

- ROTH, V. L. 1991. Homology and hierarchies: problems solved and unresolved. *J. Evol. Biol.* 5:13–24.
- SHINE, R. 1995. A new hypothesis for the evolution of viviparity in reptiles. *Amer. Natur.* 145:809–823.
- , AND J. J. BULL. 1979. The evolution of live-bearing in lizards and snakes. *Amer. Natur.* 113: 905–923.
- , AND L. J. GUILLETTE, JR. 1988. The evolution of viviparity in reptiles: a physiological model and its ecological consequences. *J. Theor. Biol.* 132:43–50.
- SITES, J. W., JR., J. W. ARCHIE, C. J. COLE, AND O. F. VILLELA. 1992. A review of phylogenetic hypotheses for lizards of the genus *Sceloporus* (Phrynosomatidae): Implications for ecological and evolutionary studies. *Bull. Amer. Mus. Nat. Hist.* 213:1–110.
- SMITH, H. M., J. L. CAMARILLO R., AND D. CHISZAR. 1993. The status of the members of the *Sceloporus aeneus* complex (Reptilia: Sauria) of Mexico. *Bull. Maryland Herpetol. Soc.* 29:130–139.
- SWOFFORD, D. L. 1993. PAUP: Phylogenetic analysis using Parsimony, version 3.1.1. Illinois Natural History Survey, Champaign, Illinois.
- TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37:221–244.
- THOMAS, R. A., AND J. R. DIXON. 1976. A re-evaluation of the *Sceloporus scalaris* group (Sauria: Iguanidae). *Southwest. Natur.* 20:523–536.
- WIENS, J. J., AND T. W. REEDER. 1995. Combining data sets with different numbers of taxa for phylogenetic analysis. *Syst. Biol.* 44:548–558.

Accepted: 13 April 1997.

Journal of Herpetology, Vol. 31, No. 3, pp. 364–368, 1997
Copyright 1997 Society for the Study of Amphibians and Reptiles

A New Species of Frog from the Sierra Maestra, Cuba (Leptodactylidae, *Eleutherodactylus*)

ALBERTO R. ESTRADA¹ AND S. BLAIR HEDGES^{2,3}

¹Instituto de Investigaciones Forestales, Apartado Postal 5152, La Habana 5, CP 10500 Cuba

²Department of Biology, 208 Mueller Laboratory, Pennsylvania State University,
University Park, Pennsylvania 16802, USA

ABSTRACT.—A new species of *Eleutherodactylus* is described from the upper elevations of the Sierra Maestra in eastern Cuba. It is a common and widespread species that calls from arboreal sites and is very similar, morphologically, to the common lowland species *E. auriculatus*. However, the two species occur sympatrically at intermediate elevations in the Sierra Maestra and have distinctive calls.

During an expedition to Pico Turquino in the Sierra Maestra of eastern Cuba in August, 1989, we encountered two common species of frogs on vegetation along trails and in the forests of the upper elevations. One was found almost exclusively in bromeliads, and the other occurred low on bushes and other vegetation. The calls of both upland forms were similar to their lowland counterparts, *Eleutherodactylus ionthus* and *E. auriculatus*, respectively, but differed in significant ways. However, because such differences might be attributed to elevation (and temperature), we made a nocturnal descent of Pico Turquino in order to hear and record calls emitted at different elevations. As we decreased in

elevation, we found that the calls of the upland forms did not change significantly. Moreover, we discovered a zone of sympatry between the upland forms and their lowland counterparts in the vicinity of 800–1100 m elevation. Initially, our recordings and collection data were more extensive for the bromeliad-dwelling species, which we described as *E. melacara* (Hedges et al., 1992). Since then, we have made additional collections of the other upland form elsewhere in the Sierra Maestra, and describe that new species here.

MATERIALS AND METHODS

The following abbreviations are used: SVL, snout–vent length; HL, head length; HW, head width; TYM, tympanum width; EL, eye length; EN, eye–naris distance; IOD, interorbital dis-

³ Address for correspondence and reprints. E-mail: sbh1@psu.edu.

