

Spectacular New Gliding Species of *Ecnomiohyla* (Anura: Hylidae) from Central Panama

JOSEPH R. MENDELSON III,^{1,2} JAY M. SAVAGE,³ EDGARDO GRIFFITH,⁴ HEIDI ROSS,⁴ BRIAN KUBICKI,⁵
AND RONALD GAGLIARDO⁶

¹Zoo Atlanta, 800 Cherokee Avenue Southeast, Atlanta, Georgia 30315 USA; E-mail: jmendelson@zoatlanta.org

³Department of Biology, San Diego State University, San Diego, California, 92182 USA

⁴El Valle Amphibian Conservation Center, El Valle de Anton, Panama

⁵Costa Rican Amphibian Research Center, Guayacán, Limón, Costa Rica

⁶Atlanta Botanical Garden, 1345 Piedmont Avenue, Atlanta, Georgia 30309 USA

ABSTRACT.—We describe a new species of *Ecnomiohyla* from the vicinity of El Valle de Anton, Coclé, Panama. This is a large species that differs from similar species in the genus by details of the prepollex, webbing, and by the presence of a distinct expanded crista lateralis with medial proximal point. We provide descriptions of the adult and subadult, as well as the tadpole. We provide natural history information including observations of individuals gliding from the forest canopy, reproduction in tree holes, and male territoriality and care of the tadpoles. This species is currently known only from the immediate vicinity of El Valle de Anton, and we have observed numbers of this species in the wild to decrease dramatically following the recent epidemic of amphibian chytridiomycosis in the region.

RESUMEN.—Describimos una especie nueva del género *Ecnomiohyla* de la región de El Valle de Antón, Coclé, Panamá. Esta es una especie que difiere de otras especies de su género por las características del prepollex, membranas interdigitales, presencia de una distinta crista lateralis expandida con punto próximo medial. Brindamos descripciones de la forma adulta, sub-adulta, y además su forma larval. También se incluye información sobre la historia natural, tales como observaciones de individuos planeando desde la copa de los árboles, reproducción en los huecos de los árboles, territorialidad y cuidado parental de las larvas. Actualmente esta especie solamente esta conocida en la región de El Valle de Antón, donde las poblaciones parecen estar sufriendo declives debido a las recientes epidemias de chytridiomycosis en los anfibios de la región.

As the wave of amphibian chytridiomycosis moved eastward along the Serranía de Tabasara of Panama (Lips et al., 2006), we began intensive efforts to work ahead of the frontline of the disease to document the still-intact amphibian assemblage of the uplands around El Valle, Coclé, Panama, and to collect individuals to be maintained alive in an attempt to initiate long-term survival assurance colonies representative of the region (Gagliardo et al., 2008). During the pre-chytridiomycosis months of May to December 2005, we encountered multiple individuals of a spectacular, large species of frog referable to the genus *Ecnomiohyla* Faivovich, Haddad, Garcia, Frost, Campbell, and Wheeler, 2005. Subsequent comparisons of this material with known species in the genus indicated that the animals from El Valle represent a new species, which is described herein.

Duellman (1970, 2001) and Savage (2002) recognized the several species of fringe-limb hylids as a distinctive cluster of taxa, informally called the *Hyla miliaria* or *Hyla tuberculosa*

group, respectively. Favovich et al. (2005), based on genetic evidence, proposed the name *Ecnomiohyla* for the group. At the same time they assigned *Hyla dendrophasma* Campbell, Smith, and Acevedo, 2000, to *Ptychohyla*; it was originally placed in the *miliaria* group by Campbell et al. (2000). In addition, Faivovich et al. (2005) included *Hyla miotympanum* Cope, 1863 in *Ecnomiohyla*. They further noted that additional data and analyses may find the species included in *Ecnomiohyla* represent two or three different clades.

Nine of the 10 species referred to *Ecnomiohyla* by Favovich et al. (2005) are characterized by having scalloped dermal fringes on the outer margin of the forearm and foot, large digital disks, and enlarged prepollices. Because the taxon *miotympanum* lacks these features, we do not consider it further in the following account.

MATERIALS AND METHODS

General terminology and format for the diagnoses and description follow that of Duellman (2001); terminology specific to the tadpoles

²Corresponding Author.

is that of McDiarmid and Altig (1999). Foot-webbing formulae follow the system summarized by Savage (2002). In making comparisons of webbing on the hands or feet in this species group, we use the following terminology: considerable = webbing not extending to base of disc on any digit; substantial = webbing extending to base of disc of one digit; extensive = webbing extending to base of disc on two digits; full = webbing extending to base of disc on all digits.

