

THREE NEW SPECIES OF *ELEUTHERODACTYLUS* FROM EASTERN CUBA, WITH NOTES ON VOCALIZATIONS OF OTHER SPECIES (ANURA: LEPTODACTYLIDAE)

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ABSTRACT: Three new arboreal species of *Eleutherodactylus* are described from upland regions of eastern Cuba. *Eleutherodactylus guantanamera* is relatively widespread in Guantánamo Province and also occurs in Santiago de Cuba Province, *E. mariposa* is known only from the type-locality on the Meseta del Guaso (Guantánamo Province), and *E. melacara* is known only from Pico Turquino in Santiago de Cuba Province. Two of these species, *E. guantanamera* and *E. melacara* represent the first bromeliad specialists known from Cuba, and they possess a head shape and eye orientation found in other bromeliad-dwelling species. Call and chromosome variation are discussed for all 10 members of this arboreal subgenus in Cuba.

Key words: Caribbean; West Indies; Systematics; Vocalization; Bromeliad; Ecomorph

THE grandiose frog genus *Eleutherodactylus* (>500 species) is represented in the West Indies by two large and widespread subgenera, *Euhyas* (80 species) and *Eleutherodactylus* (44 species), and one small subgenus (*Pelorius*; six species) on Hispaniola (Hedges, 1989). Molecular evidence suggests that the divergence of the two large subgenera occurred in the late Cretaceous or early Cenozoic (Hass and Hedges, 1991). Although members of each subgenus have invaded a wide range of ecological niches, these two groups can be characterized by their predominant ecological habits. Species in the subgenus *Euhyas* usually occupy terrestrial niches and commonly are found close to the ground or on rocks. West Indian species of the subgenus *Eleutherodactylus* nearly always occupy arboreal niches. These ecological differences are especially evident when comparing Jamaican species (all *Euhyas*), which are predominantly terrestrial, with those from Puerto Rico (all subgenus *Eleutherodactylus*), which are predominantly arboreal.

Morphologically, members of the arboreal subgenus usually have an areolate venter, an externally evident vocal sac, short vomerine odontophores, reduced sexual dimorphism in body size, and a liver with a short and rounded left lobe. Species

in the terrestrial subgenus *Euhyas* usually have a smooth venter, a concealed (or absent) vocal sac, long vomerine odontophores, marked sexual dimorphism in body size, and a liver with a long and pointed left lobe (Hedges, 1989). Most Cuban species of *Eleutherodactylus* mostly belong to the subgenus *Euhyas*, although six species of arboreal frogs (subgenus *Eleutherodactylus*) presently are known from that island: *E. auriculatus* Cope, *E. bartonsmithi* Schwartz, *E. eileenae* Dunn, *E. leberi* Schwartz, *E. ronaldi* Schwartz, and *E. varians* Gundlach and Peters. Recent field work in Cuba by us and personnel from the Museo Nacional de Historia Natural has revealed an amphibian and reptilian fauna that is considerably more diverse than previously known. Among the newly discovered snakes, lizards, and frogs are three arboreal species of *Eleutherodactylus* belonging to the *auriculatus* section of the subgenus *Eleutherodactylus*.

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; THL = thigh length; SHL = shank length; and FTW = fingertip (III) width. Museum abbreviations follow stan-

standardized usage (Leviton et al., 1985), except for MNHNCU, which refers to the newly formed collection of the Museo Nacional de Historia Natural, Cuba (Havana). Measurements were taken with digital calipers (0.01 mm accuracy) and live masses were taken with a Pesola spring scale (0.01 g accuracy). Specimens examined that are not listed in the descriptions are in Appendix I.

Calls were recorded with a Sony TCM 5000 recorder and Electrovoice 635A microphone. Analyses were made with a Digital Sona-Graph 7800 and Kay Sona-Graph 7900 printer. Terminology for call parameters follows Duellman and Trueb (1986). In the case of continuous calls (e.g., *E. auriculatus*), each note was considered a separate call in the analyses.

Measurement of eye orientation was made in the following manner. A mylar film was placed lightly on the head of the moist, preserved specimen and the lines formed by the upper eyelids were traced. The two resulting lines were extended with a ruler, past their point of intersection, and the interior angle was measured with a protractor. Greater angles correspond to eyes with a more anterior (as opposed to lateral) orientation (see below).

