, round, present on all but distal segments; palmar tubercle low, flat, bifid; prepollex massive, bifid, with nuptial excrescences (in some males);

webbing absent between first and second fingers; outer fingers about one-fourth webbed; webbing formula for outer fingers **II**2—3½**III**3—2½**IV.** Hind limbs moderately long, robust; tibia length about 53% of SVL; foot length about 47% of SVL; outer tarsal fold absent; inner tarsal fold low, extending full length of tarsus; outer metatarsal tubercle absent; inner metatarsal tubercle elongate, quadrangular, flat, visible from above; toes moderately long, slender, bearing discs only slightly smaller than those on fingers; relative lengths of toes 1<2<3=5<4; subarticular tubercles moderately small, round; supernumerary tubercles small, present only on proximal segments; toes about four-fifths webbed; webbing formula **I**1—2-**II**1—2**III**1—2**IV**1—1**V.**

Skin on dorsum finely tuberculate (body smooth with scattered tubercles in some individuals); skin on throat, belly, and ventral surfaces of thighs granular; skin on ventral surfaces of forelimbs and shanks smooth. Anal opening directed posteroventrally at midlevel of thighs, bordered laterally by diverging dermal folds; anal tube short. Dentigerous processes of vomers strongly protuberant, each bearing 3–6 teeth, narrowly separated medially, slightly inclined posteromedially between posterior margins of moderately large, ovoid choanae. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind; vocal slits and vocal sac absent.

Coloration in preservative: Dorsum dark bluish gray with or without irregular, large brown spots; anterior and posterior surfaces of thighs and inner surfaces of shanks black with broad cream (usually vertical) marks; venter dull creamy gray.

Coloration in life: Dorsum dull olive-brown, olive-green, or pale green; about 20% of the specimens with irregular pale bronze-tan spots on the dorsal surfaces of the body and limbs; anterior and posterior surfaces of thighs and inner surfaces of shanks boldly mottled with pale cream and black or dark green; ventral surfaces pale gray; iris bronze (Fig. 9).

Measurements: Morphometric data are summarized in Table 1. Males attain a greater size than females.

TADPOLES.—Series of tadpoles from two streams in Departamento Baja Verapaz and one locality in Departamento Zacapa, Guatemala, are available. A tadpole in Stage 25 has a body length of 12 mm and a total length of 35 mm; a tadpole in Stage 26 has a body length of 15 mm and a total length of 40 mm; a tadpole in Stage 27 has a body length of 15 mm and a total length of 44 mm; a tadpole in Stage 28 has a body length of 16 and a total length of 48 mm, and a tadpole in Stage 30 has a body length of 20 mm and a total length of 60 mm. Seven recently metamorphosed young have SVL of 17.8–19.0 mm ($\bar{x}$ = 18.4).

Body robust, depressed, slightly wider than deep; snout in dorsal view broadly rounded or truncate, in profile gradually inclined anteroventrally from nostrils to tip of snout; posterior edge of body bluntly rounded in dorsal view; eyes small, widely separated, directed dorsolaterally; nostrils directed anterodorsally at point about one-fourth of distance from eyes to tip of snout. Opening of sinistral spiracle directed posterodorsally below midline at point about two-thirds of length of body; anal tube long, dextral. Caudal musculature robust, extending almost to tip of acutely rounded tail; depth of caudal fins slightly less than depth of caudal musculature at midlength of tail; dorsal fin extending onto body; gut arranged in spiral coils.

In preservative, body dark brown above, pale gray laterally and ventrally; caudal musculature pale yellowish brown with irregular dark blotches interspersed by tan dorsally; periphery of caudal fins and tip of tail flecked with black (Fig. 10).

Oral disc ventral, huge, lacking lateral folds; single row of small labial papillae completely fringing disc; row of large, discrete papillae medial to anterolateral part of lip; 6–8 large papillae medially between third posterior tooth row and posterior edge of disc. Jaw sheaths robust with short, blunt serrations; upper jaw sheath in form of acutely rounded, inverted V, lacking lateral processes, with well-developed yellowish posterior cusp; lower jaw sheath broadly V-shaped. Two upper and three lower labial tooth rows extending laterally to lips; second upper row interrupted medially by extension of pocket above upper jaw sheath; other rows complete (Fig. 10).

DISTRIBUTION.—The known range is discontinuous. The species occurs at elevations of 1000–2134 m on the Pacific slopes of the Sierra Madre de Chiapas and extreme eastern Oaxaca, Mexico, at elevations of 925–1730 m on the northern slopes of the Sierra de los Cuchumatanes in northwestern Guatemala, at an elevation of 2520 m in El Quiché, Guatemala, and at elevations of 1460–1900 m in the Sierra de Las Minas in eastern Guatemala and 1920–2700 m on Cerro Celaque in southwestern Honduras (Fig. 11).

REMARKS.—There seems to be some geographic variation in size. One male and three females from the Sierra de los Cuchumatanes have SVL of 68.1 mm and 70.4–75.8 mm ($\bar{x}$ = 73.1), respectively, whereas 16 males and 18 females from Sierra de las Minas have SVL of 64.7–74.9 mm ($\bar{x}$ = 68.4) and 56.3–69.5 mm ($\bar{x}$ = 63.5), respectively. Four males and one female from the Sierra de Omoa in Honduras have SVL of 68.4–73.6 mm ($\bar{x}$ = 70.4) and 68.2 mm, respectively. Only one adult male (SVL = 63.8 mm) and one adult female (SVL = 66.4 mm) are available from the Sierra Madre de Chiapas.

As now recognized, *P. hartwegi* has a wide and disjunct geographic range. Our concept of this species is based mostly on specimens from the Sierra de las Minas in eastern Guatemala. Once comparable series of specimens from other regions are available, the species as we recognize it may be shown to be a composite.

The larvae of *P. hartwegi* and *P. teuchestes* are unique among hylid tadpoles in nuclear Central America and Mexico by having a greatly enlarged suctorial oral disc and cannot be confused with tadpoles of any other species. Nonetheless, the tadpoles of these two species of *Plectrohyla* can be distinguished from one another by several morphological characters (Table 3).

Plectrohyla ixil Stuart

Plectrohyla ixil Stuart, 1942:4.—Holotype: UMMZ 89092, from Finca San Francisco, 1175 m, 25 km north of Nebaj, Departamento El Quiché, Guatemala.

DIAGNOSIS.—(1) Maximum SVL 41.6 mm in males, 46.5 mm in females; (2) prepollical spine pointed; (3) tubercles present on dorsal surfaces of head and limbs; (4) rostral keel

FIG. 9. *Plectrohyla hartwegi*, UTA A–5362, male, 67.8 mm SVL.

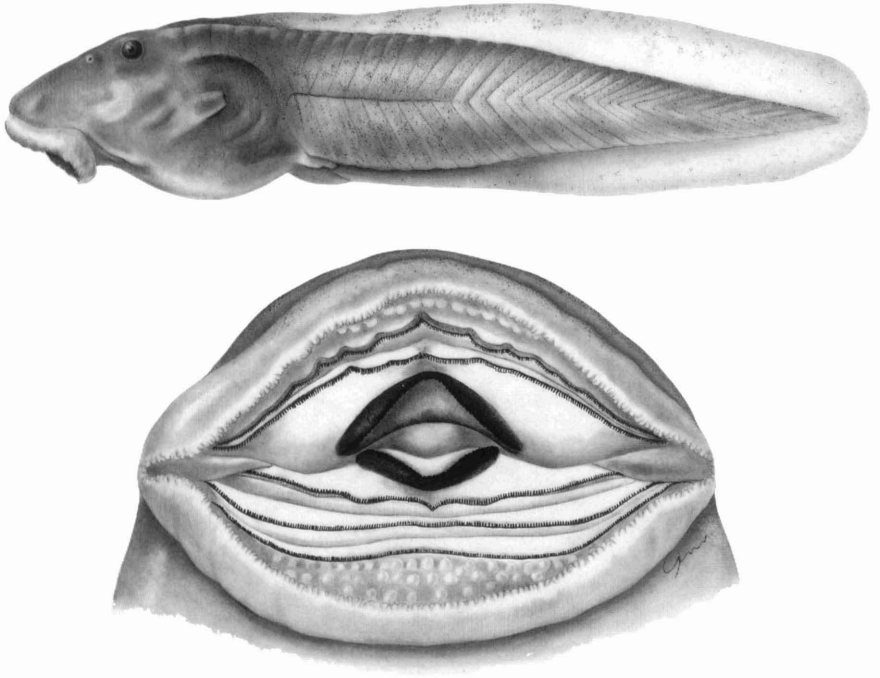

FIG. 10. Tadpole of *Plectrohyla hartwegi*, KU 191258, 60.0 mm total length.

absent; (5) vocal slits present; (6) dorsum tan or olive brown with yellowish orange lateral stripe bordered below by dark brown line; (7) tadpoles with unenlarged oral disc and enlarged fanglike serrations on upper jaw sheath.

Plectrohyla ixil is most like *P. matudai* but differs in having an acutely rounded snout, weakly tuberculate dorsum, and a broad, pale, lateral stripe. Other species of *Plectrohyla* having a long, pointed, prepollical spine have a vertical rostral

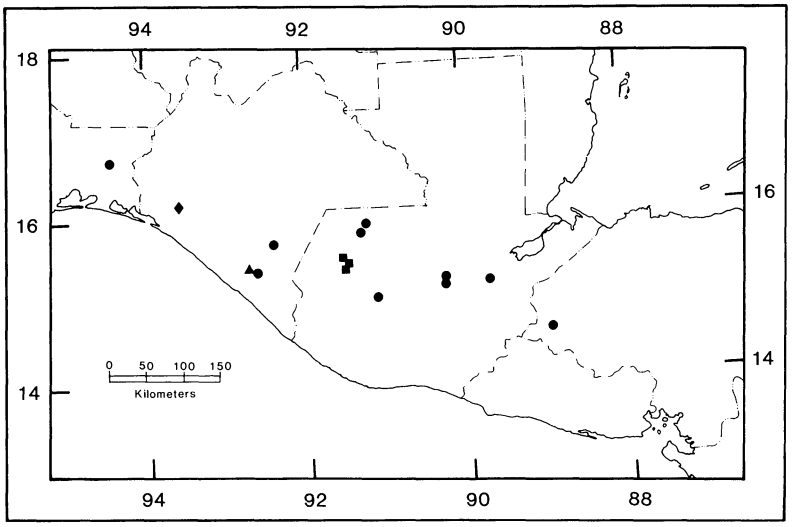

FIG. 11. Distribution of *Plectrohyla hartwegi* (circles), *P. lacertosa* (triangle), and *P. tecunumani* (squares); diamond indicates locality for *P. hartwegi* and *P. lacertosa*. In instances where several localities are in close proximity, a single symbol is used.

Table 3. Comparison of tadpoles of *Plectrohyla hartwegi* and *P. teuchestes*

Character	*P. hartwegi*	*P. teuchestes*
Size	Maximum size probably exceeds 65 mm (Stage 30)	Maximum size about 50 mm (Stage 38)
Coils of gut	Circular	Parallel, transverse loops
Snout	Broadly expanded, but not as wide as head	Broadly expanded, equal to greatest width of head
Size of disc	Disc covering snout in ventral view, extending laterally beyond side of snout	Snout apparent in ventral view, disc not extending laterally beyond side of snout
Upper jaw sheath	Sharply inflected posteriorly; rounded inverted V-shape; cavity in which upper jaw sheath is set extends beyond lower anterior tooth row	Not so sharply inflected posteriorly; broadly rounded arch-shape; cavity in which upper jaw sheath is set not extending to lower anterior tooth row
Oral papillae	One row of large, discrete papillae between fringing papillae and anterior tooth row; numerous smaller papillae between fringing papillae and large row of papillae; 6–8 papillae between posterior lower tooth row and marginal papillae	Distinct smooth, sharply raised fold between fringing papillae and anterior tooth row; fold becoming large papillae laterally; no smaller papillae between fringing papillae and fold; 4–5 papillae between posterior lower tooth row and marginal papillae

keel (*P. quecchi* and *P. sagorum*) or attain a much greater size and have a green dorsum (*P. avia*).

DISTRIBUTION.—This species inhabits cloud forests at elevations of 1175–1690 m on the Caribbean slopes of the Meseta Central in Chiapas, Mexico, and the highlands of northwestern Guatemala (Fig. 12).

Plectrohyla lacertosa Bumzahem and Smith

Plectrohyla lacertosa Bumzahem and Smith, 1954:64.—Holotype: UIMNH 33693, from "Region de Soconusco," Chiapas, Mexico.

DIAGNOSIS.—(1) Maximum SVL 47.8 mm in males; 48.1 mm in females; (2) prepollical spine blunt, with nuptial excrescences in male; (3) tubercles present on head and flanks; (4) rostral keel absent, but snout pointed; (5) vocal slits present or absent; (6) dorsum tan with dark brown markings in preservative; (7) tadpoles unknown.

Plectrohyla lacertosa differs from all other *Plectrohyla* by having a smooth dorsum with tubercles on the head. The other species that have blunt prepollical spines have distinctly tuberculate dorsal skin (*P. pychnochila* and *tecunumani*), vocal slits (*P. dasypus*), or an outer tarsal fold (*P. glandulosa*).

DISTRIBUTION.—The species is known only from two lo-

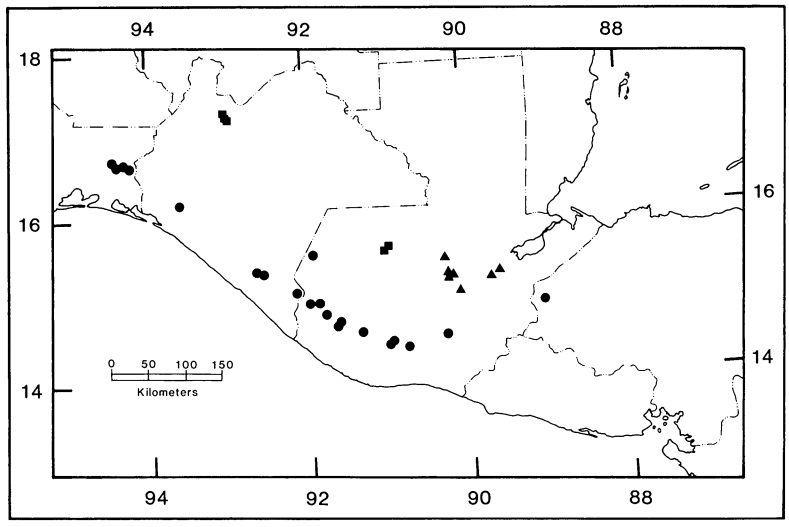

FIG. 12. Distribution of *Plectrohyla ixil* (squares), *P. matudai* (circles), and *P. pokomchi* (triangles). In instances where several localities are in close proximity, a single symbol is used.

calities in the Sierra Madre in Chiapas, Mexico—the type locality and Cerro Tres Picos, 2134 m (Fig. 11).