The following morphological measurements were taken with digital calipers to 0.1 mm: snout-vent length (SVL), head length (HL), head width (HW), length of crus (TI), length of foot (FL), width of tympanum (TYM), diameter of eye (E). The relationship of tympanum width to the diameter of eye (TY/E) is expressed as a percentage of eye diameter. The relationship of remaining measurements is expressed as a percentage of SVL. Sex of preserved specimens was determined by direct examination of gonads. Sex of living specimens was determined by the presence/absence of male sexual secondary characters (i.e., nuptial excrescences, humeral projections). Museum abbreviations are those of Leviton et al. (1985), with the addition of the following: CHP (Circulo Herpetológico Panamá; located at Smithsonian Tropical Research Institute) and CRE (Costa Rica Expeditions; located at LACM). See Appendix 1 for a complete list of specimens examined.

SYSTEMATIC ACCOUNT

Ecnomiohylla rabborum sp. nov.

Figures 1–4

Holotype.—UTA-A 58572, an adult female from Panama: Coclé: near El Valle de Anton, Rio de Jesus, 990 m. 08°37.968'N 080°04.604'W. Obtained as a larva on 15 July 2005 by E. Griffith and H. Ross; raised in captivity until its death on 3 July 2007.

Paratypes.—CHP 7489, UTA-A 58574, 58575, all from the same locality as the holotype. All were raised from the same group of tadpoles collected on 15 July 2005. CHP 7489 is a subadult female that died on 20 July 2007; UTA-A 58574 is a subadult male that died on 6 March 2007; UTA-A 58575 is a subadult female that died on 15 May 2007.

Referred Specimens.—UTA-A 58573, a juvenile specimen from the type locality; raised from same group of tadpoles as were the type specimens. UTA-A 58576, 58577, larvae from Panama: Coclé: near El Valle de Anton, Altos de Maria, 1,000 m, 08°38.078'N 080°04.686'W.

Diagnosis.—A large species, males 62–97 mm SVL, females between 61 and 100 mm, differing

from other species of *Ecnomiohylla* in the following combination of characters: (1) fingers with substantial webbing, web reaching base of disk on one finger (Fig. 1; Table 1); (2) toes with extensive webbing, web reaching base of disk on two toes (Fig. 1; Table 1); (3) skin of dorsum granular; (4) no cranial or dorsal osteoderms; (5) skin on upper surface of head not co-ossified to underlying cranial elements; (6) humerus in adult males massive with ridge formed by expanded crista lateralis with medial proximal point, skin covering projection with black, keratinized spines; (7) prepollex well developed, with a blunt distal projection and covered dorsally with keratinized black spines in adult males; (8) nuptial excrescences in males are keratinized black spines situated on the enlarged prepollex, over the medial projection of the crista lateralis of the humerus, and with a small patch over the pectoral girdle; (9) distal margin of bony large prepollical projection rounded in adult males; (10) heel smooth without fleshy flaps or pointed tubercles; (11) upper surfaces mainly brown or brown and green in life, with marked metachrosis.

Diagnostic comparisons are made below to other members of *Ecnomiohylla* with contrasting features for *E. rabborum* in parentheses. The only other *Ecnomiohylla* species having both a humeral projection and black spines on the prepollex in adult males are *Ecnomiohylla minera* (Wilson, McCranie, and Williams, 1985; Belize, Guatemala) and *Ecnomiohylla salvaje* (Wilson, McCranie, and Williams, 1985; Guatemala, Honduras). They differ from *E. rabborum* in having the cephalic skin co-ossified with the dorsal surface of the skull, extensive finger webbing and the toes with full webbing (not co-ossified, substantial webbing on hands, extensive webbing on feet). Other species similar to *E. rabborum* in lacking extensive finger webs include *Ecnomiohylla echinata* (Duellman, 1961; Mexico), *Ecnomiohylla fimbrimembra* (Taylor, 1948; Costa Rica, Panama), *Ecnomiohylla phantasmagoria* (Dunn, 1943; Colombia), *Ecnomiohylla tuberculosa* (Boulenger, 1882; upper Amazon), and *Ecnomiohylla valancifer* (Firschein and H. M. Smith, 1956; Mexico). Of these species, *E. fimbrimembra* has the skin co-ossified to the upper surface of the skull and only considerable toe webbing (not co-ossified, extensive webbing); *E. phantasmagoria* has the dorsum tuberculate and the cephalic osteoderms on the upper surface of head (granular, no osteoderms); *E. tuberculosa* does not have a prepollical projection or keratinized black spines on the prepollex in adult males, the dorsum is strongly tuberculate and has pointed tubercles on the heel (prepollical projection and black spines present, dorsum granular, heel smooth); *E. valancifer* has a tuberculate dorsum,