Chromosomes were prepared in the field and the laboratory. Field preparations were made by injecting the frog with colchicine (0.1 mg/g mass in a concentration of 1 mg/ml), sacrificing after 4–8 h, placing testes (if male) and intestines in distilled H₂O for 10–15 min, and then fixing in ethanol:acetic acid (3:1) (J. P. Bogart, personal communication). In the case of animals returned to the laboratory, the corneal epithelium method (Bogart, 1981) was used to obtain the karyotype.

SYSTEMATIC ACCOUNTS

Eleutherodactylus varians

Before describing the three new species, it is necessary to discuss briefly the taxonomic history and present status of one arboreal Cuban species, *E. varians*. This species was reviewed by Schwartz (1960). He separated the small, common and widespread *E. auriculatus* Cope from the larger, tree-dwelling *E. varians*, and recognized four isolated races of the latter

species: *E. v. varians* in central Cuba (Cienfuegos Prov. to Camagüey Prov.), *E. v. olibrus* Schwartz in the west (Pinar del Río Prov.), *E. v. ionthus* Schwartz in the east (Santiago de Cuba and Guantánamo Provinces), and *E. v. staurometopon* Schwartz (Isla de la Juventud). There are large hiatuses in the ranges of the three subspecies on Cuba, with slightly over 200 km separating the easternmost *E. v. varians* (Banao, Camagüey) from the westernmost *E. v. ionthus* (Pico Turquino, Santiago de Cuba). All of the subspecies typically occur high in trees and often can be found in bromeliads during the day, although they may occupy a variety of arboreal calling sites. The call is typically a one-, two-, or three-note hollow, metallic "tock".

Schwartz (1960) distinguished the eastern subspecies, *E. v. ionthus*, from the others by its tan dorsum with little or no pattern (versus a boldly patterned dorsum). Additionally, from *E. v. olibrus*, it differs in having a longer shank [50.1% (46.7–52.0%) SVL versus 46.9% (44.4–49.0%) SVL] and longer fourth toe. From *E. v. varians*, it differs in having a lighter venter (not uniformly pigmented) and in having a relatively larger tympanum [5.9% (5.3–6.4%) SVL versus 5.2% (4.7–5.7%) SVL]. From *E. v. staurometopon*, it has a longer head [41.4% (40.0–43.3%) SVL versus 35.7% (34.8–36.7%) SVL], a shorter thigh, and a shorter shank and fourth toe. Measurements for *E. ionthus* are given in Table 1. The call of *E. v. staurometopon* also differs in being more rapid and higher pitched than the other subspecies (Schwartz, 1960).

In August, 1989, we ascended Pico Turquino (1974 m), which is located in the Sierra Maestra, and collected a large, bromeliad-dwelling *Eleutherodactylus* that superficially resembles *E. v. ionthus* in coloration. However, it is larger, has a wider head (narrow and pointed in *ionthus*), and a different call (14–22 rapidly-emitted notes). It occurs syntopically with *E. v. ionthus*, a low elevation form, where the two overlap at intermediate elevations on Pico Turquino. In 1989 and 1990, we collected a third species in this complex at several upland localities in Santiago de Cuba and Guantánamo provinces. It is also

TABLE 1.—Measurements of four species of Cuban *Eleutherodactylus*. Shown are means and ranges (in parentheses) in mm.

