Zootaxa 2719: 21–34 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new species of fringe-limb frog, genus *Ecnomiohyla* (Anura: Hylidae), from the Atlantic slope of Costa Rica, Central America

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Abstract

A new moderate-sized species of fringe-limb treefrog of the genus *Ecnomiohyla* is described from the Atlantic premontane slope of central Costa Rica. It differs primarily from other members of the genus in having the combination of cephalic and dorsal osteoderms, extensive digital webbing, a pointed prepollical bony projection in adult males, and the fleshy scalloped fringe on the hindlimb continuing across the heel. Additional material of the related but much larger species, *Ecnomiohyla miliaria*, is documented from localities of virtual sympatry for the two taxa. The presence or absence of sexually dimorphic male features: bony humeral projection, prepollical bony projection, and keratinized black spines on the thumb and prepollex are summarized for the ten members of the genus. *Hyla tuberculosa*, recently referred to the genus does not belong to this clade and is regarded as *incertae sedis*.

Key words: Anura, Central America, Costa Rica, Guayacán, *Ecnomiohyla miliaria*, *Ecnomiohyla sukia* **sp. nov.**, new species

Resumen

Describimos una nueva especie de rana del género *Ecnomiohyla* de la vertiente Atlántica central de Costa Rica. Esta nueva especie se diferencia de las otras especies del género por la combinación de las siguientes características: osteodermos cefálicos y dorsales presentes; membranas interdigitales extensas; presencia de una estructura prepólica ósea y protuberante en machos adultos; un pliegue ondulado que se extiende desde el talón hasta la parte distal del dedo V. Reportamos material adicional de la especie relacionada y de mayor tamaño, *Ecnomiohyla miliaria*, de localidades donde aparece en simpatría con la nueva especie. También presentamos un resumen sobre la presencia o ausencia de la estructura prepólica, caraterística sexualmente dimórfica, para las diez especies del género *Ecnomiohyla*. Además, concluimos que la especie *Hyla tuberculosa*, que fue recientemente incluida en *Ecnomiohyla*, no pertenece a este género y debe ser considerada como *incertae sedis*.

Palabras Claves: América Central, Anura, Costa Rica, *Ecnomiohyla miliaria*, *Ecnomiohyla sukia* **sp. nov.**, especie nueva, Guayacán

Introduction

Among the most distinctive members of the Neotropical anuran fauna are the moderate to very large species of canopy inhabiting frogs of the genus *Ecnomiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005. Members of the genus, as currently understood following Mendelson *et al.* (2008), are immediately recognizable by having immense hands and feet, large digital disks, scalloped fleshy fringes along the outer margins of the forearm and foot, and enlarged prepollices in adult males. The first species of this group to be recognized was described as *Hypsiboas miliarius* by Cope (“1885”, 1886) from a single moderate sized male (USNM 14193) collected by Dr. John F. Bransford of the Nicaragua Canal Surveying Expedition of 1885 along the Río San Juan between El Castillo and San Juan del Norte, southern Nicaragua

Accepted by S. Castroviejo: 21 Oct. 2010; published: 10 Dec. 2010

(Savage, 1973). A second individual of the group was described as *Hyla phantasmagoria* by Dunn (1943) based on a single adult male (95 mm in standard length) from Colombia having a pointed and recurved prepollical spine.

No additional examples of these elusive frogs were discovered in Mesoamerica during the intervening 64 years following Cope's description of *Hypsiboas miliarius* until Edward H. Taylor collected two specimens of the species now called, *Ecnomiohyla fimbrimembra* (Taylor, 1948) on the Atlantic slope of the Cordillera Volcánica of Costa Rica. He described the adult female as *Hyla richardi* and the juvenile as *Hyla fimbrimembra*. The name *H. richardi* was preoccupied so Taylor (1954) renamed the species *H. richardtaylori*. The two nominal forms are now considered synonyms (Duellman, 1970, 2001; Savage, 2002) but as *H. fimbrimembra* predates *H. richardtaylori* the former is the applicable name. Later, in 1951, Taylor (1952) collected a single spectacular large male (100 mm in standard length) of fringe-limb frog with a pointed and recurved prepollical spine from a locality at a somewhat lower elevation on the Atlantic slope of Costa Rica, which he named *Hyla immensa*. Taylor made reference to Dunn's Colombian species, stated it was a female, but did not comment on possible diagnostic features separating the two nominal taxa. Taylor (1954) listed *Hyla miliaria* Cope (1886) as distinct from the three nominal taxa that he described from Costa Rica.

Subsequently, as additional specimens were collected, Duellman (1970; 2001) in his classic monograph on the hylid frogs of Mexico and Central America, concluded that both *Hyla immensa* and *Hyla phantasmagoria* were conspecific with Cope's *Hypsiboas miliarius* and applied the name *Hyla miliaria* to the species.

During the 1990's fieldwork by several individuals (e.g., Solórzano, "1997", 1998; "2001", 2002; Kubicki, 2008) working with Miguel and Norberto Solano discovered an extremely rich hot spot for amphibians and snakes in the region near Guayacán. Limón Province, Costa Rica. Early on, among the frequently heard and often collected frogs, were large males identical in significant features with the holotype of *Hyla immensa* Taylor. At the same time it appeared that a second smaller species of fringe-limb frogs occurred in the Guayacán area. W.W. Lamar provided a photograph of this form for Duellman's (2001) updated *Hylid frogs of Middle America* athat served as the basis for the painting labeled *Hyla fimbrimembra* (pl.74, fig.2) in that book. Since that time additional material and information has been gathered in the field by the junior author that fully confirms that two species are involved and neither is conspecific with *E. fimbrimembra*. In the present paper we review the application of the name *E. miliaria* as a senior synonym to *E. immensa* and *E. phantasmagoria* and describe the small fringe-limb frogs from Guayacán as a new species.

Savage and Heyer ("1968", 1969) and Duellman (1970, 2001) recognized the several species of fringe-limb hylids as a distinctive cluster of taxa, that they informally called the *Hyla miliaria* group. Savage (2002) used the term *Hyla tuberculosa* group for the same species. Faivovich *et al.* (2005) based on genetic evidence proposed the name *Ecnomiohyla* for the group. At the same time they assigned *Hyla dendrophasma* Campbell, E. Smith, and Acevedo, 2000, originally placed in the *miliaria* species group by its authors to *Ptychohyla*. In addition, Faivovich et. al. (2005) included *Hyla miotympanum* Cope, 1863 in *Ecnomiohyla*. They further noted that their putative new genus probably was non-monophyletic (= non-holophyletic) and probably would be found to consist of two or three clades.