REMARKS.—This species has been known only from the holotype, a poorly preserved adult male having greatly swollen lips and hypertrophied arms. We have examined eight adult males and two adult females (CAS 169859–61, 169853–69) from Cerro Tres Picos, Chiapas, Mexico, that we tentatively refer to *P. lacertosa*. This assignment is tentative because the males differ from the holotype by having vocal slits. Also, the tympanum is not visible in the holotype, whereas it is distinct in the females and three males and indistinct in the other five males. The labile nature of vocal slits in *Plectrohyla* suggests that this character may vary intraspecifically, as well as interspecifically. Following is a description of the specimens from Cerro Tres Picos.

Body moderately robust; average SVL 40.1 mm in males, 48.0 mm in females; head slightly wider than long, about as wide as body; snout short, pointed in dorsal view with round margin to lips, truncate in profile in males, bluntly rounded in females; nostril about two-thirds of distance from eye to tip of snout; eye-nostril distance slightly less than diameter of eye; canthus rostralis rounded, straight; loreal region barely concave; lips round; interorbital area flat; internarial area depressed; nostril slightly protuberant, directed dorsolaterally; eye moderately large; supratympanic fold moderately heavy, curving from posterior corner of orbit to point above insertion of forelimb; tympanum and tympanic annulus distinct in females and three males, indistinct in five males, upper edge covered by supratympanic fold.

Upper arm slender; forearm slender in females, robust in males; axillary membrane extending onto proximal one third of upper arm; row of low, round tubercles on ventrolateral edge of forearm; hand moderately large; fingers long, slender, bearing broad, dermal fringes laterally and round discs terminally; diameter of disc on third finger equal to about 50% of diameter of eye; relative lengths of fingers 1<2<4<3; subarticular tubercles large, round; distal tubercle on fourth finger bifid in 70%; supernumerary tubercles small, subconical, numerous on proximal segments; palmar tubercle moderately elevated, bifid; prepollical tubercle large, quadrangular, blunt distally, bearing horny, brown nuptial excrescences, also extending along medial surface of thumb to disc; webbing vestigial between Fingers I and II; webbing formula for outer fingers **II**(2–2$^+$)—(3$^-$—3)**III**(3$^-$—3)—(2–2½)**IV**. Hind limb moderately robust; tibia length about 55% of SVL; foot length about 47% of SVL; outer tarsal fold absent; inner tarsal fold broad, flaplike, extending full length of tarsus, scalloped proximally, broadest distally; outer metatarsal tubercle absent; inner metatarsal tubercle elevated, ovoid, not visible from above; toes moderately short, bearing discs slightly smaller than those on fingers; relative lengths of toes 1<2<5<3<4; subarticular tubercles moderately large, round; supernumerary tubercles small, subconical, in single row of proximal segments; toes about two-thirds webbed; webbing formula: **I**(1½–2)—**2II**1—**2III**1—**2IV**2—1**V**.

Skin on dorsum smooth with scattered low tubercles, most numerous on head and flanks; skin on belly and ventral surfaces of thighs coarsely granular; other surfaces smooth. Anal opening directed posteroventrally at midlevel of thighs; anal sheath short, bordered above by transverse dermal fold; pair of elongate tubercles below anal opening. Dentigerous processes of vomers short, elevated, bearing 2 or 3 teeth each, posteromedially inclined between posterior margins of round choanae, widely separated medially. Tongue broadly cordiform, shallowly notched posteriorly, free behind for about one third of its length; vocal slit extending from midlateral base of tongue to angle of jaw; vocal sac single, median, subgular.

Measurements: The measurements (mm with means in parentheses) of eight males are followed by those of two females: SVL 38.9–41.5 (40.1), 47.9–48.1 (48.0); tibia length

21.3–23.5 (22.0), 22.8–24.0 (23.4); foot length 16.0–20.1 (18.7), 21.1–22.4 (21.8); head length 13.2–14.5 (14.0), 16.1–16.3 (16.2); head width 13.9–15.0 (14.6), 17.0; eye diameter 4.5–4.9 (4.7), 5.5; tympanum diameter 1.7–2.1 (1.8), 2.1–2.3 (2.2).

Coloration in preservative: Dorsum tan to reddish brown with irregular darker brown blotches or spots; dark markings absent in CAS 169859; dorsum mostly dark with tan spots in CAS 169861; flanks creamy tan with small brown spots or dashes; venter and hidden surfaces of thighs creamy tan.

Plectrohyla matudai Hartweg

Plectrohyla matudai Hartweg, 1941:5.—Holotype: UMMZ 88863, from Cerro Ovando, 1800 m, Distrito Soconusco, Chiapas, Mexico.

Plectrohyla brachycephala Taylor, 1949:16.—Holotype: AMNH 53761, from a tributary of the Río Ostuta, at the foot of the Sierra Madre between the Sierra Madre and Cerro Atravesado, Oaxaca, Mexico.

DIAGNOSIS.—(1) Maximum SVL 46.0 mm in males, 49.0 mm in females; (2) prepollical spine pointed; (3) tubercles present on dorsal surfaces of head and limbs; (4) rostral keel absent; (5) vocal slits present; (6) dorsum pale brown with dark brown or black flecks and dark brown dorsolateral, irregular stripe or series of flecks; (7) tadpoles with unenlarged oral disc and fanglike serrations on upper jaw sheath.

Plectrohyla matudai is most like *P. ixil,* which has an acutely rounded snout and a broad, pale, lateral stripe; also, *P. matudai* has a more tuberculate dorsum than *P. ixil.* Other species having long, pointed, prepollical spines differ by having a rostral keel (*P. quecchi* and *P. sagorum*) or much larger size and green dorsum (*P. avia*).

DISTRIBUTION.—*Plectrohyla matudai* is widely distributed in cloud forest at elevations of 700–2300 m along the Pacific versant from extreme southeastern Oaxaca, Mexico, through south-central Guatemala to the Las Nubes block. The species also occurs in pine-oak forest in the Grijalva Depression in western Guatemala and in cloud forest at an elevation of 1370 m on Cerro Azul in northwestern Honduras (Fig. 12).

Plectrohyla pokomchi Duellman and Campbell

Plectrohyla pokomchi Duellman and Campbell, 1984:394.—Holotype: KU 190231, from the Río Sananjá, 1585–1707 m, 3.5 km east of La Unión Barrios, Departamento Baja Verapaz, Guatemala (15°11′N, 90°10′W).

DIAGNOSIS.—(1) Maximum SVL 55.2 mm in males, 49.0 mm in females; (2) prepollical spine bifid; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits present; (6) dorsum bright green with darker green or gray tubercles, and red webbing on feet; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla pokomchi can be distinguished from other *Plectrohyla* with bifid prepollices by having vocal slits. Furthermore, the species is unique in the genus by having bright red webbing on the feet.

DISTRIBUTION.—This species occurs in cloud forests at elevations of 1400–1900 m in the Sierra de las Minas and the contiguous Sierra de Xucaneb in eastern Guatemala (Fig. 12).

Plectrohyla pychnochila Rabb

Plectrohyla pychnochila Rabb, 1959:45.—Holotype: AMNH 62667, from "Coyame, Veracruz, Mexico."

DIAGNOSIS.—(1) Maximum SVL 60.5 mm in males; females unknown; (2) prepollical spine blunt, with nuptial excrescences in males; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum grayish brown with a few scattered bluish tan flecks in preservative; (7) tadpoles unknown.

Plectrohyla pychnochila can be distinguished from other *Plectrohyla* with a short, blunt, prepollical spine by having small, pale, flecks on the dorsum. It differs further from *P. tecunumani,* which it is most like in size and structure, by having small, scattered tubercles, instead of many larger tubercles, on the dorsum.

DISTRIBUTION.—This species is known definitely from only one locality in pine-oak forest at an elevation of 2400 m in the Meseta Central of Chiapas, Mexico (Fig. 6).

REMARKS.—As noted by Duellman (1970), the type locality is highly questionable. *Plectrohyla* is unknown from the Sierra de Los Tuxtlas in southern Veracruz. Moreover, extensive field work in central Chiapas has revealed no additional specimens.

Plectrohyla quecchi Stuart

Plectrohyla quecchi Stuart, 1942:1.—Holotype: UMMZ 89086, from Barranca Las Palmas, 2 km north of Finca Los Alpes, 1015 m, Departamento Alta Verapaz, Guatemala.

DIAGNOSIS.—(1) Maximum SVL 44.0 in males, 46.7 mm in females; (2) prepollical spine pointed; (3) tubercles present on dorsal surfaces of head and limbs; (4) vertical rostral keel present; (5) vocal slits present; (6) dorsum tan with a few dark spots; flanks pale tan with dark brown spots; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla quecchi is one of two species having a vertical rostral keel; the other species, *P. sagorum,* differs by having an acutely rounded snout and weakly tuberculate dorsum.

DISTRIBUTION.—This species occurs in cloud forest at elevations of 615–1850 m on the slopes of the northern highlands in Guatemala from the Sierra de los Cuchumatanes to the highlands of Alta Verapaz and the Sierra de las Minas (Fig. 13).

REMARKS.—Specimens from Barillas on the north slope of the Sierra de los Cuchumatanes are somewhat smaller than those from more eastern localities in Guatemala. Eleven males from Barillas have SVL of 36.8–42.8 mm ($\bar{x}$ = 39.9) as compared with 8 males from Finca Los Alpes, which have SVL of 41.7–43.8 mm ($\bar{x}$ = 42.2).

Plectrohyla sagorum Hartweg

Plectrohyla sagorum Hartweg, 1941:2.—Holotype: UMMZ 88862, from Cerro Ovando [Obando], 1800 m, Distrito Soconusco, Chiapas, Mexico.

DIAGNOSIS.—(1) Maximum SVL 45.5 mm in males, 51.9 mm in females; (2) prepollical spine pointed; (3) tubercles present on dorsal surfaces of head and limbs; (4) vertical rostral keel present; (5) vocal slits present; (6) dorsum dull brown with small, irregular, darker brown spots; flanks tan with fine dark brown reticulations; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla sagorum is one of two species having a vertical rostral keel; the other species, *P. quecchi,* differs by having a bluntly rounded snout and more tuberculate dorsum.

DISTRIBUTION.—This species inhabits cloud forests at elevations of 1450–2050 m on the Pacific slopes of the Sierra Madre from southeastern Chiapas, Mexico, to the volcanos of southwestern Guatemala; a single record exists from the highlands of northwestern El Salvador (Fig. 13).

Plectrohyla tecunumani Duellman and Campbell

Plectrohyla tecunumani Duellman and Campbell, 1984:391.—Holotype: LACM 39956, from a cave 1 km east of Chemal, 3395 m, Departamento Huehuetenango, Guatemala (15°27′N, 91°31′W).

DIAGNOSIS.—(1) Maximum SVL 61.6 mm in males, 57.3 mm in females; (2) prepollical spine blunt; (3) tubercles present on dorsal surfaces of head, body, and limbs; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum grayish tan with numerous irregular dark brown to black spots in preservative; (7) tadpole with unenlarged oral disc and jaw sheaths with short blunt serrations and short lateral processes.

Plectrohyla tecunumani is distinguished from other *Plectrohyla* with short, blunt, prepollices by having bold dark spots on a strongly tuberculate dorsum. *Plectrohyla dasypus* differs by having vocal slits, *P. glandulosa* by having an outer tarsal fold, *P. pychnochila* by having small scattered tubercles on the dorsum, and *P. lacertosa* by having a smooth dorsum.

DISTRIBUTION.—This species is known only from a stream flowing through a cave in pine forest and a small stream flowing through a grassy meadow at elevations of 3200–3400 m in the Sierra de los Cuchumatanes in western Guatemala (Fig. 11).

REMARKS.—The type locality was visited in late July 1989 by Campbell. The hillsides bordering the stream were devoid of forest and overgrazed. Inside the cave the water in the stream was heavily laden with silt. Despite a thorough search for adults and tadpoles, no *P. tecunumani* were found. It is our opinion that the species no longer exists at the type locality. Because there are few streams in the karstic Sierra de los Cuchumatanes and most of the natural habitats in the region have been degraded seriously within the last two decades, it is possible that *P. tecunumani* is extinct.

Plectrohyla ***teuchestes*** new species

HOLOTYPE.—KU 58831, an adult male from Finca Los Alpes, ca. 1000 m, Departamento Alta Verapaz, Guatemala (15°22′N, 90°01′W), one of a series collected on 15 July 1960 by William E. Duellman and John Wellman.

PARATOPOTYPES.—Five males and five females (see Appendix).

DIAGNOSIS.—(1) Maximum SVL 76.1 mm in males, 73.6 mm in females; (2) prepollical spine bifid; (3) skin on dorsum usually smooth; (4) rostral keel absent; (5) vocal slits absent; (6) dorsum uniformly dull olive-green; (7) tadpole with greatly enlarged oral disc and jaw sheaths with short blunt serrations and lacking long lateral processes.

The large size and uniformly olive-green coloration readily distinguish this species from other *Plectrohyla* having bifid prepollices, except *P. hartwegi,* which differs by having bold black or dark green and cream markings on the anterior and posterior surfaces of the thighs. Furthermore, *P. teuchestes* has smooth (or nearly so) skin on the dorsum, as contrasted to finely tuberculate skin in *P. hartwegi.*

DESCRIPTION.—Body extremely robust; average SVL 73.4 mm in males, 70.4 mm in females (Table 1); head noticeably wider than long, nearly as wide as body in males; snout bluntly rounded in dorsal view, inclined anteroventrally in profile; snout short; nostrils about one-half of distance from eye to tip of snout; eye-nostril distance about one-half of diameter of eye; canthus rostralis angular, curved; loreal region deeply concave; lips rounded in females, swollen anterolaterally in males; interorbital area flat, half again as wide as eyelid; internarial area barely depressed; nostrils slightly protuberant laterally. Eye moderate in size; supratympanic fold heavy, extending from posterior corner of orbit to insertion of forelimb; tympanum and tympanic annulus distinct; upper third of tympanum covered by supratympanic fold.