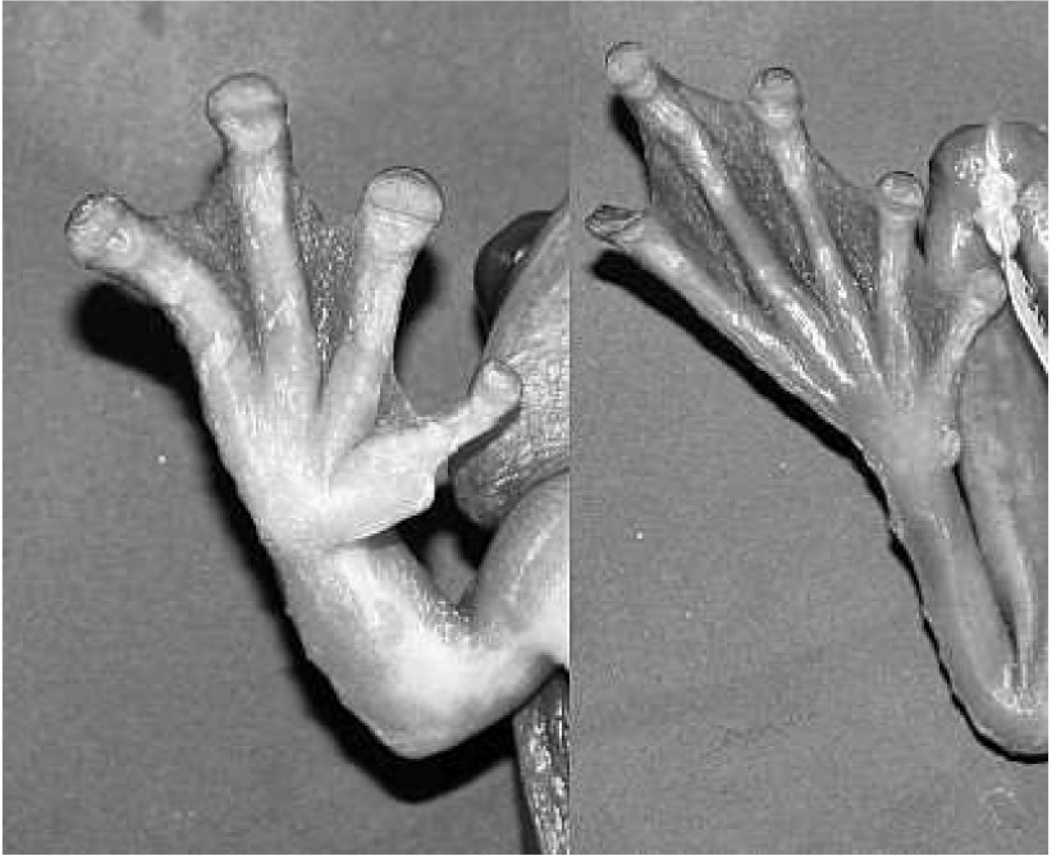


FIG. 1. Hand and foot of the holotype of *Ecnomiohylla rabborum* (UTA-A 58572). The specimen is a young adult female (SVL = 79.9 mm); photo by A. Thompson, Zoo Atlanta.

only considerable finger webbing, and large tubercles on the heel (granular, substantial webbing, heel smooth). The two remaining species, *Ecnomiohylla miliaria* (Cope "1885"; Honduras to Panama) and *E. thysanota* (Duellman, 1966; Panama) have, unlike *E. rabborum*, extensive finger webbing but are similar to the new species in having extensive toe webbing. The similarly large species *E. miliaria* has osteoderms on the upper surface of the skull and in the dorsal skin, pointed heel tubercles, strongly tuberculate skin and a recurved prepollical projection that terminates in a spine in adult males (no osteoderms, smooth heel, distal blunt and rounded prepollical projection in males). Additionally, *E. thysanota* is uniform green in life (brown or brown and green in life).