Eight of the ten species referred to *Ecnomiohyla* by Faivovich *et al.* are characterized by having scalloped dermal fringes on the outer margin of the forearm and foot, large digital disks, and enlarged prepollices. As *Hyla miotympanum* lacks these features we do not consider it further in the following account and regard its assignment to *Ecnomiohyla* as problematic. Recently, Mendelson *et al.* (2008) described a spectacular new species of fringe-limb frog, *Ecnomiohyla rabborum*, from western Panama. The authors of that paper (including us), also concluded that *Ecnomiohyla tuberculosa* (Boulenger, 1882) of the upper Amazon Basin should be considered *incertae sedis* as it lacks the enlarged prepollex and prepollical bony projection characteristic of males of this genus. However, we have included its characteristics in our comparisons to the new taxon in the current account to emphasize its distinctiveness.

Material and methods

Measurements where taken with a Vernier caliper to 0.1 mm. The following are expressed as percentage of snout-vent length (SVL): head length (HL); head width (HW); length of crus (TI); length of foot (FL). The relationship of tympanum width to the diameter of eye (TY/E) is expressed as a percentage of eye diameter.

Webbing formulae follow Savage and Heyer (1967) as modified by Myers and Duellman (1982), and Savage and Heyer (1997) and are detailed in Table 1. For descriptive purposes webbing is recorded as: considerable (C) = not extending to base of disk on one margin of any digit; substantial (S) = extending to base of disk on one margin of one digit; extensive (EX) = extending to base of disk on one margin of two to four digits; full (F) = extending to base of disk on margins of all digits.

Advertisement calls of the new species were recorded on a Sony Digital Handycam HI8mm. The call of *E. miliaria* was recorded on an unknown tape recorder by Michael Fogden. Call analyses were performed using Raven Lite ver. 1.0 software.

Institutional abbreviations follow Leviton *et al.* (1985) and Frost (2009) with the addition of CHP for the Circulo Herpetólogico de Panamá and KRL for the field numbers of K. R. Lips.

Description

***Ecnomiohyla sukia* sp. nov.**
Shaman Fringe-limb Frog
(Figs, 1, 2, 3, 4)

Hyla fimbrimembra Duellman, 2001:898, pl. 74, fig. 3 (in part).

Holotype. UCR 14119, an adult male from Costa Rica: Provincia de Limón: Cantón de Siquirres: Distrito de Siquirres: Guayacán: Alto Colorado, 710 m (N 10˚ 02’ 13.7” W 83˚31’ 22.4”) obtained by Miguel Solano on the 25th of March, 1999.

FIGURE 1. *Ecnomiohyla sukia* new species. Hand (left) and foot (right). Uncataloged paratype.

FIGURE 2. *Ecnomiohyla sukia* new species; a = adult male (basis for pl. 74, fig. 3 in Duellman, 2001) courtesy of W.W. Lamar; b = adult male in essentially uniform color phase; c = adult male in patterned color phase; d = adult male in reddish color phase. All specimens from Costa Rica: Limón: Guayacán: Alto Colorado.

Paratypes. All from Costa Rica: Provincia de Limón: UCR 10966, an adult female: 5km from Moravia de Siquirres toward Turrialba (= Guayácan area) (N 10˚ 02’ W 83˚31’); UCR 15361, an adult female and UCR 15561, an adult female: Guayacán: Alto Colorado, 710 m (N 10˚ 02’ W 83˚31’); UCR 16753, an adult male & UCR 17024, an adult female: S Río Blanco (town): Fila Asunción, (N 9° 54’ W 83° 10’) 400–500 m.

Referred specimen. Costa Rica*: Provincia de Alajuela*: UCR 11176 (metamorph), Reserva San Ramón: Colonia Palmeraña, (no coordinates available) 900 m.

Diagnosis. A moderate sized species of the genus *Ecnomiohyla*, adult males 56.7–63.3 mm in standard length, females 58.1–68.7 mm, differing from other species in the genus by the following combination of characters: 1) fingers extensively webbed (fig. 1a), web reaching base of disk on one margin of two fingers (see Table 1); 2) toes extensively webbed (fig. 1b), web reaching base of disks on one margin of three or four toes (see Table 1); 3) skin on dorsum with many scattered tubercles; tips of granules on venter not tipped with black keratin; 4) cranial and dorsal osteoderms present; 5) skin on upper surface of the head not co-ossified with cranium; 6) humerus without enlarged *crista lateralis*; 7) prepollex well developed, without keratinzed, black spinous excrescences in adult males; 8) prepollical bony projection directed laterally, pointed but not forming a sharp spine; 9) fleshy fringe on foot continuing onto heel as a series of fleshy flaps; 10) upper

surfaces uniform brown, tan or gray or with irregular darker and/or green markings in life; capable of considerable metachrosis.

TABLE 1. Modal webbing formulae for species of *Ecnomiohyla.*

		FINGERS				TOES			
Species	Extent	I – II	II – III	III – IV	Extent	I – II	II – III	III – IV	IV – V
E. echinata	C	2^{+} - 2 ½	1–2	2–1 ½	S	1–2	1–2	1–2	2 – ¾
E. fimbrimembra	C	2 ¼–3	1–2	2–1 ¼	C	1^{+}–2^{+}	1–2	1–2^{-}	2–1
E. miliaria	EX	1 ¾ -2	¾–1 ¼	1 ¼–¾	EX	1–1 ¼	¾–1 ½	¾–1	1–¾
E. minera	EX	2–2	¾–2	2–¾	F	¾–¾	¾–¾	¾–¾	¾–¾
E. phantasmagoria	C	1 ¼ –2	1 – 1^{+}	1 ½–1	EX	¾–1^{+}	¾–1	½–1	1^{+}–¾
E. rabborum	S	2–2 ¼	¾–1 ¼	1–1	EX	1–¼	¾–1 ¼	¾–1	1 ¼–1
E. salvaje	EX	2–2 ½	¾–2	2–¾	F	¾–¾	¾–¾	¾–¾	¾–¾
E. sukia	EX	1 ¾–2	¾–1	1– ¾	EX	¾–1	¾–1	¾–1	1^{+}–¾
E. thysanota	EX	2–2 ¼	¾–1 ½	1–¾$^{+}$	EX	1–1^{+}	¾–1 ¼	¾–1	1–¾
E. tuberculosa	S	2–2 ¼	¾–2 ¼	2–1	EX	¾–2	¾–2	1–2	2–¾
E. valancifer	C	2–2 ½	1 ¾–1	1 ¾–1	EX	1–2	¾–1 ¾	1^{-}–1 ¼	2^{-}–¾

C = considerable = not to base of disk on any digit; S = substantial = to base of disk on one digit; EX = extensive = to base of disk on two to four but not all digits; F = full = to base of disk on all digits.