Upper arm and forearm moderate in females, robust in males; axillary membrane absent; row of small tubercles along ventrolateral edge of forearm, most distinct in females; hand large; fingers long, bearing thick dermal fringes laterally and round discs; diameter of disc on third finger equal to one half of diameter of eye; relative lengths of fingers 1<2<4<3; subarticular tubercles large, subconical; supernumerary tubercles large, subconical, present only proximally; palmar tubercle low, flat, bifid; prepollex massive, bifid, with faint nuptial excrescences dorsally and on inner proximal surface of thumb; fingers unwebbed except basally between third and fourth fingers. Hind limbs long, moderately robust; tibia length about 56% of snout-vent length; foot length about 48% of snout-vent length; outer tarsal fold absent; inner tarsal fold curved, extending entire length of tarsus; outer metatarsal tubercle small, round; inner metatarsal tubercle elliptical, round, visible from above; toes long, slender, bearing discs as large as those on fingers; relative lengths of toes 1<2<3=5<4; subarticular tubercles large, subconical; supernumerary tubercles large, round, present only on proximal segments; toes about three-fourths webbed; webbing formula **I**1—1½**II**1—1½**III**1—2**IV**2—1**V.**

Skin on dorsum of head, body, and limbs smooth with small tubercles, most numerous on head, most prominent on shanks and forearms, small tubercles widely scattered on body, thighs, and upper arms in some specimens; skin on flanks smooth; skin on throat, belly, and proximal ventral surfaces of thighs granular; skin on other ventral surfaces smooth. Anal opening directed posteriorly at upper level of thighs, bordered laterally by single dermal fold and numerous large tubercles. Dentigerous processes of vomers strongly protuberant, bearing 3–6 teeth each, widely sepa-

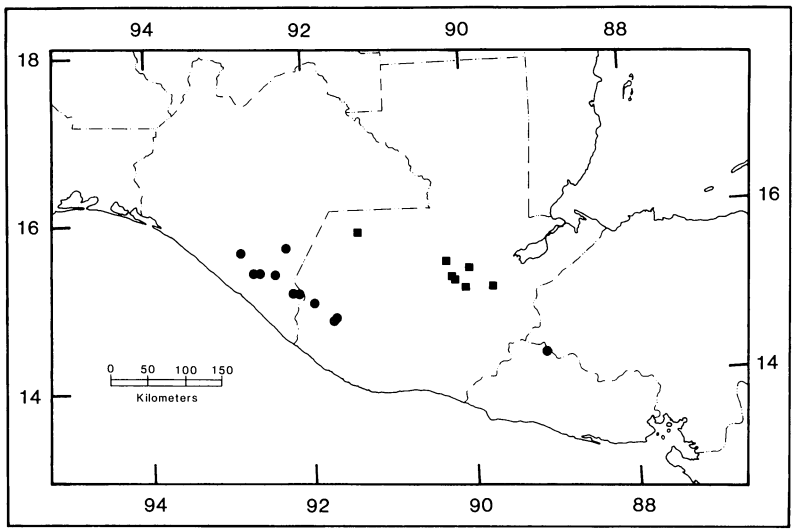

FIG. 13. Distribution of *Plectrohyla quecchi* (squares) and *P. sagorum* (circles). In instances where several localities are in close proximity, a single symbol is used.

rated medially, transverse, situated posterior to level of large, round choanae; maxillary and premaxillary teeth spatulate, bifid. Tongue ovoid, broader than long, barely free posteriorly; vocal slits absent.

Coloration in preservative: All dorsal surfaces and side of head dark, dull brownish gray; flanks slightly paler (large, faint, pale spots in KU 64102); venter dull creamy brown; webbing brownish gray.

Coloration in life: Dorsum dull olive-green; venter grayish white; iris golden yellow (Fig. 14).

Measurements: Morphometric data are summarized in Table 1. The measurements (in mm) for the holotype are: SVL 73.8, tibia length 42.1, foot length 36.2, head length 21.3, head width 25.6, diameter of eye 8.4, diameter of tympanum 2.8.

TADPOLES.—A series of 48 tadpoles from Arroyo Las Palmas at Finca Los Alpes, Departamento Alta Verapaz, Guatemala, collected on 1 August 1961 are available (Table 4). A single tadpole from this locality was collected on 15 July 1960.

Body robust, depressed, slightly wider than deep; snout broadly rounded in dorsal view, sloping anteroventrally from nostrils in profile; posterolateral edge of body bluntly rounded in dorsal view; eyes small, widely separated, directed dorsolaterally; nostrils directed anterodorsally at point about one-fourth of distance from eye to tip of snout. Opening of sinistral spiracle directed posterodorsally below midline at point about two-thirds of length of body; cloacal tube long, dextral. Caudal musculature robust, extending almost to tip of acutely rounded tail; depth of caudal fins equal to depth of caudal musculature at midlength of tail; dorsal fin extending onto body. Gut coiled in parallel, tranverse loops.

In preservative, body dark brown above, pale gray laterally and ventrally; caudal musculature pale tan with elongate, dorsal, dark brown blotches narrowly separated by tan in most specimens (Fig. 15). In small specimens (Stages 25–28), tip of tail darker than rest of tail. In life, body dark olive-brown dorsally; dark brown and yellowish tan blotches on dorsum of caudal musculature; iris pale bronze.

Oral disc ventral, huge, lacking lateral folds; single row of small marginal papillae completely fringing disc; distinct, sharply raised fold present medial to anterolateral part of lip; fold becoming discrete, large papillae laterally; four or five large submarginal papillae between posterior labial tooth row and posterior margin of lip. Jaw sheaths robust with short, blunt serrations; upper jaw sheath broadly bell-shaped, lacking long lateral processes, with well developed, yellowish, posterior cusp; lower jaw sheath broadly V-shaped. Two upper and three lower labial tooth rows, all complete and extending laterally to lips (Fig. 15).

DISTRIBUTION AND ECOLOGY.—This species is known only from two localities (Fig. 4). The type locality is a coffee finca at an elevation of 1000 m on the south slope of the Sierra de Xucaneb. These slopes drop steeply into the valley of the Río Polochic. There are many rivulets and one larger stream, the Río Chanchunac (also called the Río Quebrada), that cascade down precipitous limestone cliffs above the finca. The frogs were found during the rainy season on 15 July 1960 and 31 July–1 August, 1961. At those times, six were on branches of bushes overhanging the Río Chanchunac at night, and two were there by day; all were at places receiving mist from a cascade. Four others were by a waterfall by day; three of these were on rocks behind the falls, and one was on a rock in the splash zone of the falls. Tadpoles were found on the same dates in a quiet pool in the stream, where they adhered to stones on the bottom of the pool. The second locality is a stream (1530–1570 m) on Cerro Cusuco in the Sierra de Omoa in extreme northwestern Honduras.

ETYMOLOGY.—The specific epithet is Greek meaning an armed man. The name, as used here, has a double meaning: (1) in allusion to the bifid prepollical spines, which evidently are used by males in combat, and (2) in allusion to the late Laurence C. Stuart, who first discovered the tadpoles of this

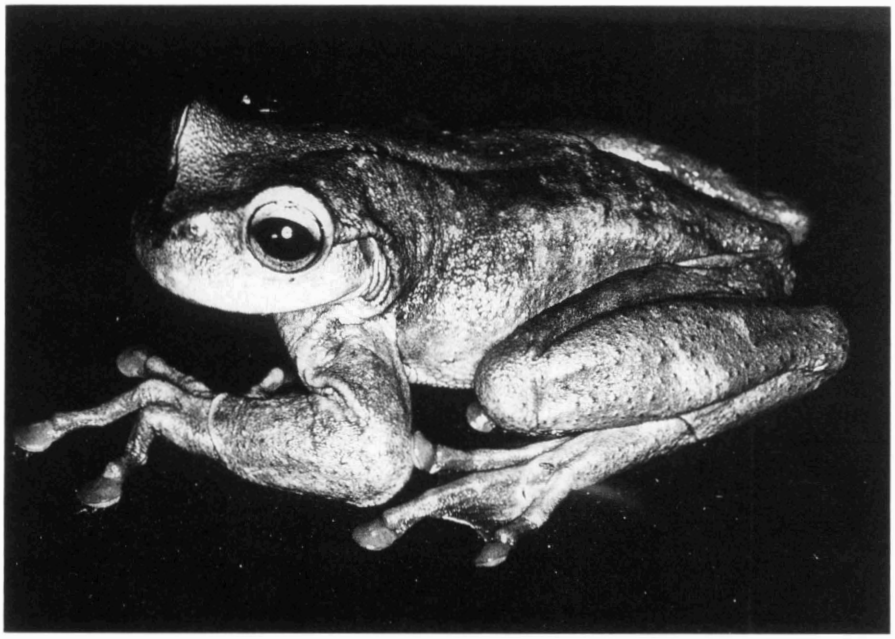

FIG. 14. *Plectrohyla teuchestes,* KU 58831, male, 73.8 mm SVL.

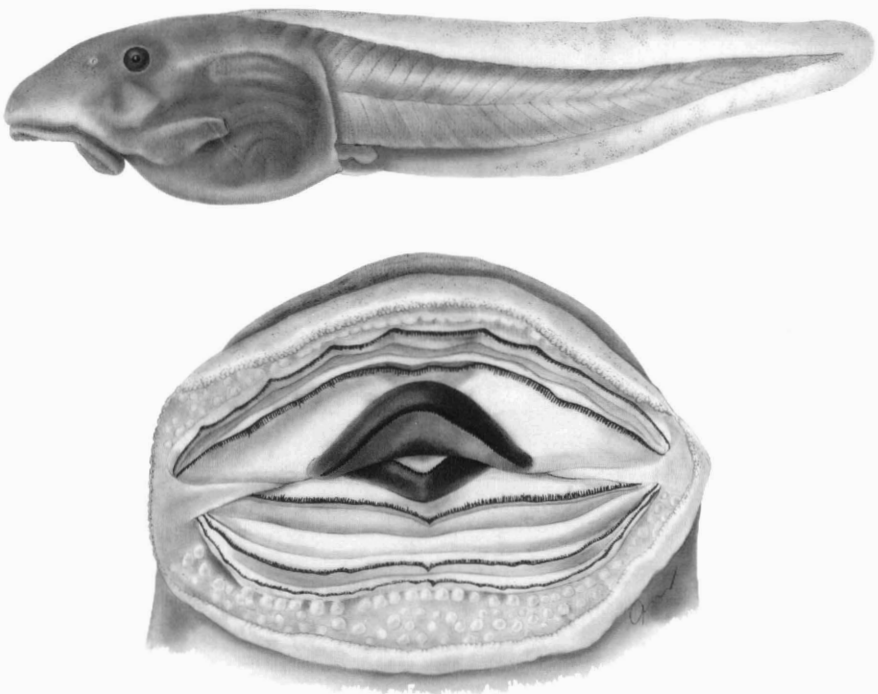

FIG. 15. Tadpole of *Plectrohyla teuchestes,* KU 68522, 46.0 mm total length.

Table 4. Measurements of tadpoles of *Plectrohyla teuchestes*. Means in parentheses.

Stage	N	Body length (mm)	Total length (mm)
25	9	9–10 (9.8)	26–30 (28.3)
26–28	23	10–14 (11.9)	27–40 (33.1)
29–31	4	13–16 (14.8)	39–45 (41.5)
32–35	4	15	4–49 (45.8)
36–38	6	15–16 (15.5)	44–50 (47.7)
39–41	2	16	48–49 (48.5)

species in 1938, and who with a pistol on his hip became a legendary figure in Alta Verapaz, where four decades later he was still known as "Pancho mata culebra."

REMARKS.—The tadpoles were described as *Hyla* sp. by Stuart (1948b), who found no adults of *Plectrohyla* at Finca Los Alpes, other than *P. quecchi*, whose tadpole he knew. Duellman (1970) reported on adult *Plectrohyla* from Finca Los Alpes, but he confused them with *P. guatemalensis*. He also reported additional tadpoles but followed Stuart in regarding them as belonging to an unknown species of *Hyla*. In the Sierra de las Minas in Baja Verapaz in 1977, Campbell found *P. hartwegi* and tadpoles resembling those from Finca Los Alpes. Subsequently, we examined the unextruded forelimbs of the tadpoles and discovered the bifid prepollex. Thus, we associate the long-known tadpole of "*Hyla* sp." from Finca Los Alpes with *P. teuchestes*, the only species of the genus in Alta Verapaz having a bifid prepollex. The tadpoles of *P. hartwegi* and *P. teuchestes* are compared in Table 3.

KEY TO THE IDENTIFICATION OF ADULTS OF *PLECTROHYLA*

1. Prepollical process bifid 2
   Prepollical process flat, blunt, or pointed, not bifid ... 6
2. Anterior and posterior surfaces of thighs with bold black or dark green and cream markings ..... *P. hartwegi*
   Anterior and posterior surfaces of thighs not so marked 3
3. Dorsum with closely packed round tubercles ..... *P. guatemalensis*
   Dorsum with scattered tubercles 4
4. Tubercles on dorsum conical; dorsum dull olive-green or gray with large olive-green spots .... *P. acanthodes*
   Tubercles on dorsum round; coloration not as described 5
5. Tubercles on dorsum small; size large (>65 mm); webbing on feet dull green; vocal slits absent ..... *P. teuchestes*
   Tubercles on dorsum large; size smaller (<60 mm); webbing on feet bright red; vocal slits present in males ..... *P. pokomchi*
6. Prepollical process pointed, knifelike 7
   Prepollical process blunt, not knifelike 11
7. Size large (>70 mm); vocal slits absent; dorsum uniformly green, smooth except for tubercles on head ..... *P. avia*
   Size smaller (<50 mm); vocal slits present in males; dorsum brown with variable tuberculation 8
8. Vertical rostral keel present 9
   Vertical rostral keel absent 10
9. Snout acuminate in dorsal view; small dark flecks on flanks ..... *P. sagorum*
   Snout blunt in dorsal view; large brown spots on flanks ..... *P. quecchi*
10. Snout acuminate in dorsal view; broad pale lateral stripe bordered below by narrow dark line usually present ..... *P. ixil*
    Snout truncate in dorsal view; lateral dark line or series of dark spots present, but broad pale lateral stripe absent ..... *P. matudai*
11. Dorsum strongly tuberculate, marked by bold, irregular, dark spots; nuptial excrescences absent ..... *P. tecunumani*
    Dorsum weakly tuberculate or smooth; pattern not as described; nuptial excrescences present 12
12. Dorsum bronze with black spots narrowly outlined with lime-green; vocal slits present ..... *P. dasypus*
    Dorsum not so marked; vocal slits absent 13
13. Dorsum tan with irregular brown markings (in preservative); inner tarsal fold flaplike ..... *P. lacertosa*
    Dorsum not tan with irregular brown markings; inner tarsal fold not flaplike 14
14. Dorsum greenish gray with or without darker markings; outer tarsal fold present ..... *P. glandulosa*
    Dorsum (in preservative) grayish brown with bluish tan flecks; outer tarsal fold absent ..... *P. pychnochila*

KEY TO THE IDENTIFICATION OF TADPOLES OF *PLECTROHYLA*

1. Oral disc greatly expanded into a suctorial structure, as wide as or nearly as wide as body 2
   Oral disc smaller, not expanded into a suctorial structure 3
2. Lips extending laterally beyond side of snout; single row of large, discrete papillae between fringing papillae and first upper labial toothrow ..... *P. hartwegi*
   Lips not extending laterally beyond side of snout; distinct smooth, sharply raised fold between fringing papillae and first upper labial toothrow .... *P. teuchestes*
3. Upper jaw sheath with enlarged pointed serrations to either side of midline 4
   Upper jaw sheath with blunt or pointed serrations subequal in size 6
4. One or two enlarged fanglike serrations on either side of upper jaw sheath ..... *P. matudai*
   Three or four enlarged fanglike serrations on either side of upper jaw sheath ..... *P. ixil*
5. Lips having two rows of small fringing papillae; lower labial rows subequal in length 6
   Lips having a single row of small fringing papillae; lower labial tooth rows subequal in length or not 7
6. Nostrils about midway between eyes and tip of snout ... *P. guatemalensis*

Nostrils about one-third distance from eyes to tip of snout ..... *P. pokomchi*
7. Lower labial tooth rows subequal in length..... 8
Third lower labial tooth row shorter than others 10
8. Lateral processes of upper jaw sheath absent . *P. dasypus*
Lateral processes of upper jaw sheath short, narrow .. 9
9. Row of discrete, large papillae between fringing papillae and outer tooth rows on both lips ..... *P. avia*
Row of discrete, large papillae between fringing papillae and outer tooth row only on lower lip .. *P. acanthodes*
10. No papillae lateral to jaw sheaths ..... *P. quecchi*
At least a few large papillae lateral to jaw sheaths.... 11
11. Lateral processes on upper jaw sheath weakly developed ..... *P. sagorum*
Lateral processes on upper jaw sheath absent 12
12. Numerous small papillae lateral to jaw sheaths ..... *P. tecunumani*
No more than two to four large papillae lateral to jaw sheaths ..... *P. glandulosa*

LIFE HISTORY AND BEHAVIOR

Reproductive Biology

Except for the few observations of amplexus, aspects of the reproductive biology of *Plectrohyla* must be inferred from diverse evidence. For example, the reproductive season in most, if not all, species is long, and may be more or less continuous throughout the year. Of those species known to vocalize, calling males have been found in February, April, June, July, and August. Gravid females (representing a total of 10 species) have been found in all months except November. Moreover, the presence of tadpoles in all stages of development at the same time of the year is suggestive of a long breeding season in *P. glandulosa* (Duellman, 1970). Tadpoles of *P. pokomchi* were found in streams in the Sierra de las Minas, Guatemala, continuously from early March through July. Metamorphosing young of *P. ixil* and *P. matudai* were found in April, June, July, and August. At the same stream near San Martín Sacatepéquez, Guatemala, tadpoles of *P. sagorum* in the same stages of development were found in February and July. All of these observations suggest that the documentation of breeding in *Plectrohyla* possibly is more accurately reflected by the activity of collectors than by the activity of the frogs.