Tadpoles for most of the large species of *Ecnomiohylla* are not known; hence, few comparisons can be made among them. In any case, the tadpole of *E. salvaje* (Wilson et al., 1985) differs by having no serrations on the beak (small serrations), 2–3 rows of lateral papillae on the oral disc (one row), labial teeth 2(2)/3(1) (in *E.*

rabborum labial teeth are 2/2[2]). The tadpole of *E. fimbrimembra* (Savage, 1981) closely resembles that of *E. salvaje* in these described features, however it is similar to that of *E. rabborum* by having fine serrations on the beak.

Description of the Holotype.—A female, SVL = 79.9; ratio of tibia length to SVL = 53.0; ratio of foot length to SVL = 46.0; ratio of head length to SVL = 34.7; ratio of head width to SVL = 39.0; ratio of diameter of tympanum to eye = 43.0.

Head wider than body; top of head flat; no cranial osteoderms; snout moderately long; nostrils protuberant laterally, near tip of snout; snout subelliptical in dorsal outline, round in profile; canthus rostralis concave in dorsal outline, somewhat thickened and rounded; loreal concave; no pointed tubercles on upper eyelid; supratympanic fold extending from eye over tympanum to angle of jaw smooth, without pointed tubercles; upper edge of tympanum obscured by supratympanic fold; tympanum distinct, slightly oblique; arms relatively short, robust; no dermal folds on wrist; low scalloped dermal fringe from elbow to near base of disc on

Finger IV; fingers relatively short; discs of Fingers II–IV equal tympanum; distal subarticular tubercle on Finger I elliptical; distal subarticular tubercles on Fingers II and III smaller than distal tubercle on Finger IV; distal subarticular tubercle on Finger IV flat; no palmar tubercle, but elongate flat tubercle on moderately enlarged prepollex; supernumerary tubercles numerous, small, round; fingers nearly fully webbed; webbing formula $I2 - 2^{1/4}II^{3/4} - 1^{1/4}III 1 - 1^{1/4}IV$; legs moderately long, slender; heels of adpressed limbs barely overlap; fibiotarsal articulation extends beyond eye; thin tarsal fold from heel to inner metatarsal tubercle; thin scalloped dermal fringe on leg present, extending from heel to base of foot, continues as low ridge to base of disc on Toe V, not extending onto heel, heel lacking pointed tubercles; discs on toes slightly smaller than discs on fingers; subarticular tubercles on foot round; distal subarticular tubercle on Toe V larger than tubercles on other toes; supernumerary tubercles numerous, small, conical; webbing formula $I1 - 1^{1/4}II^{3/4} - 1^{1/4}III^{3/4} - 1^{1/4}IV 1^{1/4} - 1V$.

Cloacal opening directed posteroventrally at midlevel of thigh; a broad glandular cloacal sheath present; skin on top of head and body smooth; venter and median posterior ventral surfaces of thighs granular; other ventral surfaces smooth; tongue round; prevomerine tooth patches ovoid, narrowly separated, lying between moderate, round choanae. We note here also that holotype has had the viscera removed, as part of a routine necropsy; the sex and maturity of this specimen were verified by direct observation (JRM) of the gonads during the necropsy.

Measurements of Holotype.—Measurements in millimeters. SVL = 79.9; head length = 27.7; head width = 31.5; tibia length = 42.6; foot length = 36.9; diameter of tympanum = 3.8; diameter of eye = 8.8.

Coloration of Holotype in Alcohol.—Dorsal surfaces brown, slightly mottled with paler shades of brown; upper surfaces of limbs blotched with dark and light brown; posterior surfaces of thighs pale yellow; upper surfaces of hands pale brown; finger and toe webs dark brown. Chin and anterior portion of chest brown; venter white with irregular brown spotting; underside of fingers dull white; underside of arms white with brown along lateral margins; underside of thighs marked like arms; remainder of hind limbs light brown.

Coloration in Life.—Coloration in life closely resembles coloration in alcohol, except that most living individuals have varying amounts of green flecking on the eyelids, upper surfaces of the limbs, the flanks, and the posterior

surface of the dorsum (Figs. 2, 3). Observations of living individuals indicate that this species is capable of considerable metachrosis, with respect to the green flecking. The distinctive ventral pattern of this species is similar in preservative and in life. The iris is uniform brown.