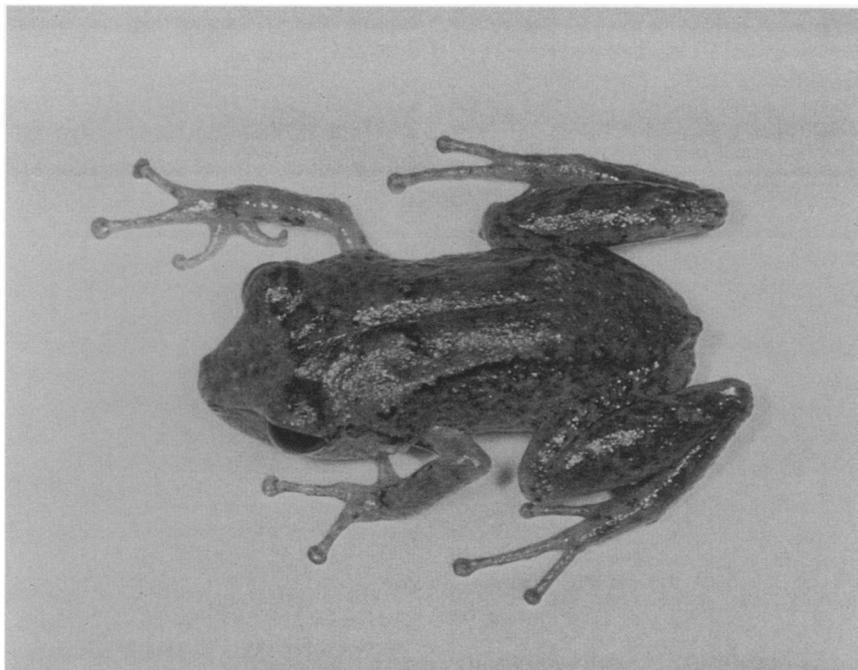


FIG. 1. *Eleutherodactylus glamyrus* from Pico Real del Turquino, Municipio Guamá, Santiago de Cuba Province, 1974 m.

tance; THL, thigh length; SHL, shank length; and FTW, fingertip (III width). Museum abbreviations follow standardized usage (Leviton et al., 1985), except for MNHNCU, which refers to the collection of the Museo Nacional de Historia Natural, Havana, Cuba; CZACC, Zoological Collection from Instituto de Ecología y Sistemática, Havana, Cuba; and CARE, Collection of Alberto R. Estrada, Havana Cuba.

Measurements were taken with calipers (0.01 mm accuracy) and an ocular micrometer. Calls were recorded with a Sony Walkman Professional cassette recorder and WM-D3 with electret condenser stereo microphone PC-62. The signal analyses were made with the use of Canary software (Cornell University). Terminology for call parameters follows Duellman and Trueb (1986).

Eleutherodactylus glamyrus, new species

Fig. 1

Holotype.—MNHNCU 660, an adult male from Pino del Agua Arriba, Sierra Maestra, Municipio Guisa, Granma Province, Cuba, 1200 m, collected by Alberto R. Estrada on 29 April 1993 (original number CARE 858).

Paratypes.—CARE 859–62, 878–82, paratypes, same collecting data as holotype; CARE 866–67, Estribo N, Pico La Bayamesa, Sierra Maestra, Municipio Guisa, Granma Province, 1600 m; USNM 509042, Pico Botella, Municipio

Buey Arriba, Granma Province, 1375 m; USNM 509044, El Joaquin, Municipio Bartolomé Masó, Granma Province, 1300–1400 m; USNM 509043, 1.4 km N Minas del Frio, Municipio Bartolomé Masó, Granma Province, 845 m; MNHNCU 112, 118, 120, 126, 131, 133, 139, 157, 159–61, USNM 509049–51, Pico Real del Turquino, Municipio Guamá, Santiago de Cuba Province, 1974 m; USNM 509052, Estribo Turquino, Municipio Guamá, Santiago de Cuba Province, 1770 m; MNHNCU 616, USNM 509045–48, Pico Cuba, Municipio Guamá, Santiago de Cuba Prov., 1720 m; MNHNCU 124, 162, Loma Redonda (near Pico Cuba), Municipio Guamá, Santiago de Cuba Province, 1700 m; MNHNCU 134, 656–8, near La Emajagua, Municipio Guamá, Province, 850 m.