Amplexus is axillary, and the arms of the male nearly encircle the body of the female. The chin and swollen upper lips of the male are pressed against the top of the head of the female. Glandular swelling of the upper lips seems to be characteristic of breeding males of all species of *Plectrohyla*. Furthermore, the maxillary and premaxillary teeth protrude through the lips and presumably contact the skin on the top of the head of the female. The glandular development and enlarged teeth are reminiscent of the conditions in plethodontid salamanders, in which males "inoculate" females with the secretions of the mental glands by scraping the head of the female with their premaxillary teeth (Arnold, 1977). It is unknown if such stimulation is part of the courtship in *Plectrohyla,* but lengthy periods of amplexus, as observed in *P. quecchi,* indicate that such stimulation may be necessary to induce ovulation.

Little information is available on oviposition and developing eggs of *Plectrohyla.* McCranie et al. (1987) reported a clutch of 240 eggs presumably deposited by *P. guatemalensis;* the eggs were adherent to the roots of a shrub on the bottom of a shallow stream, and each egg had a diameter of about 3.4 mm. A captive pair of *P. quecchi* was observed in amplexus on the night of 2 March; amplexus continued through 3 March. Oviposition began at 14:50 h on 3 March and continued through the night. Most of the 92 eggs were laid singly. The fertilized eggs were creamy white and 3.3 mm in diameter. The gelatinous capsules were sticky and 5.5–6.0 mm in diameter. On 9 March the eggs were in Stage 18; the embryos were about 6.5 mm in total length. On 16 March the eggs were in Stage 22; the embryos were about 9.8 mm in total length, and the filamentous external gills were well developed. The eggs hatched on 22 March, 19 days after deposition. Hatchlings are in Stage 25 and contain a large amount of yolk; coils of the gut are not visible. Ten hatchlings have body lengths of 4.0–4.6 mm ($\bar{x}$ = 4.48), tail lengths of 7.3–8.0 mm ($\bar{x}$ = 7.76), and total lengths of 11.5–12.6 mm ($\bar{x}$ = 12.04).

In order to ascertain the numbers of eggs deposited by different species of *Plectrohyla,* gravid females were dissected and the ovarian eggs counted and measured (Table 5). These counts revealed considerable variation in ovarian complement (88–442). Small sample sizes preclude meaningful, intraspecific statistical analyses. However, it is evident that the large species, *P. hartwegi* and *P. teuchestes,* have much larger ovarian complements than the smaller species. Furthermore, the largest ova occur in the largest species. The eggs of all species lack black pigment; the ova are cream, and the "gray" crescent is pale brown. This is typical of the coloration of eggs not deposited in direct sunlight.

Male-Male Interactions

Females are larger than males in most species of anurans; however, in some species, males are equal to, or slightly larger than, females. Wells (1978) suggested that large male size in territorial frogs may be an adaptation for aggressive defense of territories against other males. Shine (1979) analyzed sexual dimorphism in size among frogs and showed the existence of significant correlations between large size in males (relative to females) and (1) male-male combat and (2) presence of spines or tusks in males.

The hypothesis that selection favors large size in males, thereby affording them an advantage in intraspecific male-male interactions, implies that males are defending territories or fighting over mates. Generally, hyline frogs that breed in ponds migrate to breeding sites and spend a relatively short time there. This short-term residence at breeding sites contrasts with the situation in stream-breeding hylines inhabiting cloud forests. The latter species remain along the streams throughout most, if not all, of the year. Some individuals of some species may be active during the day, whereas at other times they may seek nearby diurnal shelters, such as bromeliads or crevices under rocks. Our field observations in the Sierra de Las Minas, Guatemala, of *P. hartwegi,*

Table 5. Ovarian complements and sizes of ovarian eggs in *Plectrohyla*. Means given in parentheses after observed ranges.

Species	N	Female SVL	Number eggs	Ovum diameter
P. acanthodes	1	60.4	149	2.9
P. glandulosa	7	42.0–47.3 (44.0)	88–108 (98.1)	1.3–2.1 (1.6)
P. guatemalensis	5	42.1–44.9 (43.3)	140–252 (197.2)	1.4–2.3 (2.0)
P. hartwegi	9	60.6–68.5 (65.5)	191–352 (278.7)	1.8–3.1 (2.5)
P. ixil	4	42.5–49.5 (47.2)	98–130 (116.0)	1.2–2.8 (1.8)
P. matudai	4	40.7–49.3 (42.1)	101–144 (121.8)	1.9–2.5 (2.1)
P. quecchi	1	43.1	97	3.1
P. sagorum	5	40.0–45.0 (43.1)	114–168 (129.8)	1.3–2.0 (1.7)
P. tecunumani	3	54.8–58.6 (56.2)	103–123 (113.0)	1.2
P. teuchestes	4	72.0–78.4 (74.2)	327–442 (366.5)	2.5–3.4 (3.0)

P. pokomchi, and *P. quecchi* indicate that, compared to migratory pond-breeders, males of stream-breeding species are more likely to utilize the same feeding or calling site for long periods of time and thereby are more likely to defend such sites against other males. Thus, males of stream-breeding species might be expected to be be larger (relative to females) than pond-breeding species.

Comparisons of relative snout-vent lengths of males and females of nine groups of stream-breeding and 10 groups of pond-breeding hylines (Table 6) show that the differences between the mean ratios for stream-breeders (0.893) and pond-breeders (0.877) is not significant. Males of some members of the *Hyla boans* group are the same size as females; males of these species construct basinlike nests, which they defend (Kluge, 1981). Males and females are nearly the same size in the pond-breeding *Hyla godmani* group; these species form breeding aggregations at temporary ponds in lowland rainforest; there is no evidence of male-male aggression.

Among stream-breeders, the male:female ratio in snout-vent length is 0.83–0.89 in seven groups of hylines. Two groups fall well beyond this range. Males of the *Hyla miotympanum* group are much smaller than females (mean ratio = 0.73). Compared with other stream-breeders, male *Plectrohyla* are relatively large with respect to females (mean ratio = 0.98). Considerable variation in sexual dimorphism in size exists among the species of *Plectrohyla*. Also, there seems to be a correlation between the amount of sexual dimorphism and the structure of the prepollex (Table 7). Species having a prepollex consisting of a simple spine exhibit the greatest sexual dimorphism, whereas in those species having a blunt prepollex or bifid prepollex, males and females are about equal in size, or males are larger than females.

Theoretically, male-male aggression is to be expected in those species of *Plectrohyla* in which males are large relative to females. No combat has been observed in any species of *Plectrohyla*, but males of two species in which males are larger than females (*P. hartwegi* and *P. teuchestes*) have scars on the bodies and forelimbs that presumably resulted from wounds caused by the prepollical spines of other males (Fig. 16). The scars are most common on the head and forelimbs, but one individual has several scars on the middle and posterior part of the dorsum of the body. No similar scars have been observed on female *Plectrohyla*. We interpret these observations to indicate male-male combat in these two species of *Plectrohyla*.

Among species in the *Hyla boans* group, males of which have long prepollical spines, males of *Hyla faber* (Lutz, 1960) and *H. rosenbergi* (Kluge, 1981) have been observed to inflict injuries on one another during combat, and preserved specimens exhibit scars resulting from wounds inflicted by prepollical spines. Cocroft and Heyer (1988) noted scratches on the heads and shoulders of male *Thoropa miliaris* (Leptodactylidae) that correspond to the clusters of nuptial spines on the prepollices of breeding males; they argued that these wounds resulted from male-male combat.

When *Plectrohyla* (especially those species having single spines or bifid prepollices) are handled, they commonly jab the prepollical spines into a person's fingers; therefore, the spines also may be used in defense. Compared with other hyline frogs, the maxillary and premaxillary teeth are long in *Plectrohyla* (Duellman, 1970); the teeth are pointed in *P. avia, P. glandulosa, P. lacertosa, P. sagorum,* and *P. tecunumani,* and weakly spatulate in the other species. Furthermore, at least in breeding males with swollen lips, the teeth protrude through the lips. Several species of *Plectrohyla* have been observed to press their jaws against the collector's hand; the teeth are readily felt when this is done.

A few individuals of both sexes exhibited scars on the dorsum of the head and body at the time of capture; these may be the result of scratches inflicted by the teeth (Fig. 17). If this interpretation is correct, the teeth may be used in male-male combat as well as in courtship. (See preceding account of reproductive biology.)

PHYLOGENETIC RELATIONSHIPS

Two levels of phylogenetic analyses were performed. The first involved one set of characters that were used to determine out-group relationships and diagnose *Plectrohyla* as a monophyletic group. The second analysis was based on characters of the in-group, *Plectrohyla*.

DETERMINATION OF OUT-GROUPS

Duellman (1970) considered *Plectrohyla* and the *Hyla bistincta* group to be allopatric ecological counterparts. The

Table 6. Comparative ratios of male and female snout-vent lengths in hylid frogs.
* = montane stream-breeding taxa; N = number of species.

Taxon	N	Range	Mean	Reference
Hyla bistincta group*	7	0.80–0.96	0.89	Duellman (1970)
Hyla boans group	4	0.89–1.00	0.97	Kluge (1979)
Hyla bogotensis group*	6	0.85–0.96	0.89	Duellman (1972)
Hyla eximia group	6	0.81–1.01	0.93	Duellman (1970)
Hyla godmani group	2	0.97–1.01	0.99	"
Hyla microcephala group	4	0.80–0.93	0.86	"
Hyla miotympanum group*	2	0.72–0.74	0.73	"
Hyla mixomaculata group*	3	0.80–0.92	0.86	"
Hyla parviceps group	6	0.71–0.91	0.83	Duellman and Crump (1974)
Hyla picta group	2	0.88–0.92	0.90	Duellman (1970)
Hyla sumichrasti group*	2	0.87–0.87	0.87	"
Hyla taeniopus group*	3	0.80–0.98	0.89	"
Osteocephalus	5	0.70–0.87	0.80	Trueb and Duellman (1971)
*Plectrohyla**	12	0.84–1.13	0.98	Present data
*Ptychohyla**	6	0.80–0.92	0.87	Duellman (1970); Duellman and Campbell (1982)
Smilisca	4	0.79–0.83	0.80	Duellman (1970)
*Smilisca**	2	0.80–0.85	0.83	"
Triprion	2	0.77–0.82	0.80	"

Table 7. Sexual dimorphism in snout-vent length in *Plectrohyla*, type of prepollex, and evidence of male-male combat.*

Species	SVL ♂:♀	Prepollex	Combat
P. dasypus	1.04	blunt	-
P. glandulosa	1.01	blunt	-
P. tecunumani	1.13	blunt	-
P. ixil	0.84	simple spine	-
P. matudai	0.87	simple spine	-
P. quecchi	0.90	simple spine	-
P. sagorum	0.88	simple spine	-
P. acanthodes	0.99	bifid spine	-
P. guatemalensis	0.98	bifid spine	-
P. hartwegi	1.05	bifid spine	+
P. pokomchi	1.05	bifid spine	-
P. teuchestes	1.04	bifid spine	+

*Adult females unknown for *P. avia*, *P. lacertosa*, and *P. pychnochila*.

former is restricted to the uplands of Nuclear Central America east of the Isthmus of Tehuantepec, and the latter occurs only in the Mexican highlands to the west of the isthmus. For reasons discussed below, the *Hyla bistincta* group is considered to be the first out-group of *Plectrohyla*. The monophyly of the *Hyla bistincta* group seems to be assured, but the limits of the group remain to be ascertained. Duellman (1970) included two small species, *Hyla charadricola* and *H. chryses*, in the group; both of these species lack the thick, glandular dorsal skin characteristic of the other, larger species in the group. Consequently, we have not included these two species in our out-group comparisons.

The choice of a functional second out-group (Watrous and Wheeler, 1981) is frought with uncertainty. Because of the absence of phylogenetic analyses of the diverse groups of hylids, we limited our search for a second out-group to groups of stream-breeding hylids that occur in Mexico and Nuclear Central America (Duellman, 1970). Some of these have highly specialized tadpoles with greatly enlarged oral discs (e.g., *Hyla pictipes* and *H. rivularis* groups, which have many enlarged, accessory labial papillae) and also many tooth rows (e.g., *Hyla mixomaculata* and *H. sumichrasti* groups) or umbelliform oral discs with few tooth rows (e.g., *Ptychohyla schmidtorum* group *auctorum*). In contrast, the species of the *Hyla bistincta* group and *Plectrohyla* retain the generalized hylid tadpole tooth row formula of two upper and three lower rows; only one or two rows of enlarged, accessory papillae are present, and the oral disc is only moderately expanded in most species. Consequently, we chose for a functional second out-group *Hyla miotympanum*, which occurs in the highlands of Mexico and Nuclear Central America; this species has a generalized stream-type tadpole with two upper and three lower tooth rows, and a relatively small oral disc with a median papillary hiatus on the upper lip (Duellman, 1970:377; fig. 185).