Variation.—Morphometric variation among specimens is presented in Table 1. The coloration in alcohol of most of the paratypes, both females and male, closely resembles that of the holotype. The distinctive ventral coloration, as described for the holotype, of this species seems to be remarkably invariant among specimens of either sex (Fig. 3). In life, dorsal skin texture granular. In captive males, the nuptial excrescences appear gradually through February and March, and recede similarly in August and September.

Description of the Tadpole.—Based on a preserved specimen (UTA-A 58576; Fig. 4) at Stage 37 with a body length of 16.1 mm and a total length of 56.9 mm. Body compressed, much wider than deep; snout truncate in dorsal outline, sloping anteroventrally and bluntly rounded in profile; eyes moderate, directed dorsolaterally, not visible from below; nostrils directed anterolaterally, situated about two-thirds distance from eye to tip of snout; flanks smooth; opening of the short sinistral spiracle directed posterolaterally, situated at midline of body; cloacal tube short, medial; caudal musculature moderately slender, extending nearly to tip of pointed tail; dorsal fin does not extend onto the body; at midlength of tail, depth of dorsal fin about two-thirds depth of caudal musculature; depth of ventral fin about two-thirds depth of caudal musculature.

In preservative, dorsum, flanks, sides of body, and anterior ventral surfaces pale brown; posteroventral area of body translucent; underside of limbs white; caudal musculature uniformly pale brown, except distal myocomata unpigmented; scattered melanophores on anterior dorsal fin, becoming sparse posteriorly; ventral caudal fin translucent. Coloration in life is similar to that in preservative (Fig. 3).

Oral disc small, directed anteroventrally; oral disc not emarginate; median portion of upper lip lacking papillae; laterally upper lip with one row small papillae; two rows small papillae along lateral and ventral margins of oral disc; upper and lower beaks about equally robust, with small serrations; upper beak shallowly arched; lower beak broadly U-shaped; labial teeth 2/3(2), tiny; P-2 gap about one-fourth length of each lateral section; Rows A-2 and P-1 converging laterally; Row P-3 median, very short.

Distribution and Ecology.—This species has been found only in the cloudforest habitat on



FIG. 2. Specimens of *Ecnomiohyla rabborum* in life, from the living collections of Atlanta Botanical Garden and Zoo Atlanta, showing variation in coloration and development of the nuptial excrescences. Upper left: an adult male, showing the pronounced development of the humeral spine and nuptial excrescences appearing over it (photo by J. Alison, Zoo Atlanta); Upper right: an adult male, showing the early stages of the nuptial

the mountains in the immediate vicinity of the town of El Valle de Anton, in both Coclé and Panama provinces at elevations between about 900 and 1,150 m. These sites lie within the Tropical Premontane Rain Forest (Holdridge, 1967). Most animals have been found in primary forest, but some have been found in secondary forests of varying characteristics. In this region, the extreme daily temperatures are between 17°C and 25°C. All localities known at this time are on the Pacific versant, but it is possible that this species may be found on the Atlantic slope near Altos de Maria. On Cerro Gaital, individuals have been found between 1,075 and 1,150 m. Based on field experience in other areas of Panama, it is our impression that *E. rabborum* is endemic to the vicinity of El Valle; however, only additional fieldwork will confirm our suspicion.

The advertisement call consists of a single "grrrrrck" repeated at regular intervals with a longer separation in the notes between intervals at the beginning. Calling bouts may last up to 1–2 min. Just prior to a calling bout, the males emit a "warm up" owl-like call of 3–5 notes. Males usually call from a position on a branch or vine that is situated near a tree hole of the type in which their tadpoles may be found. Sometimes the males call from the actual opening of the tree hole, a behavior also documented in *E. miliaria* (McCranie et al., 2003). We assume these calls that we are describing here are advertisement calls, however it is possible that there are additional, unknown calls or that the calls may have multiple purposes. The males appear to be highly territorial; thus, it is possible that some of the calls are associated with such behaviors. Our anecdotal observations suggest that males call from the vicinity of a tree hole to attract females to that site for egg deposition, and it appears that an individual male may mate with several females using the same tree hole throughout the year. Males call throughout the year, but there appears to be a peak of reproductive activity at the onset of the rainy season (mid-March to May). Anecdotal observations suggest that calling activity increases two or three days before and after the full moon. Males call only at night, with individuals sometimes beginning right at dusk.