Diagnosis.—*Eleutherodactylus glamyrus* is a small member of subgenus *Eleutherodactylus* on Cuba (16.6–20.0 mm SVL males; 18.8–24.1 SVL females) having a short and rounded left lobe of the liver, short vomerine odontophores, areolate venter, external submandibular vocal sac, and enlarged digital pads. It is most closely related to *E. auriculatus*, with which it shares a small body size, general body shape, and a single note call that is repeated continuously. It differs from that species in having a yellow vocal sac (in males) rather than brown and a call with a lower mean dominant frequency (3.21–3.30 kHz in *E. glamyrus* versus 3.78–3.86 kHz in *E.*

auriculatus), longer note duration (79.4–94.8 mS in *E. glamyrus* versus 7.3–8.9 mS in *E. auriculatus*), and slower call rate (67.6–78.6 calls/min in *E. glamyrus* versus 229–276 calls/min in *E. auriculatus*). Additionally (although not completely diagnostic), *E. glamyrus* typically is mottled in yellows and greens (dorsally) and has a white venter, whereas *E. auriculatus* tends to be more uniformly brown and tan, with brown ventral stippling.

Description.—Head as wide as body, width greater than length; snout acuminate in dorsal view, subacuminate in lateral view, overhanging lower jaw; nostrils strongly protuberant, directed laterally; canthus rostralis moderately sharp, slightly concave in dorsal view; loreal region concave, sloping abruptly; lips not flared; upper eyelid bearing several rounded tubercles; interorbital space without tubercles; supratympanic fold well defined, concealed upper edge of tympanic annulus; tympanum small, rounded, separated from eye by a distance more than its own diameter; two or three small, subconical, post-auricular tubercles; choanae moderate-sized, oval, partially concealed by palatal shelf of maxillary arch when roof of mouth is viewed from below; vomerine odontophores posterior to choanae, each about the same size as a choana, separated widely at midline; tongue longer than wide, posterior edge with notch, posterior three-fourths not adherent to floor of mouth; males with vocal slits; vocal sac median subgular.

Skin of dorsum moderately tuberculate, with dorsolateral folds; skin of flanks similar to dorsum; skin of venter moderately areolate, with discoidal folds; anal opening not extended in sheath; no glandular areas present, although moderate-sized postscapular tubercles present, followed by a dorsolateral fold; ulnar tubercles low, flat; palmar tubercle single, larger than the nar, thenar tubercle oval, low; several small supernumerary palmar tubercles; subarticular tubercles of fingers round and flat; no lateral ridge on finger; all fingers with expanded tips; fingertips rounded, semicircular pad on ventral surface of fingertip; circumferential groove bordering distal two-thirds of finger pad; width of largest pad (III) same size as tympanum; first finger shorter than second when adpressed; heel tubercles small and flat; no tubercles along outer edge of tarsus; metatarsal tubercles low, inner (oval) twice size of outer (subconical); several small, low, supernumerary plantar tubercles; subarticular tubercles of toes oval and flat; toes unwebbed; weak lateral ridge on toe; fifth toe longer than third when held parallel to fourth toe; all toes with expanded tips; toetips pointed; semicircular pad on ventral surface of toetip; circumferential groove bordering distal two-thirds of toe pad; heels overlap when flexed

legs are held at right angles to sagittal plane; liver shape “*auriculatus*-type” (Hedges, 1989b).

In life, dorsal ground color brown-coppery delimited by two dorsolateral discontinuous black lines that follow dorsolateral folds; a faint brown interocular bar or triangle; head color light brown; eyelids greenish-gray; white mid-dorsal hair line extending from snout to vent, where it forks and continues onto each thigh along the ventral face of shank; brown X (diffuse or absent in some animals) behind interocular bar; loreals brown-coppery with a black stripe from snout to supratympanic fold (interrupted on eyes); upper lip greenish-brown with black spots, lower yellowish-brown with black spots; tubercles below tympanum golden yellow; lateral ground color yellowish with brown and black markings; vent black-bordered; thighs dark brown, with three light cross bars; shank brown with two cross bars; forearms brown with two yellow cross bars; arms yellow; vocal sac yellow, with scattered brown spots in some animals; venter whitish-translucent.