Four synapomorphies unite *Plectrohyla* and the *Hyla bistincta* group as sister-taxa:

1. Medial ramus of pterygoid (MRP).—In many species of hylids, including *Hyla miotympanum*, the medial ramus of the pterygoid is short and not in contact with the otic capsule. In *Plectrohyla* and the *Hyla bistincta* group, the medial ramus is long and articulates with the otic capsule. This condition is viewed as a synapomorphy of these two groups of species, but it occurs in other presumably unrelated groups of hylids (e.g., *Smilisca* and *Hyla albopunctata* group). The elongation of the medial ramus as a derived condition is based on developmental evidence in *Smilisca baudinii* (Duellman and Trueb, 1986) and *Hyla lanciformis* (de Sá, 1988). In both of these taxa, ossification occurs last in the medial ramus and expands toward the otic capsule.

2. Dorsal skin (DOS).—In most species of hylid frogs, including *Hyla miotympanum*, the skin on the dorsum is thin. The skin in anurans is thickened by a great increase either in the number of granular (= poison) glands (as in *Phrynohyas*, Duellman, 1956) or of mucous glands in other hylids. The thick skin on the dorsum in *Plectrohyla* and the

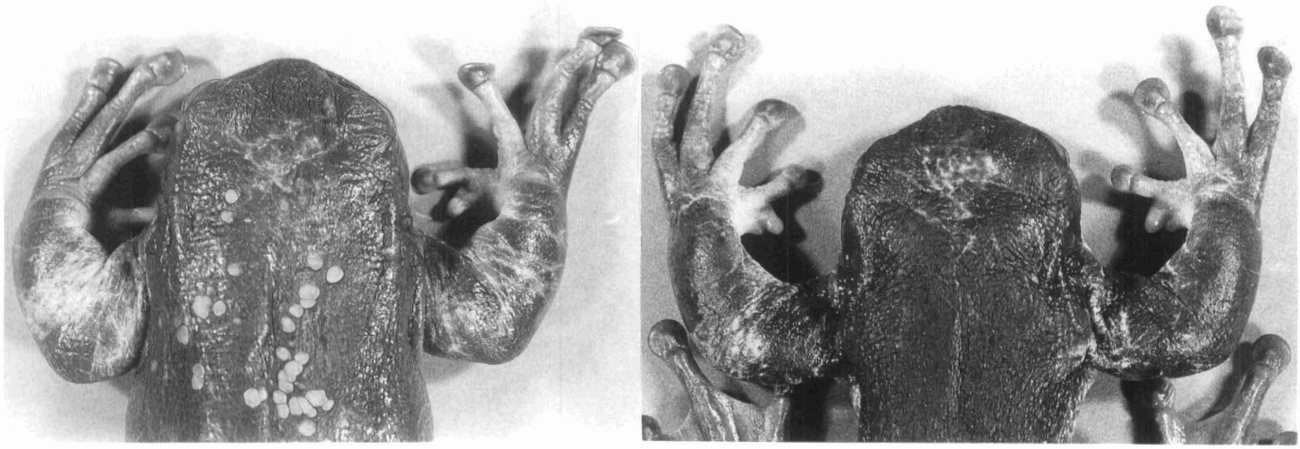

FIG. 16. Adult males of *Plectrohyla* showing scars of male-male combat. Left—*P. teuchestes,* KU 58831. Right—*P. hartwegi,* KU 190241.

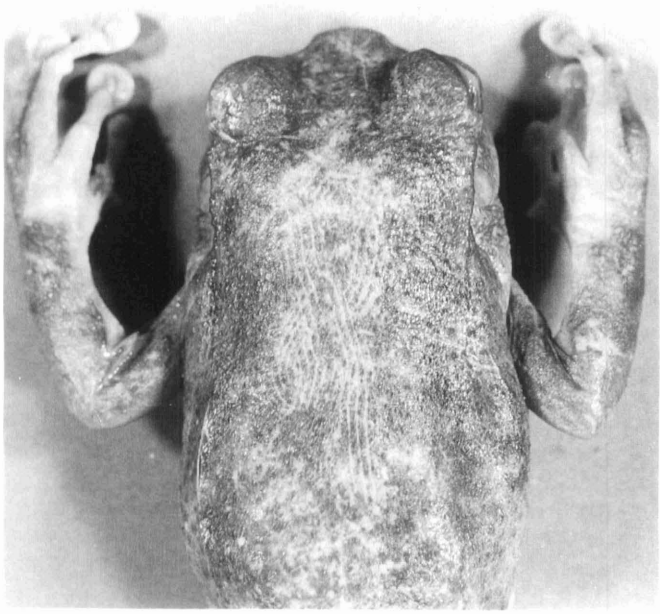

FIG. 17. Adult female *Plectrohyla hartwegi,* UMMZ 152864, showing scratches on dorsum.

Hyla bistincta group is considered to be a synapomorphy. A positive correlation between the number and size of mucous glands and the thickness of the skin has been demonstrated in various African ranids (Le Quang Trong, 1971, 1975a,b). Presumably the thickening of the dorsal skin in *Plectrohyla* and the *Hyla bistincta* group is the result of increased size and/or number of mucous glands. Commonly, these frogs secrete large quantities of mucus when disturbed; the secretion does not have the noxious properties of the secretion of the poison glands characteristic of *Phrynohyas.*

3. Median papillary hiatus (MPH).—Pond-type and generalized stream-type hylid tadpoles, including those of *Hyla miotympanum,* have a median hiatus in the fringing papillae on the upper lip. In diverse groups of hylids having specialized stream-type tadpoles, the fringing papillae are continuous on the upper lip (Duellman, 1970). The latter condition is considered to be a synapomorphy of *Plectrohyla* and the *Hyla bistincta* group, but the condition is not unique to them.

4. Accessory labial papillae (ALP).—Pond-type and generalized stream-type hylid tadpoles, including those of *Hyla miotympanum,* have relatively unspecialized labia and no large accessory papillae between the marginal papillae and the peripheral rows of labial teeth. In *Plectrohyla* and the *Hyla bistincta* group, the labia are expanded and have one or more rows of large submarginal papillae medial to the fringing papillae (Duellman, 1970).

MONOPHYLY OF *Plectrohyla*

Polarization of character transformations using the *Hyla bistincta* group as the first out-group and *Hyla miotympanum* as the second out-group resulted in the discovery of six synapomorphies of the species of *Plectrohyla.* These include four osteological characters, one feature of soft anatomy, and one larval character.

5. Alary process of premaxilla (APP).—The alary process (= pars dorsalis) of the premaxilla provides an abutment supporting the cartilages of the nasal capsule. The processes are simple, vertical or posterodorsally inclined struts in all hylids except *Plectrohyla,* in which the process is bifurcate (Duellman, 1970). In *Plectrohyla* the anterodorsal tip of the bifurcate alary process lies adjacent to the nasal cartilage anteroventral to the nasals, and the posteroventral ramus extends beneath the anterior part of the sphenethmoid.

6. Sphenethmoid (SPH).—The extent of ossification of this endochondral element is highly variable in anurans. In many taxa the anterior part of the sphenethmoid is unossified. In some other taxa, including *Plectrohyla,* the sphenethmoid is ossified anteriorly to incorporate the septum nasi and projects forward to the leading margins of the nasals.

7. Frontoparietals (FRO).—These paired, dermal roofing bones overlie the sphenethmoid and the prootics. In most hylids the frontoparietals do not have a complete median articulation with one another and therefore expose all, or

part, of the underlying frontoparietal fontanelle (i.e., the dorsal neurocranial fenestra formed in the sphenethmoid and prootics). In *Plectrohyla,* the frontoparietals abut broadly both anteriorly and posteriorly, thereby exposing only a small area of the frontoparietal fontanelle.

8. Prepollex size and shape (PRS).—The prepollex is only slightly enlarged and exists as a flat, elliptical, cartilaginous or ossified plate in most anurans. In various unrelated groups of anurans, males (and in some cases, females) have enlarged prepollices. The prepollex is enlarged and ossified in both sexes in *Plectrohyla.*

9. Forearm (FOR).—Characteristically, the forearms are moderately slender in anurans, but in breeding males of some species of frogs (e.g., *Leptodactylus* and *Plectrohyla*) the forelimbs are greatly hypertrophied (Duellman and Trueb, 1986).

10. Lateral labial folds (LAF).—The generalized pond-type and stream-type hylid tadpoles have lateral folds in the labia. One of the types of modifications in bottom-dwelling, stream-type tadpoles, including those of *Plectrohyla,* is the loss of the lateral folds.

INTERGENERIC RELATIONSHIPS

Four subfamilies are recognized in the Hylidae. The many species of the morphologically and ecologically diverse subfamily Hylinae have been grouped into genera and species groups on the basis of overall similarity, not on the basis of descent. Certainly the large and diverse genus *Hyla* is paraphyletic with respect to many recognized genera of hylines. This is true for the relationships between *Hyla* and *Plectrohyla,* for we have discovered synapomorphies that identify *Plectrohyla* as the sister-group of the *Hyla bistincta* group (Fig. 18).

We have not studied thoroughly all of the species in the *Hyla bistincta* group and have discovered no synapomorphies of the species in that group that are not shared with *Plectrohyla.* Thus, in the present treatment, the *Hyla bistincta* group may be paraphyletic with respect to *Plectrohyla.* However, further taxonomic rearrangement is unwarranted until the characters of the species in the *Hyla bistincta* group are studied in more detail and analyzed phylogenetically with respect to other hylines.

In the proposed phylogeny (Fig. 18), at Node 1 four synapomorphies (Characters 1–4) identify a clade [*Hyla bistincta* group + *Plectrohyla*] distinguished from other hylines. At Node 2 six synapomorphies (Characters 6–10) distinguish *Plectrohyla* from the *Hyla bistincta* group.

CHARACTER STATES AND THEIR POLARITIES IN *Plectrohyla*

After study of preserved specimens of adults and tadpoles and skeletal preparations of adults, 11 characters were determined to be analyzable phylogenetically within *Plectrohyla.* These include three osteological characters, three soft morphological characters of adults, and five larval characters. The primitive condition (that found in both the first and second out-groups) is designated as "0" and the derived condition as "1"; in each transformation series the direction of change is 0→1, except for Characters 13 and 20, in which it is 0→1→2. Tadpoles of two species of *Plectrohyla* are unknown; for those species, the larval characters were coded as "9" (= missing). The character states for the 11 characters in *Plectrohyla* and the out-groups are given in Table 8.

11. Squamosal (SQU).—The otic ramus of the squamosal normally articulates with the crista parotica, but in some taxa the dorsal part of the squamosal is poorly developed and not in contact with the crista parotica.

0 = otic ramus of squamosal articulating with the crista parotica.

1 = otic ramus of squamosal not articulating with the crista parotica.

12. Humerus (HUM).—Normally, the humerus is nearly round in section, but in some frogs in which the forelimbs are greatly hypertrophied in breeding males (e.g., *Leptodactylus* and *Plectrohyla*), the humerus is massive and has well developed flanges for muscle attachment (Duellman and Trueb, 1986).

0 = humerus round in section.

1 = humerus having well developed flanges.

13. Prepollex (PPS).—The prepollex in *Plectrohyla* may be blunt or pointed; if it is pointed, it may be simple or bifid (Duellman, 1970). These states are considered to be a transformation series from simple to complex. The shape of the prepollex is evident even before the emergence of the forelimbs at metamorphosis.

0 = prepollex blunt.

1 = prepollex pointed, simple.

2 = prepollex pointed, bifid.

14. Rostrum (ROS).—Normally the rostrum in anurans lacks dermal modifications. However, dermal appendages may be present in the form of a fleshy proboscis (e.g., *Hemiphractus;* Trueb, 1974) or a vertical rostral keel (e.g., some *Hyla* and some *Plectrohyla;* Duellman, 1970).

0 = rostrum plain.

1 = rostrum having a vertical keel.

15. Linea masculinea (LIN).—These bands of fibrous connective tissue extending along the entire dorsal and ventral edges of the *M. obliquus* occur in males of diverse species of frogs and seem to have been derived independently (Duellman and Trueb, 1986).

0 = linea masculinea absent.

1 = linea masculinea present.

16. Vocal slits (VOC).—The vast majority of anurans possess vocal slits and a vocal sac as structural modifications for the resonance of advertisement calls. Some frogs, principally those inhabiting the edges of cascading mountain streams, lack vocal slits and a vocal sac; most of these are not known to have advertisement calls (Duellman and Trueb, 1986). The coding for this character in *P. lacertosa* follows the condition in the holotype (absent). (See account of that species for possible variation.)

0 = vocal slits present.

1 = vocal slits absent.

17. Rows of accessory papillae (RAP).—Pond-type hylid tadpoles and generalized stream-type hylid tadpoles have no large accessory papillae between the fringing papillae and the peripheral rows of labial teeth. In *Plectrohyla,* one or more rows of large accessory papillae are present medial to the fringing papillae.

Table 8. Character states of the species of *Plectrohyla*. See text for abbreviations.

Species	11 SQU	12 HUM	13 PPS	14 ROS	15 LIN	16 VOC	17 RAP	18 EXP	19 SER	20 LAT	21 LLT
Ancestor	0	0	0	0	0	0	0	0	0	0	0
ACAN	0	1	2	0	0	1	0	0	0	0	0
AVIA	0	1	1	0	0	1	0	0	0	1	0
DASY	0	1	0	0	0	0	0	0	0	2	0
GLAN	0	1	0	0	0	1	0	0	0	2	0
GUAT	0	1	2	0	0	1	0	0	0	0	0
HART	0	1	2	0	0	1	1	1	0	2	1
IXIL	1	0	1	0	1	0	1	0	1	2	0
LACE	0	1	0	0	0	1	9	9	9	9	9
MATU	1	0	1	0	1	0	1	0	1	2	0
POKO	0	1	2	0	0	0	1	0	0	1	0
PYCH	0	1	0	0	0	1	9	9	9	9	9
QUEC	0	1	1	1	0	0	0	0	0	2	0
SAGO	0	1	1	1	0	0	0	0	0	2	0
TECU	0	1	0	0	0	1	0	0	0	2	0
TEUC	0	1	2	0	0	1	1	1	0	2	1

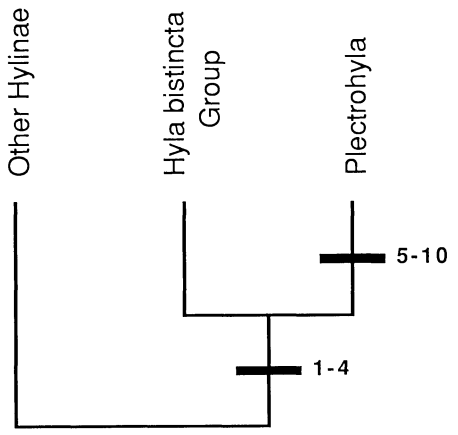

FIG. 18. Cladistic relationships of *Plectrohyla* and *Hyla bistincta* group in relation to other hylines. Numbers by crossbars refer to numbered characters in text.

0 = one row of accessory papillae on each labium.