The eggs are deposited just above the water line on the exposed wood or bark inside the tree hole. We estimate that clutches range from

about 60–200 eggs. The males remain at the hole and attend the eggs and tadpoles. The female disperses soon after oviposition. In captivity, we have observed behaviors that we can only interpret as direct feeding of tadpoles by the males. Attendant males spend the day with their body half submerged in the water with the tadpoles. During this time, the tadpoles may be seen constantly swimming around the submerged regions of the male's body and eating small flecks of what appears to be skin coming off of his body.

We have found recently metamorphosed young in two different tree holes 10 July 2005 and 15 July 2006; we presume these young developed from eggs deposited in late March or early April (i.e., during the apparent peak of reproductive activity; see above). We have observed water levels to vary considerably in a single tree hole over time; hence, it may be that timing of the development of the young may be somewhat controlled by resources available. The SVL of two recently metamorphosed individuals collected in the wild were 27.1 mm and 25.8 mm, with mass of 1.8 g and 1.5 g, respectively. We collected premetamorphic tadpoles from this clutch at the same time (Table 2).

This species lives in the forest canopy, with the exact location seemingly being determined by the presence of suitable tree holes. They have evident abilities to glide through the air, and when threatened, they leap from their perch and glide with outstretched limbs. We have observed them on several occasions to glide out of trees from heights up to 9 m to land on the ground.

Although this species was uncommon in the region during our field surveys in 2005 and 2006, we usually could hear at least one or two individuals calling each night during that time. Subsequently, after the appearance of the fungal pathogen *Batrachochytrium dendrobatidis* in the region (Gagliardo et al., 2008), they are evidently much less common. We no longer hear them at known localities, but in December 2007, one individual was heard in deep forest on Cerra La Gaita (P. Crump, B. Wilson, and R. Hill, pers. comm.).

Etymology.—The specific epithet for this spectacular amphibian honors George B. and Mary S. Rabb for their career-long contributions to conservation of all biodiversity, and especially for their substantial support of programs to

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excrescences over the humeral spine (photo by B. Wilson, Atlanta Botanical Garden); Lower: a large adult male (approximate SVL = 97 mm) showing some of the ventral coloration, and also the humeral spine (photo by B. Wilson, Atlanta Botanical Garden).



FIG. 3. Upper: An adult male of *Ecnomiohyla rabborum* in life, showing the ventral coloration and full development of the nuptial excrescences over the humeral spines, on the chest, and partially on the prepollex (photo by J. Alison, Zoo Atlanta); Lower: dorsal and ventral views of a living tadpole (approximate Gosner stage 25).

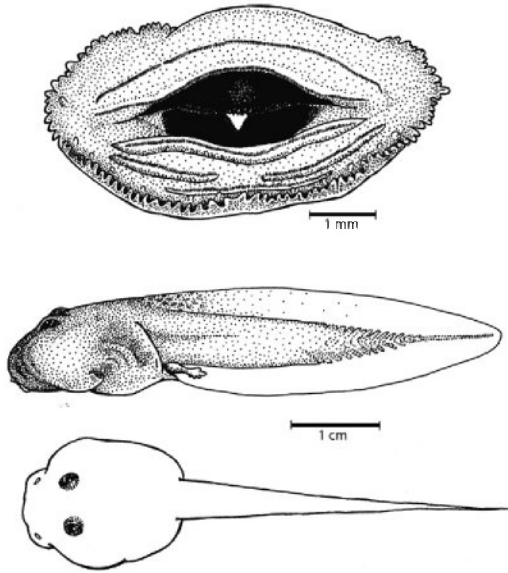


FIG. 4. The tadpole of *Ecnomiohylla rabborum* (UTA-A 58576; total length = 52.7 mm, Stage 36); illustration by P. C. Ustach.

conserve the amphibians of the world. Additionally, with their direct support, there is now not only a greater understanding of the amphibians of the El Valle region of Panama but also some hope for their recovery in the wake of yet another example of the destructive power of an epidemic of chytridiomycosis.

TABLE 1. Measurements (in millimeters) of specimens of *Ecnomiohylla rabborum*. Range, mean \pm SD are given. SVL = snout-vent length. *Measurements for males were taken from a single preserved subadult specimen, and approximate SVL measurements were taken from four large, mature living individuals. Measurements for females were taken from three large subadult specimens, the small, mature holotype, and an approximate SVL measurement was taken from a single large, mature living individual.