Measurements.—The mean (± 1 SE) and range (in parentheses) of 21 adult males and six adult females are (in mm): SVL 18.7 ± 0.22 males, (16.6–20.0), 21.7 ± 0.78 females (18.8–24.1); HL 6.7 ± 0.06 males (6.2–7.4); 8.2 ± 0.41 females, (6.4–9.3); HW 7.7 ± 0.06 males, (7–8.1), 9.1 ± 0.35 females (7.7–10.4); TYM 1.01 ± 0.03 males (0.7–1.4), 1.3 ± 0.11 females (0.9–1.6); TYM-EYE 1.02 ± 0.02 [11] males. (0.8–1.1), 0.8 [1] female; EYE 2.9 ± 0.07 males (2.5–3.7), 3.6 ± 0.19 females (2.8–4.1); E-N 2.1 ± 0.03 males (2–2.5), 2.5 ± 0.06 females (2.3–2.8); IOD 2.7 ± 0.05 males (2.2–3.1), 3.1 ± 0.17 females (2.7–3.9); THL 9.01 ± 0.14 males (7–10), 10.4 ± 0.34 females (9.5–11.4); SHL 9.6 ± 0.14 males (8.1–11.2), 11.3 ± 0.17 females (10.7–11.8); FTW 0.8 ± 0.02 [15 males] (0.5–1), 0.9 ± 0.05 [5 females] (0.7–1); TTW 0.99 ± 0.013 [12 males] (0.7–1.1), 0.96 ± 0.05 [5 females] (0.8–1.1); live mass 0.47 ± 0.01 (0.40–0.55) g males (N = 13), and 0.88 ± 0.05 (0.78–1.12) g females (N = 6).

Etymology.—From the Greek *glamyrus*, meaning bleary-eyed or watery-eyed; in allusion to the misty, cloud forest habitat of this species.

Natural History.—During the night, *Eleutherodactylus glamyrus* typically calls from horizontal surfaces of leaves and ferns about 0.5–2 m above the ground, although during the day it calls from more concealed sites. In contrast, *E. auriculatus* did not show that preference for horizontal surfaces, but rather often was found calling from twigs of bushes or stems of ferns low to the ground. The female from Estribo N of Pico La Bayamesa (CARE 866) was collected during the day on leaf litter. Another female (MNHCU 131), on the main trail to Pico Real del Turquino, was collected in a hole in the

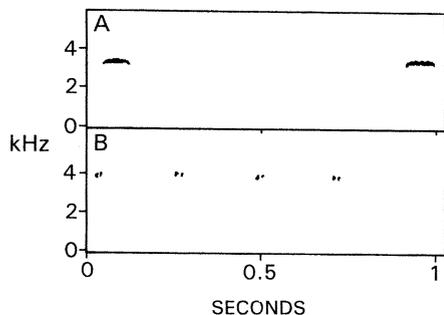


FIG. 2. Audiospectrograms (filter bandwidth 353 Hz) of two Cuban species of *Eleutherodactylus*: (A) two calls of *E. glamyrus* from the type locality, and (B) four calls of *E. auriculatus* from the same locality.

ground (beneath a stone) along with a clutch of 6 eggs. A pair was found in amplexus in leaf litter during the day (9 August) on Estribo Turquino, and the female later laid 11 eggs in a bag.

Vocalization.—Both species have a call that consists, usually of a single note repeated continuously in long series. However, the call of *E. glamyrus* consists of a “ting” note that is longer in duration and lower in frequency than the “tick” of *E. auriculatus* (Fig. 2). The call has a lower mean dominant frequency (3.25 ± 0.01 [3.21–3.30] kHz in *E. glamyrus* versus 3.83 ± 0.01 [3.78–3.86] kHz in *E. auriculatus*), longer call duration (84.6 ± 2.2 [79.4–94.8] ms in *E. glamyrus* versus 8.1 ± 0.21 [7.3–8.9] ms in *E. auriculatus*), and slower call rate (72.0 ± 1.78

[67.6–78.6] calls/min in *E. glamyrus* versus 258 ± 6.3 [229–276] calls/min in *E. auriculatus*).