1 = one row of accessory papillae on upper labium and two rows on lower labium.

18. Expansion of oral disc (EXP).—Among stream-type hylid tadpoles, theoral disc is ventral and moderately large (width = 65–75% of width of head). A further specialization is the expansion of the disc (width = 100% of width of head), so as to form a suctorial apparatus.

0 = oral disc not expanded and suctorial.

1 = oral disc expanded and suctorial.

19. Serrations on upper jaw sheath (SER).—Normally the serrations on the upper jaw sheath are subequal in size and either blunt or pointed. A presumed feeding specialization is the great enlargement of some serrations into fanglike structures in some species of *Plectrohyla.*

0 = serrations on upper jaw sheath subequal in size.

1 = two or more fanglike enlarged serrations.

20. Lateral processes on upper jaw sheath (LAT).—Generalized pond- and stream-type hylid tadpoles have long, slender lateral (alary) processes on the upper jaw sheath. In some stream-type tadpoles, including some species of *Plectrohyla,* these processes are short; in others they are weak or absent.

0 = lateral processes long.

1 = lateral processes short.

2 = lateral processes weak or absent.

21. Length of lower rows of labial teeth (LLT).—Generalized pond- and stream-type hylid tadpoles have two upper and three lower labial tooth rows; the lower rows are shorter than the upper rows. In specialized stream-type tadpoles with large oral discs, including some species of *Plectrohyla,* the lower rows may be as long as the upper rows.

0 = lower labial tooth rows shorter than upper rows.

1 = lower labial tooth rows equal in length to upper rows.

CHARACTERS NOT USED IN PHYLOGENETIC ANALYSES

Various characters were deemed inappropriate for use in the phylogenetic analysis. Characters of color pattern were not used because of (1) lack of evidence for polarization, and (2) absence of information on coloration in life in some taxa. Some color characters are autapomorphies of certain species (e.g., bold black and cream marks on the flanks and hidden surfaces of the hind limbs in *P. hartwegi* and red webbing on the feet in *P. pokomchi*). The extent of webbing on the feet is nearly the same in all species of *Plectrohyla;* intraspecific variation in some species encompasses the range of interspecific variation among other species.

Keratinized pads or clusters of spines on the prepollex of breeding males are characteristic of most hylids that breed in streams (Duellman, 1970). Well developed nuptial excrescences are characteristic of breeding males of those species of *Plectrohyla* that have blunt prepollices (e.g., *P. dasypus, P. glandulosa, P. lacertosa,* and *P. pychnochila*). However, nuptial excrescences also have been observed in some males of *P. hartwegi* and *P. teuchestes,* species that have bifid prepollices. Because of the uncertainty of the occurrence of nuptial excrescences in populations not represented by series of breed-

ing males and because of the variation in occurrence in others, this character was not used.

Although notable differences exist in the dorsal skin texture among species of *Plectrohyla* (e.g., smooth with small tubercles on head and limbs in *P. avia* versus large tubercles on all dorsal surfaces in *P. pokomchi*), this character was not used in the analyses because (1) intraspecific differences may be owing to sexual dimorphism or breeding condition, and (2) nature of the texture of the skin may be owing to different techniques of preservation.

PHYLOGENETIC ANALYSES OF *Plectrohyla*

Eleven multistate characters [Characters 11–21] were used for the in-group analysis. Using the multiple parsimony and global branch-swapping options of PAUP, 100 equally parsimonious trees (maximum number generated on personal computer version) having 20 steps and a consistency index of 0.65 were found. Using the extended branch-breaking option of HENNIG86, 201 equally parsimonious trees having 20 steps and a consistency index of 0.65 were identified. In the strict consensus trees of PAUP and HENNIG86 (Fig. 19), *Plectrohyla* is diagnosed by two synapomorphies [Characters 12 (0→1) and 20 (0→1→2)]. However, *Plectrohyla* is diagnosed by six other synapomorphies [Characters 5–10] in the out-group analysis (Fig. 18). Within the strict consensus trees there exists a polytomy of 11 clades. Four sets of sister-species are identified—[*ixil* + *matudai*] characterized by derived states of Characters 11, 15, and 19; [*quecchi* + *sagorum*], characterized by the derived state of Character 14; [*hartwegi* + *teuchestes*] characterized by derived states of Characters 18 and 21; and [*acanthodes* + *guatemalensis*] characterized by a reversal in Character 20.

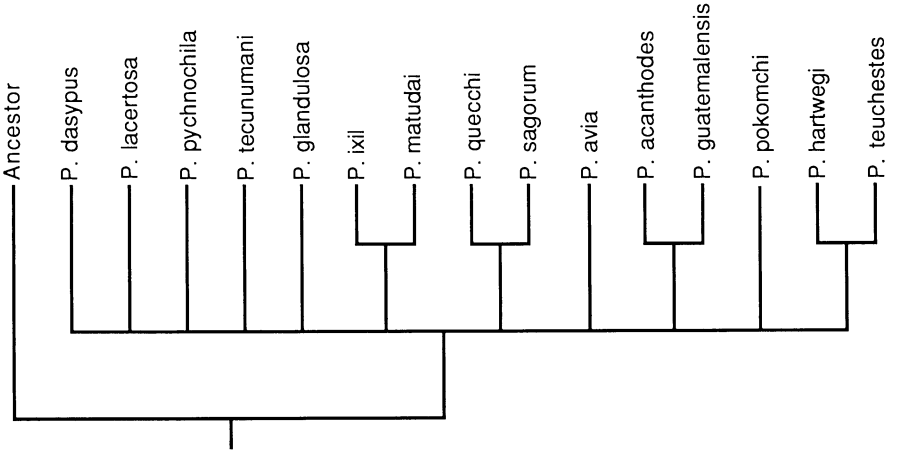

FIG. 19. Strict consensus tree of 201 equally parsimonious trees of *Plectrohyla* using ancestor rooting.

Using PAUP, an Adams consensus tree was generated. This tree differs from the strict consensus tree in that *P. pokomchi* is identified as a branch off of [*hartwegi* + *teuchestes*]; this association is based on the derived state of Character 17, which is homoplastic with respect to [*ixil* + *matudai*]. Obviously, the morphological data set that we have used is not sufficent to resolve the phylogenetic relationships among the species of *Plectrohyla*.

BIOGEOGRAPHY

Plectrohyla is endemic to the highlands of Nuclear Central America, where it is restricted to regions drained by cold mountain streams. We have suggested that the sister-group to *Plectrohyla* is the *Hyla bistincta* group, which is restricted to the Mexican highlands northwest of the Isthmus of Tehuantepec. In the Early Tertiary, the region corresponding to the Isthmus of Tehuantepec might have been inundated by a marine portal (Sykes et al., 1982; Donnelly, 1989) or, if not inundated, the isthmus was of lower relief and no more than one half of its present width (Durham et al., 1955).

Plectrohyla is associated with the historical events of the highlands of Nuclear Central America. The fragmentation of the highlands in the northeastern part of Nuclear Central America presumably had its origin with the Motagua and Polochic faults, which resulted from the tectonic events associated with the movements of the North American, Caribbean, and Cocos plates (Plafker, 1976) (Fig. 20). An estimated 200 km of lateral movement has occurred along these faults since the Miocene (Plafker, 1976).

In contrast to the more stable northwestern highlands (Meseta Central of Chiapas, Sierra de los Cuchumatanes), the southern edge of the highlands of Nuclear Central America experienced extensive vulcanism beginning in the Miocene; this volcanic region is associated with the subduction zone of the Cocos Plate where it meets the Caribbean Plate and the southwestern corner of the North American Plate (Plafker, 1976). The series of volcanoes begins in southeastern Chiapas, Mexico, and continues eastward, paralleling the Pacific coast (Fig. 21). These volcanoes mostly are isolated from one another by passes at elevations of less than 1500 m and form a series from Volcán Tacaná in southeast-

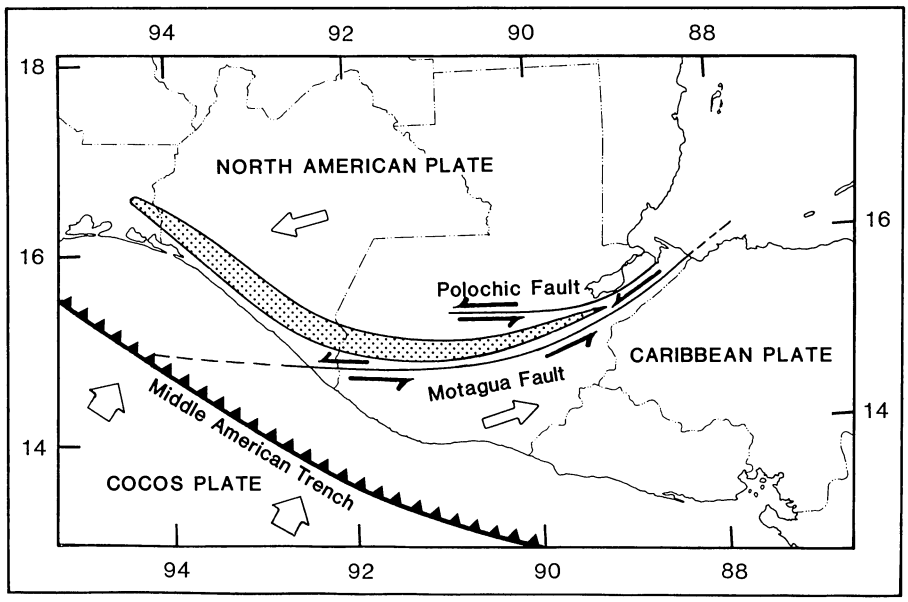

FIG. 20. Nuclear Central America showing position and direction of movement of crustal plates and location and direction of slippage of major faults. The Paleozoic core of highlands is stippled. Adapted from Plafker (1976).

ern Chiapas and Volcán Tajumulco in southwestern Guatemala to Volcán Santa Ana in El Salvador; this volcanic chain consists of lower and more widely separated volcanoes southeastward into Nicaragua.

All of these highlands reach elevations sufficient for the accumulation of clouds at least on their windward slopes; it is on these slopes that cloud forest developed. The orogeny of some of these mountains, especially the Sierra Madre del Sur and the highlands bordering the Motagua Valley, resulted in modification of wind currents so as to create rain shadows in the valleys. Consequently, with increasing elevation of highlands during the Middle and Late Tertiary, the cloud forest became fragmented. At higher elevations, especially on the limestone rocks of the Meseta Central of Chiapas and the Sierra de los Cuchumatanes, cloud forest gives way to pine forest, and at still higher elevations fir forest. Streams are numerous on most of the slopes supporting cloud forest. Streams are far less numerous in the limestone mountains of Alta Verapaz and surface streams are scarce in the porous and karsted limestone of the Meseta Central of Chiapas and the Sierra de los Cuchumatanes.

The phylogenetic analysis identified four pairs of sister-species. In two of these, one member of each pair (*P. matudai* and *P. sagorum*) occurs on the Pacific versant, and the other member of each pair (*P. ixil* and *P. quecchi*) occurs on the Caribbean versant. The sister-species *P. acanthodes* and *P. guatemalensis* occur in the western and eastern parts of the Nuclear Central American highlands, respectively. Likewise, the sister-species *P. hartwegi* and *P. teuchestes* have a similar distribution pattern, but *P. teuchestes* is restricted to the northeastern highlands. Also, *P. pokomchi* is restricted to the highlands north of the Motagua Valley, whereas *P. avia* and *P. lacertosa* are endemic to the Pacific versant. *Plectrohyla tecunumani* and *P. pychnochila* are known with certainty only from the karstic northern highlands of Nuclear Central America. *Plectrohyla dasypus* is unique in the genus by having its distribution lying entirely south of the Motagua fault zone.

In Nuclear Central America the complex topography resulting mainly from Pliocene and Pleistocene vulcanism and the presumed altitudinal fluctuations in climate and vegetation zones at times resulted in fragmentation of distributions and isolation of populations and at other times provided opportunities for dispersal. Unfortunately, few rigorous phylogenetic analyses of members of the Nuclear Central American herpetofauna are available. Of the five species of the colubrid snake genus *Adelphicos, A. quadrivirgatus* in the lowlands is the sister-species of the five highland species; vicariance events seem to have occurred in a west to east sequence (Campbell and Ford, 1982; Campbell and Brodie, 1988). Likewise, species of the *Ptychohyla schmidtorum* group (*auctorum*) and *P. euthysanota* group have representatives on both Caribbean and Pacific versants in Nuclear Central America (Duellman and Campbell, 1982).

Among amphibians, the amount of differentiation within *Plectrohyla* in Nuclear Central America is exceeded only by that in bolitoglossine salamanders (Wake and Lynch, 1976; Wake and Elias, 1983; Wake and Johnson, 1989). Although a phylogenetic analysis of these salamanders is wanting, Wake and his coworkers have hypothesized relationships that include species pairs on opposite versants of the highlands; this pattern is like that exhibited by two pairs of species of *Plectrohyla*

FUTURE RESEARCH

We consider the foregoing treatment of the species of *Plectrohyla* to be an initial step toward a realistic understand-

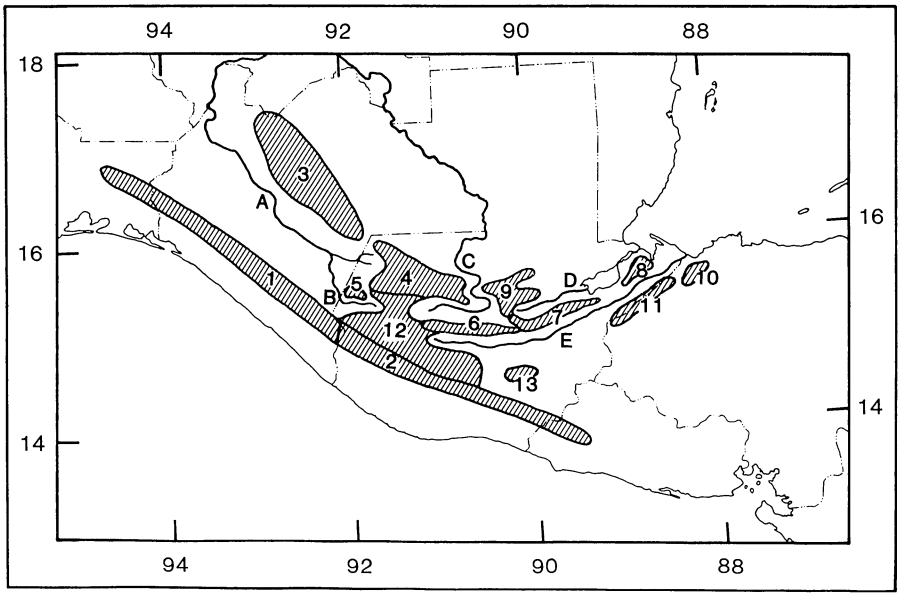

FIG. 21. Principal highlands and rivers in Nuclear Central America. Rivers are identified by letters: A = Grijalva, B = Cuilco, C = Negro, D = Polochic, E = Motagua. Highlands are identified by numbers: 1 = Sierra Madre de Chiapas, 2 = Southern volcanic chain, 3 = Meseta Central of Chiapas, 4 = Sierra de los Cuchumatanes, 5 = Montañas del Cuilco, 6 = Sierra de Chuacús, 7 = Sierra de las Minas, 8 = Montañas del Mico, 9 = Alta Verapaz highlands (Sierra de Chamá, Sierra de Pocolhá, Meseta de Cobán, Sierra de Pansal, Sierra de Xucaneb), 10 = Sierra de Omoa, 11 = Sierra de Merendón, 12 = Guatemalan Plateau, 13 = Las Nubes block.

ing of this interesting group of frogs. Much remains to be learned about their morphology, physiology, reproduction, behavior, and relationships with one another. On the basis of our own experience, we offer the following suggestions for future research.