Diagnostic comparisons are made below to other members of *Ecnomiohyla* with contrasting features for *E. sukia* presented in parentheses (see Tables 1–2 for summary). *Ecnomiohyla echinata* (Duellman, 1962) of Mexico and *E. fimbrimembra* (Taylor, 1952) from Costa Rica and Panama are immediately distinguishable from the new form by having substantially less finger and toe webbing (see Table 1). In addition they have heel tubercles, blunt, rounded prepollical bony projections and keratinized black spinous prepollical excrescences in adult males (fleshy heel flaps, prepollical bony projection pointed, no keratinized, black spines on prepollex). Other species having less extensive finger webbing than *E. sukia* but sharing extensive toe webs with the new form are *E. phantasmagoria* (Dunn, 1943) of Colombia, *E. rabborum* Mendelson, Savage, Griffith, Ross, Kubicki, and Gagliardo, 2008 of Panama, *E. tuberculosa* (Boulenger, 1882) from the upper Amazon Basin and *E. valancifer* (Firschein and H. M. Smith, 1956) of Mexico. *Ecnomiohyla phantasmagoria* has less finger webbing, the prepollical bony projection forming a spine in males, and pointed tubercles on the heel (extensive finger webbing, prepollical projection pointed, heel with fleshy flaps). In *E. rabborum* there is a bony humeral projection and the prepollex is covered with keratinized, black spines in adult males and the heel is without ornamentation (no humeral projection, no keratinized, black spines, heel with fleshy flaps). *Hyla tuberculosa* (fig. 5) lacks an enlarged prepollical bony projection in males and has large tubercles on the heel (enlarged prepollical bony projection present, heel with flesh flaps). *Ecnomiohyla valancifer* has a blunt flattened prepollical bony projection in adult males and two to three large tubercles on the heel (prepollical projection pointed, heel with fleshy flaps). *Ecnomiohyla minera* from Belize and Guatemala and *E. salvaje* from Guatemala and Honduras (Wilson, McCranie, and Williams, 1985) have the cephalic skin co-ossified to the skull, the toes fully webbed, and adult males have a humeral projection, a blunt prepollical projection and keratinized, black spines on the prepollex (no co-ossification, toes with less webbing, no humeral projection, a pointed prepollical projection, no keratinized, black spines on prepollex). The two remaining species of fringe-limb hylids placed in *Ecnomiohyla* having extensive finger and toe webs are *E. thysanota* (Duellman, 1966) of Panama and *E. miliaria* (Cope, “1885”, 1886) of Honduras to Panama. The former differs trenchantly from *E. sukia* in having a granular dorsum and a smooth heel and being uniform green in life (tuberculate dorsum, fleshy flaps on heel, not uniform green). The very large species, *E. miliaria* (to 110 mm in males, 86 mm in females) has the prepollical projection recurved and terminating in a sharp spine in adult males, pointed large tubercles on the heel which are tipped with black keratin in males,

and many large tubercles on the upper head surface and eyelids some of which are tipped with black keratin and others with a light horny material in males, and black keratin tipped over most of the venter and flanks (prepollex not recurved, prepollical projection not terminating in a sharp spine, fleshy flaps on heel, and only a few tubercles on upper surface of head and eyelids, and no ventral and flank black-tipped tubercles).

Description. Head as wide as body, upper lip round in dorsal outline; raised snout truncate in dorsal outline and profile; snout short with nearly terminal protuberant nostrils directed laterally. Top of head flat; internarial area slightly concave; canthus rostralis concave; loreal region concave; upper lip not flared. Upper and lateral surface of head and upper eyelids with scattered tubercles, a few black tipped; a discrete series of tubercles running from midpoint of posterior margin of eye to tympanum; a continuous supratympanic and postympanic series of large tubercles, under laid by bone, that overlap the upper and posterior margin of the raised tympanum and terminate in a cluster of tubercles near angle of jaw; tympanum prominent, opaque, separated from eye by a distance slightly greater than width of tympanum; TY/E 160–180% in males, 126–148 in females. Upper surfaces of body and limbs tuberculate with scattered larger tubercles. Flanks and venter granulate without black tipped tubercles. Arms short and upper arm hypertrophied in males; no distinct transverse dermal fold on wrist; a fleshy scalloped fringe extends from the elbow along the ventrolateral margin of forearm and continues along the outer edge of Finger IV to base of disk; scallops of fringe relatively weak, not deeply incised or pointed, largest on forearm, smaller scallops along finger.