Character	Females N = 4*	Males N = 5*
SVL	61.3–79.9 (preserved) 70.5 \pm 9.3 100.1 (living)	62.8 (preserved) 93.2–97.3 (living)
Head length	22.3–27.7 24.4 \pm 2.9	21.7
Head width	25.4–31.5 27.7 \pm 3.3	25.1
Tibia length	34.4–42.6 37.8 \pm 4.3	33.8
Foot length	28.9–36.9 32.7 \pm 4.0	29.1
Eye diameter	7.5–8.8 8.1 \pm 0.7	7.8
Tympanum diameter	3.0–4.3 3.7 \pm 0.7	3.8
Percentage head length/SVL	33.0–36.0	–
Percentage head width/SVL	37.1–41.0	–
Percentage tibia length/SVL	52.0–56.0	–
Percentage foot length/SVL	46.0–47.0	–
Percentage tympanum/eye	40.0–50.0	–

TABLE 2. Size and timing of metamorphosis of a group of tadpoles of *Ecnomiohylla rabborum* that were collected from the same tree hole on 15 July 2006.

Tadpole	SVL (mm)	Mass (g)	Date of metamorphosis
1	27.1	1.788	Postmetamorphic when collected
2	25.8	1.452	Postmetamorphic when collected
3	25.8	1.761	19 July 2006
4	23.3	1.433	19 July 2006
5	24.3	1.368	30 July 2006
6	21.6	1.204	30 July 2006
7	23.6	1.413	30 July 2006
8	23.8	1.450	1 February 2007

DISCUSSION

Persons working among species of *Ecnomiohylla* in the future should be aware that two representative figures in Duellman (1970, 2001) were apparently inverted during final print setup. The corrections are as follows: in both Duellman (1970:fig.166) and Duellman (2001:fig.166) the hand of *E. fimbrimembra* is illustrated in figure 166A, but the hand of *E. valancifer* is illustrated in figure 166C.

As documented in the diagnosis above, members of the genus *Ecnomiohylla* exhibit a series of differentiating features in male secondary sexual characters. Note that *E. thysanota* is not considered in the following review because the species is only known from a single female. Several species (*E. miliaria*, *Ecnomiohylla*

minera, and *E. phantasmagoria*) have the prepollex recurved and the prepollical bone terminating in a spine. In *E. tuberculosa*, the prepollex is rounded and the supporting bone does not project from the thumb base. In the remaining species, the prepollex has a blunt terminus, and the prepollical bony projection is directed parallel to the thumb and is rounded or spade-like terminally. Four species in the latter group (*E. echinata*, *E. fimbriembra*, *E. rabborum*, and *E. salvaje*) are characterized by having keratinized black spines on the prepollex and base of the thumb in adult males. However, *E. minera*, a species with a recurved prepollex and a prepollical projection terminating in a spine, also has keratinized, black spines on the prepollex and thumb. To further complicate matters, one species, *E. minera*, with a recurved prepollex and a prepollical projecting spine and two species, *E. salvaje* and *E. rabborum*, with blunt prepollices and rounded prepollical bony projections have a bony projection on the humerus in adult males.

Ecnomiohyla valancifer differs from all other members of the genus in that the adult male lacks a humeral projection and keratinized black spines on the hand but has the prepollex spadelike and the prepollical bone flattened distally. Duellman (2001) suggested that this species might be conspecific with *E. minera*, but the latter has a humeral projection and keratinized black spines on the recurved prepollex and the prepollical bone ending in a sharp spine. We have considered the possibility that the prepollex and thumb spines may only be present in the breeding males and the absence in the male holotype of *E. valancifer* might be a seasonal effect, because such variation is known in *E. rabborum*.

Savage (2002) previously suggested that these frogs could be placed into two groups, one including those species with keratinized, black nuptial spines (*E. echinata*, *E. fimbriembra*, *E. minera*, *E. salvaje*, and *E. tuberculosa*) and the other those lacking the nuptial spines (*E. miliaria* and *E. valancifer*), which would include the recently resurrected *E. phantasmagoria*. The above descriptions of the variety of male secondary characters demonstrate that the situation is more complicated than this bipartite division indicates. In addition, examination of an adult male *E. tuberculosa* shows that it does not have a greatly enlarged prepollex, there is no prepollical projection, and its nuptial ornamentation consists of a rugose brown nuptial pad containing many mucous glands. Although not conclusive, we tentatively conclude that this species does not belong to the genus *Ecnomiohyla* and should be considered *incertae sedis*.