1. Collecting.—The distributions of some species are poorly known, and some regions within the range of the genus have not been collected. An effort should be made to secure adequate series of *P. lacertosa* and *P. pychnochila,* including larvae. Detailed information on these two species might help substantially to resolve the polytomy in our phylogenetic tree. Several highland areas in Nuclear Central America need to be collected more extensively and may reveal surprises concerning *Plectrohyla.* These areas include the isolated high peaks in southeastern Guatemala (collections are available only from the Las Nubes block), the northern slopes of the Sierra de los Cuchumatanes, and the Sierra de Chuácas and Sierra de Merendón in Guatemala. Neither of these ranges has been collected, and both should be inhabited by *Plectrohyla.* Habitat destruction continues at an ever-increasing rate in the highlands of Nuclear Central America. Recent field work indicates that *Plectrohyla* has disappeared from some of the streams where previously we found them to be common.

2. Alpha taxonomy.—The status of many populations still is questionable. These include *P. acanthodes* and *P. ixil* on the Meseta Central de Chiapas, Mexico, and in the Sierra de los Cuchumatanes in Guatemala, *P. glandulosa* in the southeastern highlands of Guatemala and adjacent Honduras, and *P. sagorum* in El Salvador. The broad distribution of *P. hartwegi* and the geographic variation displayed by that species suggest that more than one species may be included therein.

3. Molecular systematics.—Analyses of allozymes and mitochondrial DNA should be helpful in detecting cryptic species and in determining phylogenetic relationships. This approach will permit a refined evaluation and reconciliation of data sets by the combination of phylogenetic trees in the manner of Hillis and Davis (1986). Molecular approaches necessitate the collection of tissues, which at the present time are available for only a few species.

4. Behavior.—Extensive field observations and controlled laboratory experiments are needed on intrapecific interactions. Several questions need to be addressed: (1) In the absence of vocalization, how are mates located? (2) Is mate selection by male choice or female choice? (3) What is the behavioral sequence leading to male-male combat? (4) Are there interspecific differences in aggressive behavior? (5) How long are individuals active at breeding sites and are territories defended? (6) What effects do aggressive behavior have on breeding populations? Two species of *Plectrohyla* have notable flash colors; *P. hartwegi* has bold dark and light bars on the flanks and hidden surfaces of the hind limbs, and *P. pokomchi* has bright red webbing on the feet. Are these colors used in advertisement of territories, in mate attraction, species recognition, or do they have some other non-reproductive function (e.g., predator avoidance)? Perhaps *P. pokomchi* displays the bright webbing in the manner de-

scribed for the Bornean ranid *Staurois parvus* (= *S. tuberilinguis*) by Harding (1982).

SUMMARY

Frogs of the genus *Plectrohyla* inhabit the uplands of Nuclear Central America from the Isthmus of Tehuantepec, Mexico, eastward to north-central Honduras. Fifteen species are recognized in the genus; two of these, *P. acanthodes* and *P. teuchestes*, are named and described herein, and expanded descriptions are provided for *P. guatemalensis*, *P. hartwegi*, and *P. lacertosa*. The species of *Plectrohyla* differ from one another in size, coloration, skin texture, nature of the prepollices, and features of the oral discs of the tadpoles. Keys are provided for the identification of adults and larvae (tadpoles of *P. lacertosa* and *P. pychnochila* are unknown).

Frogs of this genus deposit their eggs in mountain streams, where the generalized stream-type tadpoles seemingly undergo lengthy periods of development. Males of at least some species seem to be territorial and engage in male-male combat. Scars on adult males evidently result from wounds inflicted by prepollical spines.

A phylogenetic analysis of morphological characters shows that the *Hyla bistincta* group is the sister-group to *Plectrohyla;* the two lineages are united by four synapomorphies. Six additional synapomorphies diagnose *Plectrohyla* as a monophyletic group. The relationships of most of the species of *Plectrohyla* have not been resolved; a strict consensus tree reveals a polytomy of 11 clades, which include four pairs of sister-species.

Further collecting is needed in order to define the ranges of the species, to obtain additional material of some species, and to establish the occurrence of *Plectrohyla* in some previously uncollected mountain ranges. The status of some populations, especially those of *P. hartwegi*, needs to be evaluated on the basis of new kinds of data. Analyses of allozymes and mitochondrial DNA are needed to resolve some of the phylogenetic relationships. Field observations and controlled laboratory experiments are needed in order to evaluate intraspecific behavior, particularly male-male aggression.

RESUMEN

Las ranas del género *Plectrohyla* viven en los terrenos elevados de América Central Nuclear desde el Istmo de Tehuantepec, México, hacia el este hasta la región norcentral de Honduras. Se reconocen 15 especies en el género; aquí se describen dos, *P. acanthodes* y *P. teuchestes*, y se provéen descripciones nuevas de *P. guatemalensis*, *P. hartwegi*, y *P. lacertosa*.

Las especies de *Plectrohyla* se distinguen por características de tamaño, coloración, textura de la piel, condición de los prepólices, y morfología de la boca de los renacuajos. Se provéen claves para la identificación de ejemplares adultos y sus renacuajos (no se conocen los renacuajos de *P. lacertosa* ni de *P. pychnochila*).

Ranas de este género depositan sus huevos en corrientes de los altiplanos y tierras altas donde sus renacuajos generalizados (que se han adaptado a corrientes fuertes) se desarrollan por un período extenso. Los machos de algunas especies son territoriales y pelean entre ellos mismos. Las cicatrices que hemos observado en machos adultos son los resultados de heridas causadas por las espinas de los prepólices.

Un análisis filogenético de las características morfológicas demuestra que el grupo que incluye *Hyla bistincta* es el grupo-hermano de *Plectrohyla;* los dos linajes están unidos por cuatro sinapomorfias. A razón de seis sinapomorfias adicionales se declara *Plectrohyla* como un grupo monofilético. Las relaciones de la mayor parte de las especies de *Plectrohyla* no han sido resueltas; un árbol de consenso estricto revela una politomía de 11 clados, los cuales incluyen cuatro pares de especies hermanas.

Colectas más amplias son necesarias para delimitar los rangos de las especies y para confirmar la existencia del género *Plectrohyla* en las sierras y montañas aún no colectadas. Se necesita evaluar con otros datos la posición taxonómica de algunas poblaciones, sobre todo las de *P. hartwegi*. Para resolver algunos de los parentescos se necesitan análisis de alozimas y DNA mitocondrial. Es indispensable llevar a cabo observaciones cuidadosas de campo y análisis controlados de laboratorio para evaluar el comportamiento intraespecífico de los individuos, con énfasis particular en la agresión entre machos.

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APPENDIX

SPECIMENS EXAMINED

Localities followed by an asterisk (*) could not be found on available maps and are not plotted on the distribution maps.

Plectrohyla acanthodes.—GUATEMALA: HUEHUETENANGO: 9.5 km W, 8.5 km S of La Democracia, 2250 m, MVZ 114799; San Juan Ixcoy, 2200 m, KU 58835; 3 km E of San Juan Ixcoy, 2250 m, UMMZ 120083. MEXICO: CHIAPAS: Cerro Paschtal, 1500 m, UMMZ 87864; Chen Senvilmut, 3 km N Huistán, KU 125453, 125455; Cueva Mapachero, 3 km N Huistán, KU 125454; 3.6 km S of Rayón Mescalapa, 1550 m, KU 63032 (tadpoles); 5.6 km S of Rayón Mescalapa, 1680 m, KU 58822 (paratype), 60031 (tadpoles); 6.2 km S of Rayón Mescalapa, 1690 m, KU 58823 (paratype), 58824 (holotype), 58825 (paratype), 58826—29 (young), KU 59832 (skeleton), KU 60033 (tadpoles); 4.5 km N Pueblo Nuevo Solistahuacán, UTEP 4383 (tadpoles); 14.7 km NW Pueblo Nuevo Solistahuacán, 1575 m, KU 75336–38 (paratypes); 15.2 km NW Pueblo Nuevo Solistahuacán, 1540 m, CAS 122621–22 (paratypes), KU 75341–42 (paratypes); 18 km NW Pueblo Nuevo Solistahuacán, 1560 m, UMMZ 121516–17 (paratypes), 124856–57 (paratypes), 128384 (tadpoles); head of Pemex road, top of Río Hondo, E Jitotol, CAS 169855; Río Hondo, 9.5 km S of Pueblo Nuevo Solistahuacán, 1700 m, KU 58830 (tadpoles); 4 km W of San Cristóbal de Las Casas, UMMZ 94432–33.

Plectrohyla avia.—GUATEMALA: QUEZALTENANGO: Finca El Faro, south slope of Volcán Santa María, 1690 m, KU 209778 (tadpole), UTA A-24646, A-24798–800 (tadpoles); Finca El Faro, south slope Volcán Santa María, 2000 m, UTA A-15248–49 (young); Granja Lorena, 6 km SW San Martín, 1760 m, UMMZ 102280 (holotype). SAN MARCOS: Finca Insula, ca. 14 km (by road) W San Marcos, 2200 m, MVZ 104472; 2–4 km WNW Palo Gordo, 2500–2700 m, MVZ 104474. MEXICO: CHIAPAS: El Chichiquite*, UIMNH 55538; Región de Soconusco, KU 106295 (skeleton), UIMNH 33690–91; Volcán Tacaná, 8.0–8.5 km N Unión Juárez, 2000 m, KU 94016–17.

Plectrohyla dasypus.—HONDURAS: CORTÉS: El Cusuco, Sierra de Omoa, 5.6 km WSW Buenos Aires, 1530–1690 m, CAS 170006, KU 186025 (holotype), 186026–33, 186035 (tadpoles), 186036–37 (young), 186038 (tadpoles), 192879 (tadpoles), 209653–56, 209698 (skeleton), 209703–04 (young).

Plectrohyla glandulosa.—EL SALVADOR: CHALATENANGO: Cerro El Pital, KU 184948; Los Esemiles, MVZ 39858. GUATEMALA: No specific locality: BMNH 1940.2.20.40–41 (syntypes). HUEHUETENANGO: Laguna de Vejcha, 5.5 km S San Mateo Ixtatán, 3040 m, KU 104019 (young); 3 km S Paquix, 175 m, UMMZ 120085 (7); 8 km S Paquix, 3300 m, KU 58703–811, 58812 (young), 59827–30 (skeletons), 59943–47 (skeletons), 60029 (tadpoles), 104192 (tadpoles); 1.5 km E San Mateo Ixtatán, 2480 m, KU 104193; Todos Santos, 2530 m, UMMZ 120084, 120464; 2.5 km N Toquiá, 3300 m, KU 58699–700. JALAPA: 8 km E Mataquescuintla, La Soledad Grande, FMNH 68716–20, 68722–27. QUEZALTENANGO: 37 km SE Malacatancito, 2630 m, KU 68552 (tadpoles); 6 km N San Carlos Sija, 2890 m, KU 58815–21. SAN MARCOS: 1–2 km N, 1–1.5 km W El Rincón, 2800–2860 m, MVZ 109406; 2 km WSW El Rincón, 2800–2880 m, MVZ 113701–02, 113703–04; ridge above El Rincón, MVZ 149403; 1 km E Ixchiguán, 3150 m, UMMZ 98339 (tadpoles); 2 km NW Ixchiguán, 3480 m, MCZ 27800, UMMZ 95902 (holotype of *P. cotzicensis*), 95903–6, 95908; 5 km W Ixchiguán, UMMZ 98340 (tadpoles); 5.5 km (airline) W San Marcos, 2700 m, MVZ 104677; 6.5 km (airline) W San Marcos, 2650 m, MVZ 104673; 9.5 km (road) W San Marcos, 2500 m, MVZ 132359; Volcán Tajumulco, FMNH 20302. SOLOLÁ: Los Encuentros, 3190 m, UMMZ 126314 (12), 126330. TOTONICAPÁN: Desconsuelo*, UMMZ 117978; María Tecún, 21 km ESE Totonicapán, 3000 m, KU 104194 (tadpoles), MVZ 104671, UMMZ 100508, 100518–19 (tadpoles), 123338; 13.4 km N San Carlos Sija, 3000 m, KU 58813–14. HONDURAS: LEMPIRA: E slope Cerro Celaque, 2450–2700 m, KU 195455–62, 209657–62, 209699 (skeleton), 209705 (tadpoles).

Plectrohyla guatemalensis.—EL SALVADOR: MORAZÁN: Cantón Palo Blanco: 11 km NE Perquin, KU 184785. SANTA ANA: Cerro Metapán, 2200 m, KU 61950; Hacienda Montecristo, Cerro Metapán, 2200 m, KU 61945–48, 61952–54, UMMZ 118411–12; Hacienda Los Planes, Cerro Miramundo, 1950 m, KU 61951; Miramundo, FMNH 65116–18; Trifinio, 1800 m, KU 61949. GUATEMALA: CHIMALTENANGO: Tecpán, AMNH 70202 (tadpoles); Patzicía, MNHN 6332 (2) (syntypes). EL QUICHÉ: Chiul Cunén, 2500 m, KU 190233; Río Las Violetas, Nebaj, UMMZ 90220 (tadpoles). ESCUINTLA: South slope Volcán de Agua, Finca Rosario Vista Hermosa, 1600–1750 m, UTA A-25386–87. GUATEMALA: Las Nubes block, 11 km E San José Pinula, 2150 m, UMMZ 100520 (tadpoles), 100523 (tadpoles); San Jorge Muxbal, UTA A-4353–54, A-5497–99, A-5501–02, A-14647. JALAPA: Asseradero San Lorenzo, UMMZ 106782 (3), 130022 (tadpoles); La Soledad, UMMZ 130027 (tadpoles); 8 km E Mataquescuintla, La Soledad Grande, FMNH 68721. JUTIAPA: Jutiapa, UMMZ 130029 (tadpoles). QUEZALTENANGO: Granja Lorena, 13 km NNE Colombá, 1750 m, KU 103163, 117438 (skeleton), UMMZ 107734, 116565–66 (tadpoles); 10.5 km SSW San Martín Sacatepéquez, 2050 m, KU 64098. SAN MARCOS: Río Achute, below Tacaná, UMMZ 98338 (tadpoles); Tacaná, UMMZ 95911; Tejutla, UMMZ 95912. SOLOLÁ: Panajachel, MCZ 11150; falls, 2.7 km NW Panajachel, 1700 m, KU 58834, UMMZ 95913–14, 98337 (tadpoles). TOTONICAPÁN: Momostenango, UMMZ 95909–10. HONDURAS: COMAYAGUA: Montaña del Comayagua, above Río Negro, 1640 m, KU 209683–84, 209707 (tadpoles). COPÁN: Quebrada Grande, 1370 m, KU 209685, 209706 (tadpoles). FRANCISCO-MORAZÁN: Cerro Cantagallo, near Lepaterique, 1840 m, KU 209687–88. LEMPIRA: E slope Cerro Celaque, 2490 m, KU 209666–73; Naranjos, above Villa Verde, E slope Cerro Celaque, 1930–1940 m, KU 209663–65, 209700 (skeleton), 209709 (tadpoles). OCOTEPEQUE: El Chaqüitón, 18.8 km SE Corquín, Cordillera de Celaque, 1870 m, KU 209674; El Portillo de Ocotepeque, 1900 m, KU 209675–81, 209701 (skeleton); El Volcán, 1760 m, KU 209682; 20 km E Nueva Ocotepeque, LACM 47245–46. OLANCHO: Sierra de Agalta, 1000 m, KU 209686, 209708 (tadpoles). YORO: Portillo Grande, FMNH 34694–95, 34698–99. MEXICO: CHIAPAS: Chicomuselo, UMMZ 94430–31; El Chiciquite, UIMNH 55539; Letrero*, UMMZ 94429; Región de Soconusco, UIMNH 33692; Volcán Tacaná, 8–8.5 km N Unión Juárez, 2000 m, KU 94018, 94147 (tadpoles).