	<i>E. melacara</i>				<i>E. guantanamera</i>			<i>E. mariposa</i>	
	<i>E. ionthus</i> Males (12)	Males (9)	Females (8)	Holo- type	Males (12)	Females (5)	Holotype	Males (12)	Holo- type
SVL	25.9 (24.7–27.0)	27.1 (24.0–28.7)	32.2 (28.8–35.6)	35.6	30.7 (26.5–32.8)	35.0 (32.1–37.3)	32.9	32.1 (29.8–36.1)	31.0
HL	10.6 (9.94–11.2)	11.2 (9.76–12.1)	13.3 (12.7–14.4)	14.4	12.8 (10.7–14.2)	14.5 (13.2–15.9)	13.2	12.9 (11.7–13.9)	13.2
HW	10.6 (9.47–11.9)	11.4 (9.77–12.3)	13.9 (13.1–14.9)	14.9	13.1 (11.3–14.3)	14.7 (13.3–16.4)	13.5	12.8 (11.8–13.8)	13.4
TYM	1.46 (1.24–1.67)	1.47 (1.24–1.66)	1.98 (1.76–2.16)	2.08	1.82 (1.76–2.07)	2.02 (1.63–2.33)	2.33	2.23 (1.89–2.43)	2.21
EL	3.94 (3.30–4.41)	3.68 (2.97–4.27)	4.34 (3.85–4.79)	4.60	4.58 (3.96–5.12)	4.83 (4.26–5.31)	4.26	4.51 (4.14–5.02)	4.42
EN	3.30 (3.11–3.52)	3.17 (2.92–3.30)	3.80 (3.45–4.23)	4.23	3.91 (3.30–4.34)	4.35 (3.82–4.78)	3.82	3.94 (3.61–4.34)	3.74
THL	11.3 (10.8–12.2)	11.4 (9.72–12.2)	13.9 (12.9–14.9)	14.9	13.4 (12.2–14.4)	15.4 (13.5–17.0)	14.1	13.8 (12.2–15.5)	13.4
SHL	12.5 (11.7–13.1)	13.0 (12.1–14.0)	16.0 (15.4–17.1)	17.1	15.6 (14.1–16.8)	17.5 (15.2–19.1)	15.2	15.2 (14.1–16.3)	14.7
FTW	1.31 (1.06–1.68)	1.35 (1.16–1.56)	1.61 (1.38–1.80)	1.69	1.57 (1.42–1.77)	1.89 (1.68–2.00)	1.71	1.45 (1.26–1.68)	1.68

a larger species than *E. v. ionthus*, has a different head shape, and typically a four- or five-note call. It is sympatric with *E. v. ionthus*, but the two have not yet been collected syntopically. Although older specimens representing all three species have been placed under the name *E. v. ionthus*, examination of the type series and our recordings made at 0.5 km W Yerba de Guinea, near the type-locality (10 km E La Maya), indicate that the name *ionthus* belongs with the small, two-note species.

The morphological differences distinguishing *E. v. ionthus* from the other subspecies of *E. varians*, its geographic isolation, and the fact that it has a different chromosome number ($2N = 26$) from at least one of those subspecies, *E. v. olibrus* ($2N = 18$; Bogart, 1981) lead us to conclude that it is a separate species, *E. ionthus* (Fig. 1E). The diagnostic differences among *E. ionthus*, the new species from Pico Turquino, and a new five-note upland species will be discussed in detail below in the accounts of those two new species.

For the bromeliad-dwelling species from Pico Turquino, we propose the name:

Eleutherodactylus melacara sp. nov.
Fig. 2B

Holotype.—MNHNCU 252, an adult male from Estribo Turquino, 1–2 km N

Pico Turquino, Santiago de Cuba Prov., Cuba, 1770 m, collected by S. Blair Hedges and Richard Thomas on 9 August 1989.

Paratypes.—KU 217775–76, MNHNCU 253–71, USNM 309731–38, paratypes, same collecting data as holotype; USNM 309739, vicinity of Pico Cuba (near Pico Turquino), 1720 m; MCZ 21985–89, near Cueva del Aura (below Pico Turquino), 445–1212 m; UMMZ 80907 ($n = 3$), Cueva del Aura (below Pico Turquino), 455–1212 m; all from Santiago de Cuba Prov., Cuba.

Diagnosis.—*Eleutherodactylus melacara* can be distinguished from all other members of the subgenus *Eleutherodactylus* on Cuba by its large size (24.0–28.7 mm SVL, males; 28.8–35.6 mm, females), short snout, very wide and dark head (usually), tan dorsum lacking any well-defined pattern, and with concealed areas of legs uniform dark brown. The only taxa likely to be confused with *E. melacara* are *E. ionthus* and an undescribed species (see diagnosis below for comparisons with that species). Both *E. melacara* and *E. ionthus* occur in eastern Cuba and are sympatric. Although they both have large digital tips and a tan, patternless (or nearly so) dorsum, *E. ionthus* has a straight (not concave) canthus rostralis, a distinct canthal bar (only rarely present in *E. melacara*), has eyes that are oriented more laterally ($56\text{--}70^\circ$ versus $77\text{--}91^\circ$; Fig. 3), and a head