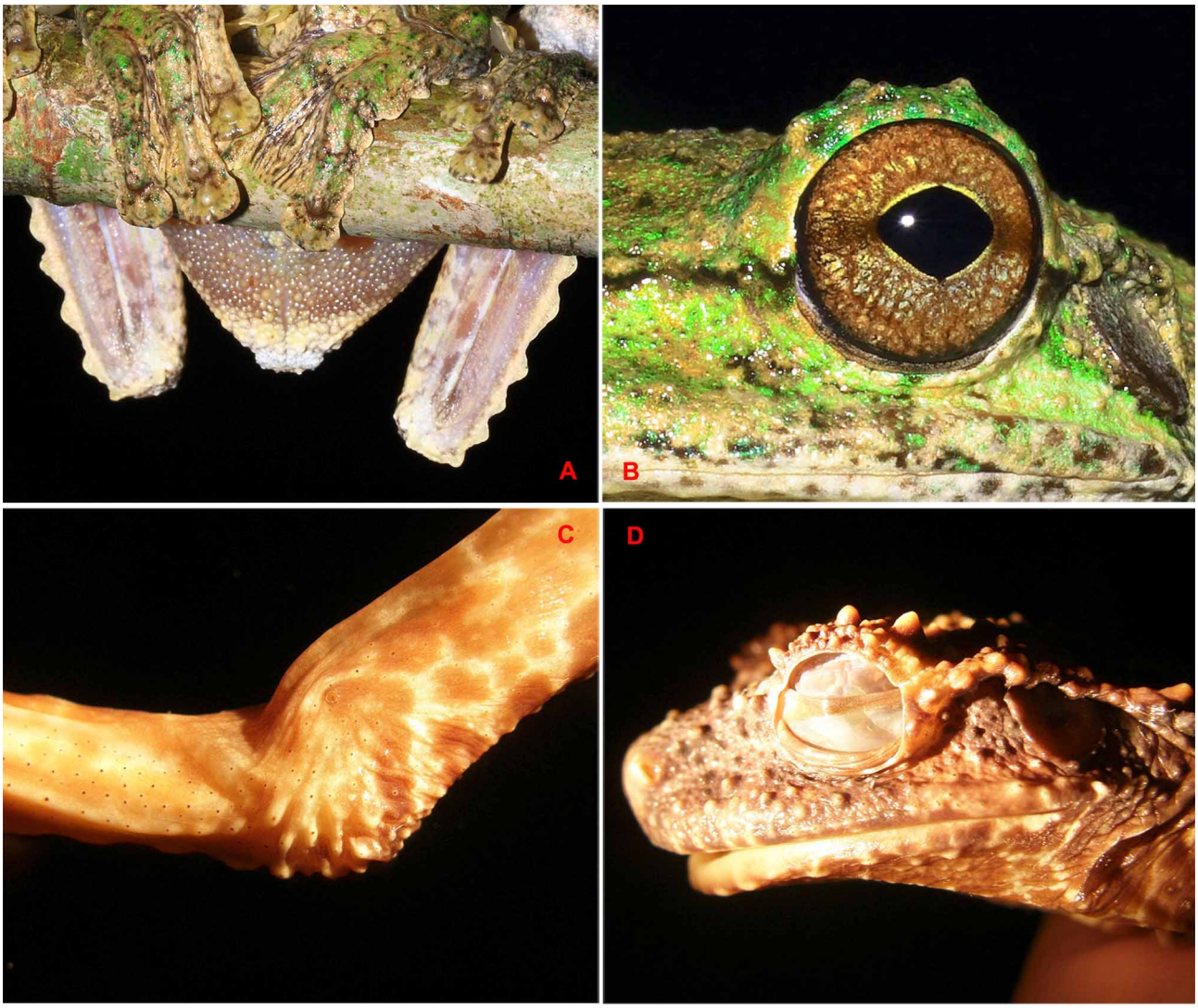

FIGURE 3. *Ecnomiohyla sukia* new species. **a =** adult male showing heel fringe; b = adult male showing low supraorbital tubercles; *Ecnomiohyla miliaria* (Cope); c = heel showing pointed tubercles; d = showing enlarged supraorbital tubercles.

Hands very large; fingers moderately long and robust; disk on Finger I much smaller than disks on Fingers II–IV; disk on Finger III largest, about equal in size to tympanum. Distal subarticular tubercles on fingers large, somewhat elliptical, larger than proximal subarticular tubercles on Fingers II–IV; accessory palmar tubercles numerous, low, small; thenar tubercle cordate, prepollex enlarged, protuberant, greatly enlarged and obtuse in males; bony prepollical projection bluntly pointed in males and directed laterally; tip rounded in females; fingers extensively webbed, web extending to base of disk on at least two fingers; web margin nearly even between Fingers II–IV; modal webbing formula: **I** $1^{3/4}$ - 2 **II** $^{3/4}$ - 1 **III** 1 - $^{3/4}$ **IV**. Legs relatively long and robust, heel of adpressed limbs overlapping about one-quarter length of crus; tibiotarsal articulation extends to eye when limb adpressed along side of body; distinct fleshy, scalloped fringe begins on heel and extends along ventrolateral margin of tarsus and outer margin of Toe V to base of disk; scallops relatively weak, not deeply incised or pointed, largest on tarsus, smaller scallops along toe; several small tubercles dorsal to fleshy scallops on heel; no tarsal fold. Disks on toes smaller than those on fingers, moderate on Toes III–V, smaller on Toes I–II; Subarticular tubercles under toes, small, round; inner metatarsal tubercle elongate, slightly raised, outer not distinct from accessory tubercles which are tiny and numerous; toes nearly fully webbed, webs extending to base of disks on at least three toes; web margin slightly concave between Toes II–V; modal webbing formula: **I** $^{3/4}$ - 1 **II** $^{3/4}$ - 1 **III** ¾-1 **IV** 1^{+} - $^{3/4}$ **V**. Chin, chest, venter and undersides of arms and thighs strongly granulate and lacking keratinized tips; cloacal opening directed posteriorly at mid-level of thighs with a distinct flap, many small tubercles below cloaca. Tongue broadly cordate; prevomerine tooth patches transversely elongate, narrowly separated, lying between the posterior margins of the moderately large ovoid choanae; paired vocal slits in adult males extending posterior from posterior lateral base of tongue towards angle of jaws; single partly distensible, median subgular vocal sac.

Coloration in life. Dorsal ground color varies from reddish-brown to brown or tan to gray, uniform or with irregular darker markings of brown, black, and/or green; usually a definite narrow interorbital dark band; dark bands often present on dorsal surfaces of arms and legs. Substantial metachrosis evident, with color and intensity varying with level of activity and environmental factors. Throat, chest, abdomen and ventral surfaces of arms and legs cream to white with irregular medium sized tan to brown spots; ventral spots often larger and more diffuse on the arms and legs; similar brown spots present on flanks and upper portion of posterior thigh. Posterior surface of thigh brown, usually with large pale spots. Iris pale tan to gold, finely reticulated with copper to dark brown and divided into upper and lower halves by solid brown horizontal band through center of eye.

Coloration in preservative. Dorsal ground color brownish and dark markings somewhat more emphasized than in life but no green markings evident.

Measurements of holotype in mm. SVL = 56.7; HL = 18.6 ; HW = 23.5; E = 6.3; TY = 3.5; C = 30.4; FL = 28.5.

Measurements of paratypes in mm. Males (N=2): SVL = 56.7–63.2; HL 32.0–33.0; HW = 40.0–42.0; C = 53.0–55.0; FL = 48.0–51.0; TY/E = 56.0–64.0; females (N=4): SVL = 62.6–68.7; HL = 33.0–40.0; HW = 40.0–46.0; C = 53.0–58.0; FL = 46.0–56.0; TY/E = 71.0–84.0.