Distribution.—*Eleutherodactylus glamyrus* is widely distributed throughout the Cordillera del Turquino, Sierra Maestra, at elevations above about 800 m (see Fig. 3 for localities). On the SW slope of Pico Turquino we found *E. glamyrus* from the top (Pico Real, 1974 m) down to a point above La Emajagua (850 m). Sympatry between *E. glamyrus* and *E. auriculatus* was noted (by vocalization) at about 850–1100 m. We also found sympatric populations from W to E in different localities along the northern slope of the Sierra Maestra: Minas del Frío (845 m), El Naranjo (850), Pico La Botella (1375 m), and Pino del Agua Arriba (1200 m).

DISCUSSION

The validity of *Eleutherodactylus glamyrus* as a species distinct from *E. auriculatus* is indicated by occurrence of the two in sympatry at intermediate elevations in the Sierra Maestra. However, their distinction at those localities is based primarily on vocalization, call site, and color of the vocal sac, traits of living males (although vocal sac color is evident also in some preserved specimens). For females and juveniles, separation of these two species will be difficult, although some of the coloration differences noted above (see Diagnosis) may help. Older museum specimens from intermediate elevations (e.g., MCZ 21985–989; USNM 137914) cannot be allocated, with confidence, to species.

The altitudinal relationship and morphologi-

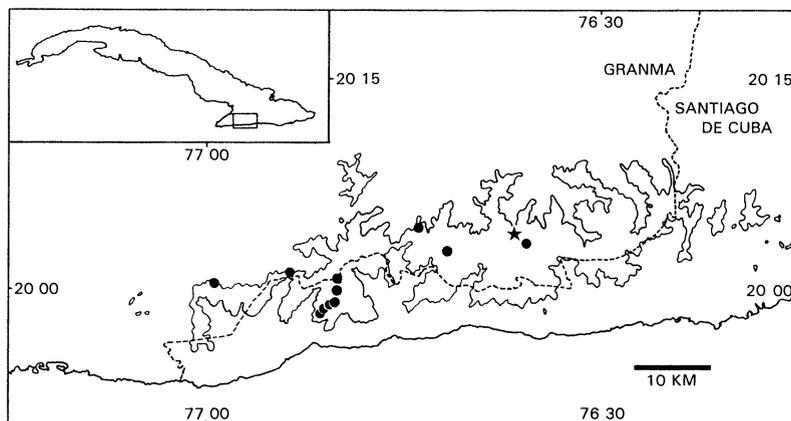


FIG. 3. Distribution of *Eleutherodactylus glamyrus* in eastern Cuba. Known localities, from west to east are 1.4 km N Minas del Frío (845 m), El Naranjo (850 m), near La Emajagua (850 m), Pico Mar Verde (“Pico Cardero,” 1285 m; vocalization only), Pico Cuba Camp (1720 m), Pico Real del Turquino (1974 m), Estribo Turquino (1770 m), El Joaquin (1300–1400 m), 2.4 km S Las Guasimas (845 m; vocalization only), Pico Botella (1375 m), Pino del Agua Arriba (1200 m), and Pico La Bayamesa (1600 m). The star denotes the type-locality, Pino del Agua Arriba; dashed line is the border between the provinces of Granma and Santiago de Cuba; narrow line indicates 800 m contour. See Schwartz and Hedges (1991) for a detailed map of collecting localities in the region of Pico Turquino and a discussion of place names.

cal similarity between *E. glamyrus* and *E. auriculatus* parallels that of two Hispaniolan species (*E. audanti* and *E. abbotti*) and two Puerto Rican species (*E. portoricensis* and *E. coqui*), also in the subgenus *Eleutherodactylus* (Hedges, 1989b). In both of those cases, the ranges of the upland species (*E. audanti* and *E. portoricensis*) overlap with those of the corresponding lowland species, morphological differences are slight, and the call differences provide about the best means of distinguishing the species in the zone of overlap (Schwartz, 1966; Thomas, 1966). As with the Cuban pair, older museum specimens of the Hispaniolan and Puerto Rican species can be difficult to correctly identify. Although the subgenus *Eleutherodactylus* does not occur (naturally) on Jamaica, there is a pair of sibling species of the subgenus *Euhyas* (*E. gossei* and *E. junori*) that also is difficult to distinguish morphologically (Schwartz and Fowler, 1973). In that case, differences in vocalization provide about the only means of identifying specimens (with confidence) in the zone of sympatry aside from karyotyping (Bogart and Hedges, 1995) or obtaining molecular data (Hedges, 1989a).