It appears that presence of nuptial spines may be a synapomorphy for a clade within *Ecnomio-*

hyla. Within the group of species having this feature, three of the species (*E. rabborum*, *E. minera*, and *E. salvaje*), also have a humeral projection—representing another possible synapomorphy. Among the species lacking the nuptial spines, the recurved prepollex plus a spinous prepollical projection is a putative synapomorphy for three species (*E. miliaria*, *E. minera*, and *E. phantasmagoria*). However, homoplasy cannot be ruled out for these features because *E. minera* has nuptial spines and a recurved prepollex and spinous prepollical process.

In any event, the new species most closely resembles *E. salvaje* of Honduras in male secondary sexual features (humeral projection, prepollex shape, shape of prepollical bony projection, and the presence of keratinized, black spines on the prepollex and thumb). Any close relationship between the two seems contraindicated by the presence of integumentary co-ossification with the skull in *E. salvaje* (absent in *E. rabborum*) and the presence of keratinized, black spines on the upper arm in the area of the humeral projection in the new species (absent in *E. salvaje*). *Ecnomiohyla fimbriembra*, another fringe-limb species known from western Panama, shares the prepollex, nuptial black spines, and prepollical projection features with *E. rabborum* but has cranial integumentary co-ossification and lacks the humeral projection and humeral keratinized spines found in males of the new species. Such recombinations of morphological characters in different pairings remains the bane of frog systematics. The question remains: will dependence on molecular analyses be able to sort out these kinds of ambiguities among these species, many of which appear to be approaching extinction?

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APPENDIX 1

Specimens Examined

Ecnomiohyla fimbrimembra.—Costa Rica: Provincia Alajuela: Volcan Poas: Isla Bonita, approximately 1,200 m (FMNH 191784, holotype, *Hyla fimbrimembra*); 3.2 km west of Isla Bonita, approximately 1,300 m (FMNH 191783, holotype, *Hyla richardi*, *H. richardtaylori*); Cinchona, 1,300 m (CRE 7015, tadpole); Provincia Heredia: northern slope of Volcan Barba: Parque Nacional Braulio Carrillo: Zona Protectora de La Selva, 1,800 m cabin (LACM 149979; MVZ 206432); southern slope of Volcan Barba: Cerro Turu: Yurro Honda, 1,900 m; Provincia Puntarenas: Monteverde: Pantanosa Trail, 1,600 m (LACM 149980). Panama: Provincia Chiriqui: Cerro Horqueta, 1,600–1,700 m (CHP1036).

Ecnomiohyla miliaria.—Honduras: Departamento Gracias a Dios: Hiltara Kiamp, 160 m (USNM 56949); Urus Tingi Kiamp, 160 m. Nicaragua: Departamento Río San Juan: between El Castillo and San Juan del Norte (USNM 4193, holotype, *Hyla miliaria*). Costa Rica: Provincia Alajuela: Rio Penas Blancas, nr. Fogden cabin, approximately 800 m (LACM 150152); Finca Francisco Orlich, 800 m (UCR 5142); Provincia Cartago: 2.5 km east of Turrialba: CATIE, 602 m (KU 30404, holotype, *Hyla immensa*); Provincia Limon: Alto Guayacan, 750 m (UCR 12787); 5 km from Moravia to Turrialba, approximately 750 m (UCR 10966); mountains north of La Bomba, 200 m (UCR 12678, 13706); 6–7 km south of Rio Blanco de Liverpool: Fila Asuncion, 400 m (UCR13254); Siquirres, 62 m (USNM 331414); Parque Nacional Hitoy-Cerere (UCR 12679); Comadre de Cahuita, approximately 20 m (UM 149201); Provincia Puntarenas: La Alturas, approximately 1,400 m (LACM 150153); Estacion Biologia Las Cruces, approximately 1,200 m (UCR 4979). Panama: Provincia Chiriqui: Finca Santa Clara, 1,140 m (KU 98451, 101610); upper Rio Chiriqui: Fortuna dam site, approximately 1,000 m (AMNH 94887); Provincia Coclé: Parque Nacional G. D.Omar Torrijos H.: Loop Trail, (SIUC H-6998).

Ecnomiohyla thysanota.—Panama: Provincia Darien: Cerro Mali (USNM 151080, holotype, *Hyla thysanota*).

Ecnomiohyla tuberculosa.—Peru: Provincia Amazonas: mouth Rio Santiago (AMNH 43479).