Advertisement call. Males of this species generally call at night from high in the forest canopy, often more than 20m above the ground. The call consists of 13 to 20 staccato barks repeated after a time gap of as much or more than an hour. A single male possibly calls only several times during one night.

The accompanying audiospectrograms of *E. sukia* (fig. 4a–b) are calls of a male that was captured at the type locality of *E. sukia*. The calls where recorded on the 28th of February, 2006 in the laboratory.

Call 1 (fig. 4a) was recorded at 22.15 hours: ambient temperature 21 C; relative humidity 95–100%. The call consists of 15 separate notes, with a total duration of 7.73 sec. having a dominant frequency of 1.15 kHz. Individual call notes lasted 0.252 sec. (average of four notes selected at random) with a 0. 287 sec. pause between notes (average of four pauses selected at random).

Call 2: (fig. 4b) was recorded at 22:53 hours: ambient temperature 21 C; relative humidity 95–100%. The call consisted of 16 separate notes, with a total duration 0f 8.29 sec. having a dominant frequency of 1.15 kHz. Individual call notes lasted 0.220 sec. (average of four notes selected at random) with a 0.302 sec pause between notes (average of four pauses selected at random).

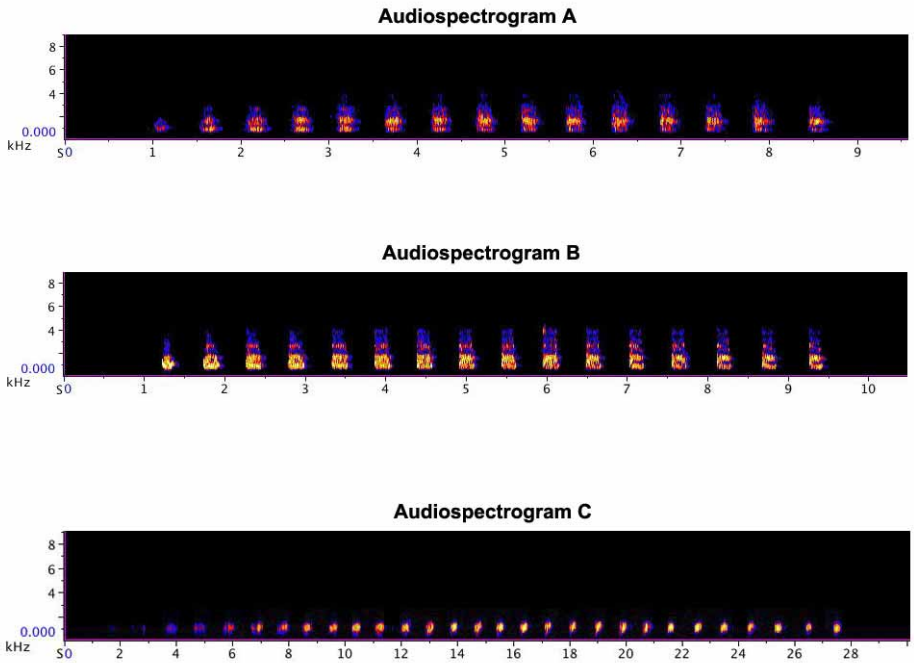

FIGURE 4. Audiospectrograms of *Ecnomiohyla* male advertisement calls. a = call one of *Ecnomiohyla sukia*; b = call two of *E. sukia;* c = call of *Ecnomiohyla miliaria*.

TABLE 2. Comparison of selected features of species of *Ecnomiohyla.*

	E. echinata	*E. fimbrimembra*	*E. miliaria*	*E. minera*	*E. phantasmagoria*
SVL (mm)					
ad M	57.0	NA	86.0–110.0	70.0–83.1	95.0
ad F	60.2	71.0–91.0	86.2	71.0–81.0	NA
Dorsum	smooth	granular	tuberculate	tuberculate	tuberculate
Cephalic skin co-ossifed to skull	no	yes	no	yes	no
Cranial osteroderms present	no	no	yes	no	yes
Dorsal osteoderms	no	no	yes	no	yes
Humeral projection present in M	no	no	no	yes	no
Prepollex M	blunt	blunt	recurved	recurved	recurved
Prepollical bony projection M	rounded	rounded	spine	spine	spine
Keratinized black spines on prepollex and thumb in M	yes	yes	no	yes	no
Finger webbing	C	C	EX	EX	C
Toe webbing	C	C	EX	F	EX
Heel	few small tubercles	several pointed tubercles	pointed tubercles	smooth	pointed tubercles
Color in life	red-brown; flanks dark brown	brown with darker markings; juv. mix of brown-yellow-green	brown to mottled brown and green with darker markings	brown to green with darker blotches	*brown with light vermiculations

continued.

	E. rabborum	*E. salvaje*	*E. sukia*	*E. thysanota*	*"E". tuberculosa*	*E. valancifer*
SVL (mm)						
ad M	62.8–97.3	84.7–86.0	56.7–63.2	NA	83.6	77.7
ad F	61.3–79.9	NA	58.1–68.7	95.0	68.5	NA
Dorsum	granular	smooth-scattered tubercles	tuberculate	granular	tuberculate	tuberculate
Cephalic skin co-ossifed to skull	no	yes	no	no	no	no
Cranial osteroderms present	no	no	yes	no	no	no
Dorsal osteoderms	no	no	yes	no	no	no
Humeral projection present in M	yes	yes	no	no	no	no
Prepollex M	blunt	blunt	obtuse	NA	rounded	spade-like
Prepollical bony projection M	rounded	rounded	pointed, directed laterally	NA	not projecting	flattened
Keratinized black spines on prepollex and thumb in M	yes	yes	no	NA	no, with brown excrescence	no
Finger webbing	S	EX	EX	EX	S	C
Toe webbing	EX	F	EX	EX	EX	EX
Heel	smooth	smooth	scalloped fringe	smooth	2–3 large tubercles	2–3 large tubercles
Color in life	brown with green or dark markings	brown with olive or dark markings	brown to gray with green or darker markings	uniform green	tan with darker spots	mottled green and brown with orange lateral spots

*color in preservative; M = Male; F = Female.

FIGURE 5. Adult male *Hyla tuberculosa* Boulenger *incerte sedis.* Peru: Loreto: Río Tigre. Courtesy W. W. Lamar.