The above examples illustrate that it is not uncommon to have a valid, reproductively isolated, species of *Eleutherodactylus* with few or no known diagnostic morphological characters distinguishing it from its closest relative. At the same time, the fact that morphologically similar species always have call differences, but not the reverse (morphologically different co-occurring species with identical calls) reinforces the close association between vocalization and speciation observed in these anurans. Although it is not yet known whether the call differences represent a genetic byproduct of other changes at speciation, or whether they are the primary character under selection, closer study of such sibling species may help provide insight into the process of speciation.

Acknowledgments.—We thank the other members of the 1989, 1990 and 1994 Penn State/Cuba herpetological expeditions (Emilio Alfaro, Riberto Arencibia, Antonio Pérez-Asso, Octavio Perez Beato, Orlando Garrido, Laredo González, Daniel McCallister, Jr., Alfonzo Silva, Alcides Sampedro, and Richard Thomas) for their assistance and support, and the collaborating Cuban scientific institutions (Museo Nacional de His-

toria Natural, and Instituto de Ecología y Sistemática); Martjan Lammertink organized the trip to Pico Bayamesa (with A.R.E.) and Bird Life International for provided funds. We thank John Lynch for helpful comments on the manuscript. The senior author was supported in part a by grant from RARE Center and Instituto de Investigaciones Forestales, La Habana, Cuba. The junior author was supported by grants from the National Science Foundation.

LITERATURE CITED

- BOGART, J. P., AND S. B. HEDGES. 1995. Rapid chromosome evolution in Jamaican frogs of the genus *Eleutherodactylus* (Leptodactylidae). *J. Zool. (London)* 235:9–31.
- DUELLMAN, W. E., AND L. TRUEB. 1986. *Biology of Amphibians*. McGraw-Hill, New York.
- HEDGES, S. B. 1989a. An island radiation: allozyme evolution in Jamaican frogs of the genus *Eleutherodactylus* (Anura, Leptodactylidae). *Carib. J. Sci.* 25:123–147.
- . 1989b. Evolution and biogeography of West Indian frogs of the genus *Eleutherodactylus*: slow-evolving loci and the major groups. In C. A. Woods (ed.), *Biogeography of the West Indies: Past, Present, and Future*, pp. 305–370. Sandhill Crane Press, Gainesville, Florida.
- , A. R. ESTRADA, AND R. THOMAS. 1992. Three new species of *Eleutherodactylus* from eastern Cuba, with notes on vocalizations of other species (Anura, Leptodactylidae). *Herpetol. Monogr.* 6:68–83.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802–832.
- SCHWARTZ, A. 1966. The relationships of four small Hispaniolan *Eleutherodactylus* (Leptodactylidae). *Bull. Mus. Comp. Zool., Harvard Univ.* 133:369–399.
- , AND D. C. FOWLER. 1973. The anura of Jamaica: a progress report. *Stud. Fauna Curacao Other Carib. Ids.* 43:50–142.
- SCHWARTZ, A., AND S. B. HEDGES. 1991. An elevational transect of Lepidoptera on Pico Turquino, Cuba. *Carib. J. Sci.* 27:130–138.
- THOMAS, R. 1966. New species of Antillean *Eleutherodactylus*. *Q. J. Fla. Acad. Sci.* 28:375–391.

Accepted: 15 April 1997.

APPENDIX 1

Specimens Examined

Eleutherodactylus auriculatus.—Cuba: Pinar del Rio Province, Soroa (USNM 509057). Granma Province; 1.4 km N Minas del Frio (USNM 509058–59).