Plectrohyla hartwegi.—GUATEMALA: BAJA VERAPAZ: Biotopo Mario Dary (Vuelta del Quetzal), UTA A-5358–64, A-5366, A-5368–69; 0.8 km NE entrance to Biotopo Mario Dary, 1676 m, KU 186464; 1 km N, 1 km E entrance to Biotopo Mario Dary, UTA A-5953–57; Cerro Verde, UTA A-5507–08; East face of Cerro Verde, UTA A-5354–55, A-5357; La Unión Barrios, 1615–1829 m, KU 190234–35; 3.5 km E La Unión Barrios, 1585–1707 m, KU 190238–40; Plantación Santa Teresa, Río Chipilín, 1615 m, KU 186469, UMMZ 152864, UTA A-5353, A-5367; 0.0–4.0 km SE Pu-

rulhá, UTA A-7653–57; 1.6–7.7 km SE Purulhá, UTA A-7658–60; 2.4–4.3 km SE Purulhá, 1524–1720 m, KU 186463, 186466–68, 186470, 190236–37, 190241–42, 190257, 190259, 192443 (skeleton), 192467 (tadpoles), UTA A-7661–72, A-8724 (tadpoles), A-8729 (tadpoles); 2.1 km S, 1.5 km E Purulhá, UTA A-17298; 2.3 km S, 2.0 km E Purulhá, UTA A-7953, A-17292, A-17294–97. EL QUICHÉ: Santa Rosa Pass, 9 km NE Santa Cruz del Quiché, 2520 m, MVZ 160444–77. HUEHUETENANGO: Barillas, 1730 m, LACM 40171; Finca Chiblac, 10 km NE Barillas, 925 m, MVZ 134651; Hacienda Santa Gregorio, near Barillas, 1350–1375 m, UMMZ 129885. ZACAPA: Finca Sitio Nuevo, Río Portón, Sierra de las Minas, 1896 m, KU 190260–62, 191258–59 (tadpoles). HONDURAS: LEMPIRA: East slope Cerro Celaque, 1920–2700 m, KU 209690–94. MEXICO: CHIAPAS: Barrejonel, UMMZ 94228 (holotype); Cerro Tres Picos, 2134 m, CAS 169870 (young); Paraje El Triunfo, N Mapastepec, 2050 m, KU 58873; Volcán Tacaná, 8.5 km N Unión Juárez, 2000 m, KU 94019. OAXACA: Cerro Azul, UIMNH 40837.

Plectrohyla ixil.—GUATEMALA: EL QUICHÉ: Finca San Francisco, 25 km NE Nebaj, 1175 m, UMMZ 89092 (holotype), 89093–94, 89168; Finca Tesoro, UMMZ 90222 (tadpoles). MEXICO: CHIAPAS: ridge between Pantepec and Tapalpa, 1768 m, CAS 169872–73; 2 km NW Pueblo Nuevo Solistahuacán, 2250 m, UMMZ 119950–51; 11–11.3 km NW Pueblo Nuevo Solistahuacán, 1540–1575 m, KU 75344–64, 75365 (tadpoles); 15 km N Pueblo Nuevo Solistahuacán, 1640 m, UMMZ 124848–49, 124850 (2), 124854 (9), 18 km N Pueblo Nuevo Solistahuacán, 1560 m, UMMZ 124851 (2), 124853 (6), 124855; 28 km N Pueblo Nuevo Solistahuacán, UMMZ 124852; 3.6 km S Rayón Mescalapa, 1550 m, KU 60034 (tadpoles); 5.6 km S Rayón Mescalapa, 1680 m, KU 58853–60, 59833 (skeleton); 6.2 km S Rayón Mescalapa, 1690 m, KU 58836–52, 58861–68 (young), 59834–36 (skeletons), 60035 (tadpoles), 101027–29, UTEP 5248–50.

Plectrohyla lacertosa.—MEXICO: CHIAPAS: Cerro Tres Picos, 2134 m, CAS 169860–61, 169865–69, KU 209804–05, 209806 (skeleton); Región de Soconusco, UIMNH 33693 (holotype).

Plectrohyla matudai.—GUATEMALA: CHIMALTENANGO: Acatenango, AMNH 128013–24; Finca Recreo, about 5 km SW Yepocapa, UMMZ 116569 (6). GUATEMALA: Las Nubes block, 11 km E San José Pinula, 2150 m, UMMZ 100521–22 (tadpoles). ESCUINTLA: South slope Volcán de Agua, Finca Rosario Vista Hermosa, 1000 m, UTA A-18201–03, A-24650–51, A-24960–61. HUEHUETENANGO: Finca Injerta, 5 km N Casa Grande, UMMZ 126451. QUEZALTENANGO: South slope Volcán Santa María, Finca El Faro, about 4 km N El Palmar, 700 m, UTA A-24648–49, A-24652–62, A-24801–02 (tadpoles), A-25388 (young). SAN MARCOS: El Porvenir, FMNH 20762 (4), 20764 (8); Finca La Paz, near La Reforma, 1325 m, KU 58869–71, 59948 (skeleton), 60037 (young), 60063 (tadpoles), UMMZ 107738 (6), 116567–68 (tadpoles); 9 km W, 3.5 km S San Marcos, 1630 m, MVZ 104675. SUCHITEPÉQUEZ: Finca El Naranjo, W slope Volcán Santa Clara, UIMNH 46200–09. HONDURAS: COPÁN: Quebrada Grande, base of Cerro Azul, 1370 m, KU 195447–54, 209711 (young). MEXICO: CHIAPAS: Cerro Ovando [=Obando], 1800 m, MCZ 25651, UIMNH 30672 (tadpoles), 30673, UMMZ 87869–70, 87875, 88365 (5), 88863 (holotype), 88864; Cerro Tres Picos, 1850 m, UIMNH 37410; Cerro Tres Picos, 2134 m, CAS 169858; northeast base Cerro Tres Picos, 1372 m, CAS 169857; El Rastrojo*, 1230 m, UIMNH 37411; Las Nubes, Cerro Obando, USNM 111094–121; Montecristo, UMMZ 88346; Municipio Motozintla, 5 km E Toliman, 1372 m, CAS 169871; Región de Soconusco, CAS 87821, MCZ 24577, UIMNH 33825–33; Rodillo*, 16 km S Chiltepec, UMMZ 87865–67; Unión Juárez, UIMNH 55338. OAXACA: Cerro Baúl, UIMNH 33835; Colonia Rodulfo Figueroa, 19 km NW Rizo de Oro, 1524 m, UTA A-13455–56; 19.2 km W Rizo de Oro, along ridge S Cerro Baúl, 1524 m, CAS 169862 (tadpoles); Río Ostuta, between Sierra Madre and Cerro Atravesado, AMNH 53758–60, 53761 (holotype of *P. brachycephala*), KU 28079; stream near Cerro Baúl, UIMNH 40787; N of Zanatepec, 925 m, UIMNH 52960; 19 km NNE Zanatepec, 1510 m, LSUMZ 7559.

Plectrohyla pokomchi.—GUATEMALA: ALTA VERAPAZ: Finca Chichén, UMMZ 90219 (tadpoles). BAJA VERAPAZ: Biotopo Mario Dary (Vuelta de Quetzal), 1615 m, UTA A-5357 (tadpoles), A-5359–60 (tadpoles), A-5365; Cerro Verde, E Unión Barrios, UTA A-5356, A-5509; 2.4 km S, 2.0 km E Purulhá, UTA A-7953; 3.4 km SE Purulhá, 1585–1676 m, KU 186715 (tadpoles); 3.8 km SE Purulhá, 1463–1615 m, KU 186713 (tadpoles), UTA A-8726–27 (tadpoles); Riachuelo Colorado, 3.8 km SE Purulhá, 1494–1707 m, UTA A-7436, KU 186714 (tadpoles), 191260–61 (tadpoles), 191266–71 (tadpoles), UMMZ 152863 (tadpoles); Riachuelo Colorado, 2.2 km S, 1.8 km E Purulhá, 1585 m, UTA A-1816–17 (tadpoles); Río Chipilín, Cerro Quisís, 1615 m, KU 190229 (skeleton); Río Chipilín, 7.7 km SSE Purulhá, 1615 m, UTA A-8731 (tadpoles); Río Sananjá, 3.5 km E La Unión Barrios, 1585–1707 m, KU 190231 (holotype), 190232, 191265 (tadpoles), UTA A-5510; vicinity La Unión Barrios, 1615–1829 m, KU 190228, 190230, UTA A-6171; 3 km ESE La Unión Barrios, 1670 m, KU 191264 (tadpoles). EL PROGRESO: Finca Bucaral, UMMZ 130030 (tadpoles), 130033 (tadpoles). ZACAPA: Finca Planada, 15 km NNE Río Hondo, 1700 m, MVZ 160443 (young), 160478 (tadpoles), 160483 (young); Finca Sitio Nuevo, Río Portón, Sierra de las Minas, 1896 m, KU 190258 (young), 191262–63 (tadpoles), 191272–76 (tadpoles).

Plectrohyla pychnochila.—MEXICO: CHIAPAS: 5 km NNW San Cristóbal de Las Casas, TCWC 17459. VERACRUZ: Coyame, AMNH 62667 (holotype).

Plectrohyla quecchi.—GUATEMALA: ALTA VERAPAZ: Finca Chichén, UMMZ 89090–91; Finca Los Alpes, 1000 m, KU 60038 (tadpoles), 64107 (skeleton), 64108–15, 68172 (skeleton), 68553–54 (young), UMMZ 89086 (holotype), 89087–89. BAJA VERAPAZ: 1.3 km SE Biotopo Mario Dary, KU 186471; Niño Perdido, UTA A-5506; Plantación Santa Teresa, Río Chipilín, 1615 m, KU 186473; 2.3 km S, 2.0 km E Purulhá, 1600 m, UTA A-5958, A-17293; 3.8–3.9 km SE Purulhá, 1585–1707 m, KU 186472, 190243–50, 190255–56, 191278–79 (tadpoles), 191280–82 (eggs), 191283–84 (tadpoles), UTA A-7433–34, A-8725 (tadpoles), A-8730 (tadpoles); Riachuelo Colorado, 2.2 km S, 1.8 km E Purulhá, 1585 m, UTA A-8717 (tadpoles); Río Sananjá, 3.5 km E La Unión Barrios, 1585–1707 m, KU 190251–54; San Antonio, 8 km ESE Chilascó, 1850 m, MVZ 160479–80; 3 km ESE La Unión Barrios, KU 191277 (tadpoles). HUEHUETENANGO: Barillas, 1730 m, LACM 40162–81, 40182–204 (tadpoles). ZACAPA: Volcán de Cos, 11 km W Santa Cruz, 615 m, MVZ 160481–82.

Plectrohyla sagorum.—EL SALVADOR: CHALATENANGO: Los Esemiles, MVZ 39859. GUATEMALA: QUEZALTENANGO: Granja Lorena, 13 km NNE Colombá, 1750 m, KU 103164–66, 104195 (tadpoles), 117439 (skeleton), MVZ 113702, UMMZ 107735 (2), 107736 (3), 107737, 116563–64 (tadpoles); 10.4 km WSW San Martín Sacatepéquez, 2000 m, KU 60039 (tadpoles); 10.5 km WSW San Martín Sacatepéquez, 2050 m, KU 68555 (tadpoles). SAN MARCOS: Volcán Tajumulco, 1700 m, FMNH 20392, 20653 (3), 24104. MEXICO: CHIAPAS: Cerro Ovando [=Obando], 1800 m, MCZ 24538, UIMNH 15187, 30671, UMMZ 87868, 87871, 87872 (5), 87873, 87874 (7), 88862 (holotype), 89757; Chicomuselo, UMMZ 94418–27; Colonia Talquian, Volcán Tacaná, 1450 m, MVZ 159513; El Chiciquite*, UIMNH 55535–37; El Fenix, 8 km N Monserrate, UMMZ 107987–89; Las Nubes, Cerro Ovando [=Obando], USNM 111122–38, 118659; Montecristo, UMMZ 89758; Paraje El Triunfo, N Macastepec, 2050 m, KU 58872, UMMZ 95172; Región de Soconusco, UIMNH 33821–24, 33854; Volcán Tacaná, 8 km N Unión Juárez, 2000 m, KU 94020–32.

Plectrohyla tecunumani.—GUATEMALA: HUEHUETENANGO: 1 km E Chemal [=Xemal], 3395 m, KU 192454–57, 192458 (skeleton), 192459 (tadpoles), LACM 39934–55, 39956 (holotype), 39957–61, 39962–72 (tadpoles); 12.9 km N Chiantla, UTA A-24803–06 (tadpoles); 2.6 km N Huehuetenango, 3200 m, TCWC 23602.

Plectrohyla teuchestes.—GUATEMALA: ALTA VERAPAZ: Finca Los Alpes, 1000 m, FML 3500/1–2 (paratypes), KU 58831 (holotype), 58832–33 (paratypes), 59831 (skeleton), 60054 (tadpoles), 64099–104 (paratypes), 68522 (tadpoles), UMMZ 128404 (tadpoles), 139509 (tadpoles). HONDURAS: CORTÉS: El Cusuco, 5.6 km WSW Buenos Aires, Sierra de Omoa, 1530–1640 m, KU 192880–84, 194178 (tadpoles), 209695–97, 209710 (young).