The only recorded call of *E. miliaria* (fig. 4c) consists of a series of 29 slurred bar-aks with a total duration of 26.03 sec having a dominant frequency of 1.05 kHz. Individual call notes lasted .323 sec (average of four notes selected at random) with a 0.562 sec pause between notes (average of four pauses selected at

random).

Larva. See following paper by Hoffmann and Kubicki (2010).

Etymology. The name *sukia* is a noun in apposition and is derived from the Costa Rican name for the Amerind shamans of this region. We imagine that the call of the new species speaks, like those of the shamans, to communicate with the mysterious and unknown forces in the forest of the night.

Habitat and ecology. *E. sukia* is a nocturnal frog that inhabits mature secondary and primary humid broadleaf evergreen forests. It is a habitué of the canopy and individuals have been found in water-filled cavities, on the surface of vegetation and on tree branches. The junior author has seen about 20 individuals captured by Miguel Solano and his associates and heard about 10 individual males calling over the past decade. The species seems to be generally most active at the drier times of the year (February to April) but may be heard calling more or less randomly throughout the year. Five were kept in captivity but only one would feed under conditions in a large terrarium with ample water and hiding places. The single male, whose call was recorded, lived four year in the terrarium and ate crickets. The species uses water-filled cavities in living trees as sites for egg deposition and probably these are the places where amplexus takes place. We wish to point out that no individuals of the larger species, *Ecnomiohyla miliaria* have been seen nor heard subsequent to 1999 at Guayacán or elsewhere in the larger study area.

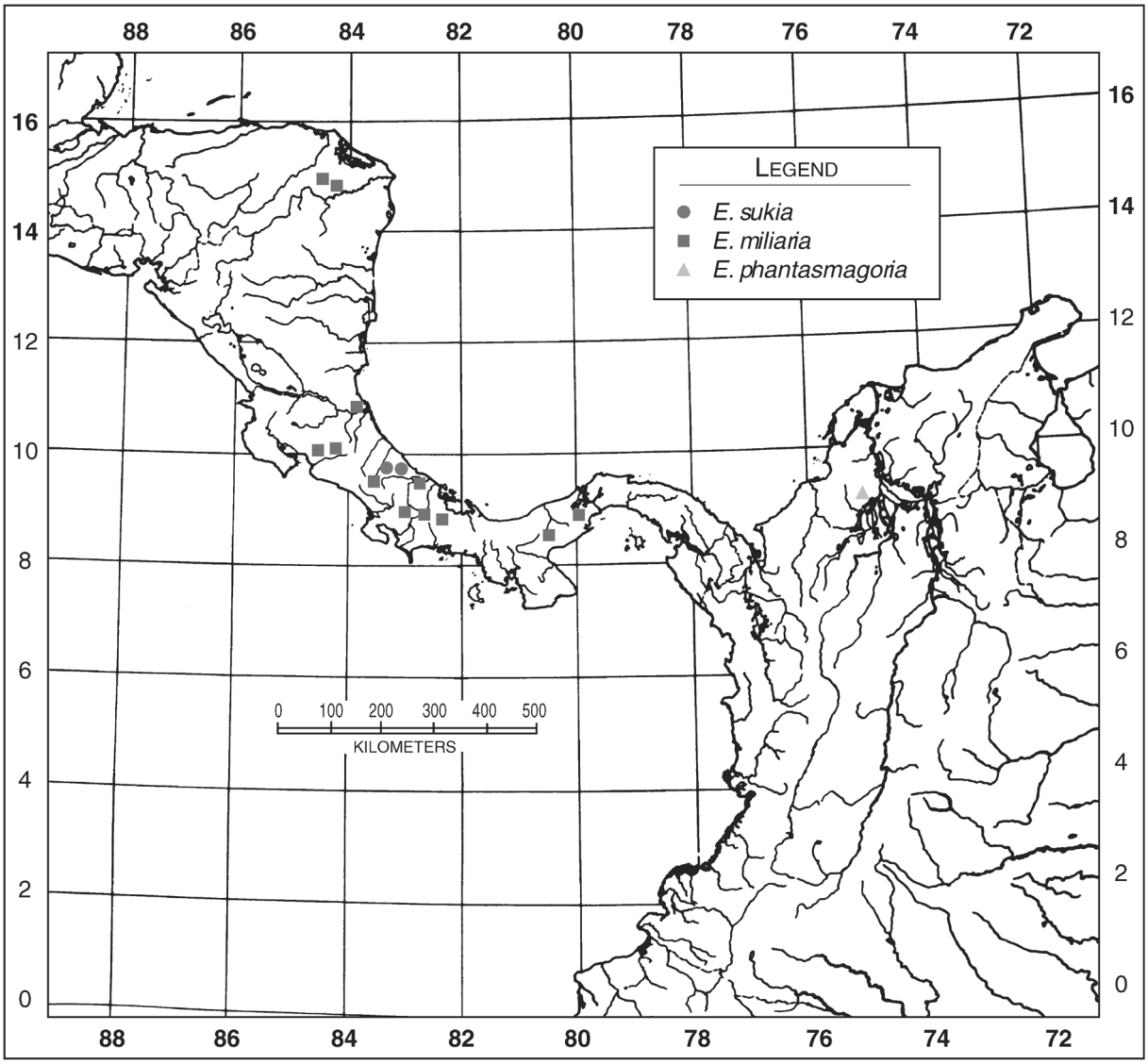

FIGURE 6. Distribution of *Ecnomiohyla sukia* new species (circles), *E. miliaria* (Cope) (squares), and *E. phantasmagoria* (Dunn) (triangle); one symbol may represent more than one locality.

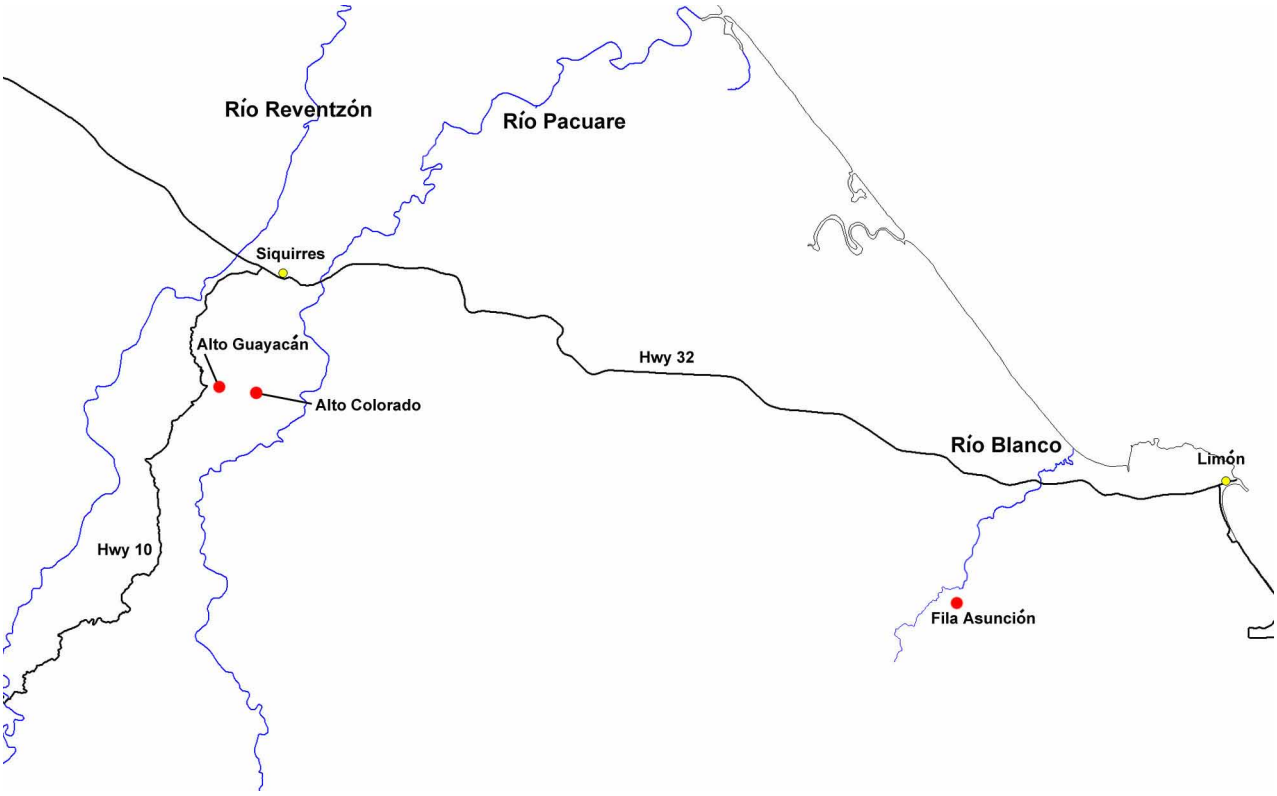

FIGURE 7. Detail of distribution of *Ecnomiohyla sukia* new species (circles) and *E. miliaria* (Cope) (squares) in Atlantic slope central Costa Rica, showing location of principal localities mentioned in the text.

Distribution. Definitely known from two localities on the Atlantic slope in Tropical Lowland Wet Forest and Tropical Premontane Rainforest zones (*sensu* Savage, 2002, modified from Holdridge, 1967), Limón Province, Costa Rica (400–710 m; possibly to 900 m in northeastern Costa Rica). This species was recently found but not collected on the private reserve Las Brisas, at an elevation near 1000 m (Erick Berlin pers. comm.). The private reserve of Las Brisas is located on the Atlantic slopes of the Turrialba Volcano, Limón Province.

Discussion

As this discovery unfolded, we originally thought that the smaller of the two fringe-limb species in the Guayacán area was a representative of *E. miliaria.* However, direct comparison of the types of *E. sukia* to the male holotype of *E. miliaria* (USNM 14193) on several occasions convinced us that two distinct taxa were involved. The holotype of *E. miliaria* is a subadult male (86 mm in standard length) that lacks vocal slits. It differs most obviously from *E sukia* in having heel tubercles rather than a fleshy heel fringe and enlarged pointed tubercles on the upper eyelid rather than low ones. Eight additional adult males and one subadult female of *E. miliaria* over those seen by Duellman (2001) were examined in the course of this study. Three other adult males (UTA-A 52783-85) from the Guayacán area and two adult males from Honduras (UF 137207-08) with verified identifications by Eric Smith (pers. comm.) and McCranie *et al.* (2003), respectively, have been reported subsequent to Duellman's (2001) account. This brings the known examples to 23 adult and one subadult male, one adult and two subadult females and two juveniles. Our analysis confirms the conclusion of Duellman (1970, 2001) that the type of *E. miliaria* is conspecific with the specimen described by Taylor (1952) as a new form, *Hyla immensa* (holotype, KU 30404), with which it agrees in all features except those reflecting ontogenetic variation.

Members of the genus *Ecnomiohyla* may be placed into three groups based upon the presence or absence of a pointed bony humeral projection and the presence or absence of keratinized black spines on the prepollex and thumb of adult males. Frogs in Group 1 have a spiny humeral projection and black nuptial spines: *Ecnomiohyla minera*, *E. rabborum*, and *E. salvaje*. Members of Group 2 lack the humeral projection but have black nuptial spines: *E. echinata* and *E. fimbrimembra*. There is no humeral projection or black nuptial spines in species of Group 3: *E. miliaria*, *E, phantasmagoria*, *E. sukia*, and *E. valancifer*). It is not possible to assign *E. thysanota* to any group as the species is known only from the female holotype. It is clear that the Amazonian species *Hyla tuberculosa* should not be included in *Ecnomiohyla* as males of that species do not have an enlarged prepollex, no prepollical projection, and its nuptial excrescences consists of a rugose brown nuptial pad.

The groupings defined above are compromised by the variation in the occurrence of cranial co-ossification with the cephalic integument and the presence of cranial and dorsal osteoderms and two other sexually dimorphic adult male features, the shapes of the prepollex and prepollical bony projection. Cranial co-ossification is present in only three species (*E. fimbrimembra, E. minera*, and *E. salvaje*) and three others have cranial and dorsal osteoderms (*E. miliaria, E. phantasmagoria*, and *E. sukia*). However, *E. miliaria, E. minera* and *E. phantasmagoria* have recurved prepollices and a prepollical bony spine whereas *E. fimbrimembra* and *E. sukia* do not. The probable relationship among *E. miliaria, E. phantasmagoria*, and *E. sukia* is supported by their sharing of cranial and dorsal osteoderms while all other members of the genus lack them.

E. miliaria occurs sympatrically, but not syntopically, with *E. sukia* in the vicinity of the type locality of the latter (fig. 6). All examples of the former from the general area of Siquirres and Guayacán were collected prior to 1999, while specimens of the latter are mostly from post-1999. Some confusion has related to the geographic source of specimens of the two species. Examples of *E. miliaria* have been cataloged variously as from Alto Guayacán, Guayacán, Guayacán de Turrialba or Guayacán de Siquirres, and 5 km from Moravia de Siquirres toward Turrialba. Nearly all of these specimens were collected by Miguel and/ or Norbert Solano (pers. comm. regarding localities). In this region *E. sukia* is known from to Alto Colorado, the surrounding forest patches of Bajo Huacas, and the upper Río Siquirres Valley. Two paratypes of the new form are cataloged as being from “Río Blanco” or “Río Blanco de Liverpool” but were actually collected on a ridge, Fila Asunción (470 m), above of the river (Río Blanco), 6–7 km south of the village of Río Blanco (16 m). Similar confusion relates to examples of *E. miliaria* collected by the Solanos from this region. Those cataloged as from Río Blanco and Liverpool actually were collected to the south on Fila Asunción. Those recorded from La Bomba were collected to the west of that site also on Fila Asunción

In western Panama single male specimens of *E. miliaria* have been collected near the Costa Rica border at Chiriquí Province: Finca Santa Clara (KU 30404) and Coclé Province: Parque Nacional G. D. Omar Torrijos, northwest of El Copé (KRL 758). We have seen photographs of what seems to be a second species of fringe-limb frog from the latter area. It does not appear to be a representative of the recently described *E. rabborum* from Coclé Province: near El Valle de Antón. Superficially, the animal resembles *E. sukia* but it is not possible to make a definitive identification based on the photographs. This frog shows considerable resemblance to the adult female fringe-limb frog from Chiriquí Province: upper Río Chiriquí, Fortuna dam site (AMNH 94887) referred to *E. miliaria* by Myers and Duellman (1982) and Duellman (2001). This specimen, as noted by these authors, does not show the characteristic tuberculation of the upper surfaces of the head, eyelids and body typical of adult *E. miliaria*. However, it is clearly differentiated from *E. sukia* in having the heel covered with large pointed tubercles as in *E. miliaria*. It seems possible that the second species in the vicinity of El Copé and this female may represent another, as yet unrecognized, species of the fringe-limb clade.

Acknowledgments

We first thank Manuel and Nobert Solano, who collected most of the examples of the new form and

Ecnomiohyla miliaria examined in this study. We are also indebted to Alejandro Solórzano and Mahmood Sasa for their foresight that led to the material collected by the Solanos being deposited in museum collections. William W. Lamar expedited this study by providing photographs of the new species and other aid. We were further aided by the loan of critical material by F. Bolaños and Gerardo Chaves (UCR), J. Campbell and E. Smith (UTA), D. Kizirian (AMNH), K. Lips (KRL), R. McDiarmid (USNM), G. Schneider (UMMZ), and L. Trueb (KU).

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Appendix I. Specimens examined.

Ecnomiohyla fimbrimembra

COSTA RICA: *Provincia Alajuela*: FMNH 191784 (holotype of *Hyla fimbrimembra*), Volcán Poás: Isla Bonita, ca. 1200m; FMNH 191783 (holotype of *Hyla richardi* and *H. richardtaylori*), 3.2 km W Isla Bonita, ca. 1300m; CRE 7015 (tadpole), Cinchona, 1300 m. *Provincia Heredia*: LACM 149979; MVZ 206432), N slope Volcán Barba: Parque Nacional Braulio Carrillo: Zona Protectora de La Selva: 1800m cabin; UCR 5976, S slope Volcán Barba: Cerro Turú: Yurro Honda, 1900m. *Provincia Puntarenas:* LACM 149980, Monteverde: Pantanosa Trail, 1600m.

PANAMA; *Provinica Chiriqui*: CHP1036, Cerro Horqueta, 1600–1700m.

Ecnomiohyla miliaria

HONDURAS: *Departamento Gracias a Dios:* USNM 563949, Hiltara Kiamp, 160 m; USNM 563950, Urus Tingi Kiamp, 160 m.

NICARAGUA: USNM 30404 (holotype of *Hyla miliaria*), *Departamento Río San Juan*: btwn. El Castillo and San Juan del Norte.

COSTA RICA: *Provincia Alajuela:* LACM 150152, trail along Río Peñas Blancas, nr. Fogden cabin , ca. 800 m; UCR 5142, Finca Francisco Orlich, ca. 800 m; *Provincia Cartago:* KU 304042 (holotype of *Hyla immensa*), 2 *km* E Turrialba, Instituto Interameicano de Ciencias Agricolas, 602 m *Provincia Limón*, UCR 12678, UCR 13254, Río Blanco area (not the village), Fila Asunción, ca. 450m ; UCR 13706, W La Bomba, Fila Asunción, ca. 450m; UCR 12679, Reserva Biologica Hitoy-Cerere; UCR12787, Guayacán, 750 m; UMMZ 149201, Comadre de Cahuita, 20 m;USNM 331414, Siquirres, 62 m. *Provincia Puntarenas:* UCR 4979, Estación Biológico Las Cruces,1200m; LACM 150153, Las Alturas, ca. 1400m. We have seen photographs of specimens of this species from Costa Rica: *Provincia Limón:* Pacuare, ca 740 m and Panama: *Provincia Chiriquí:* Fortuna, 1000 m.

PANAMA: *Provincia Chiriquí:* AMNH 94887, upper Río Chiriquí, Fortuna dam site; KU 98451, 101610, Finca Santa Clara. *Provincia Cocle:* KRL loop trail, Parque Nacional G. D. Omar Torrijos.

Ecnomiohyla rabborum

PANAMA: *Provincia Cocle:* AMNH 55532, El Valle de Antón; UTA-A 58572 (holotype), UTA-A 58573-75; CHP 7489, nr. El Valle de Anton, Rio de Jesus, 990 m.

Ecnomiohyla thysanota

PANAMA*: Provincia Darién*: USNM 151080, (holotype of *Hyla thysanota)* Cerro Malí, 1265 m.

Ecnomiohyla tuberculosa

PERU: *Provincia Amazonas*: mouth Río Santiago (AMNH 43479).