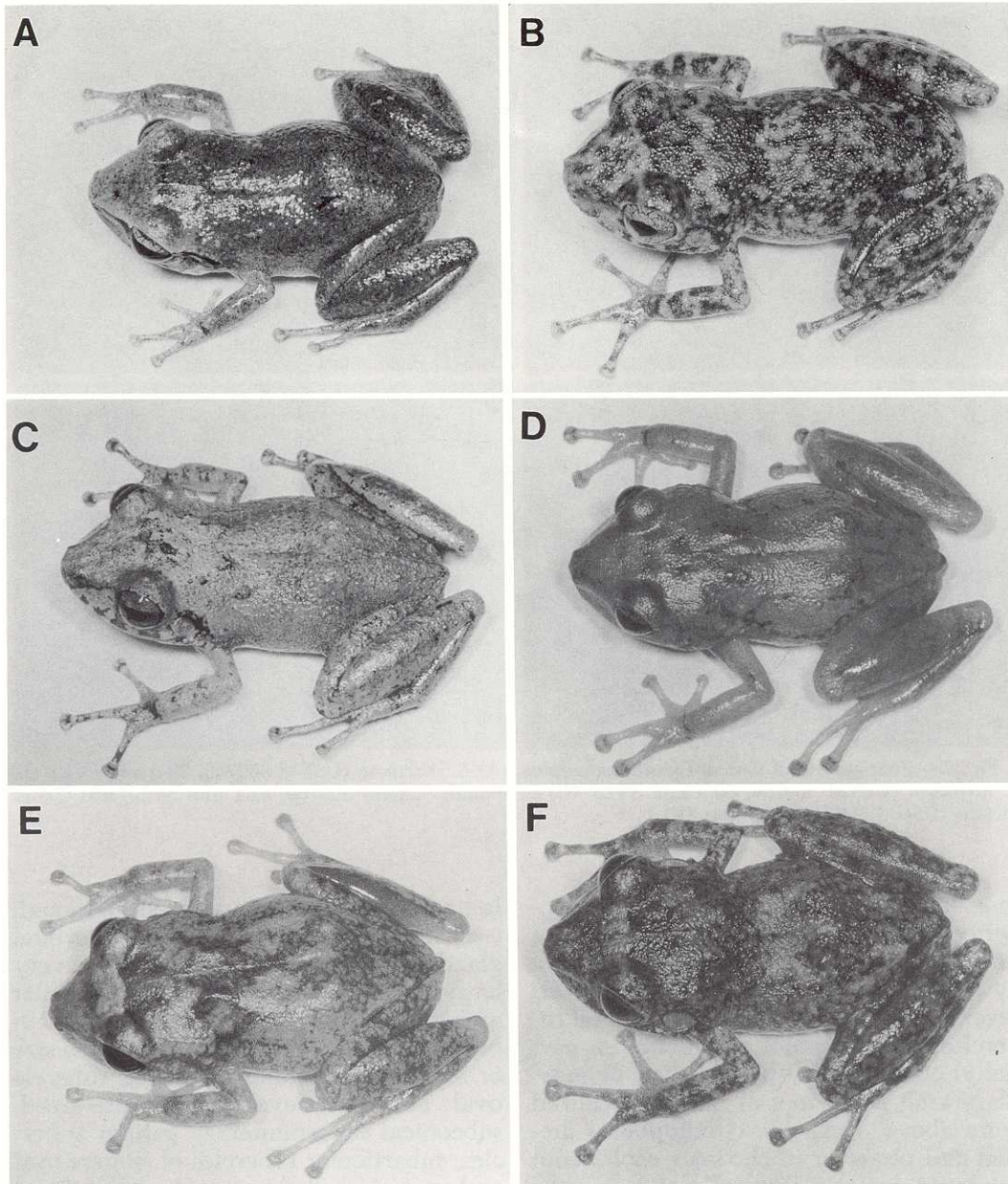


FIG. 1.—Six species of Cuban *Eleutherodactylus*: (A) *E. auriculatus* (USNM 309752, 17.4 mm SVL), (B) *E. bartonsmithi* (USNM 309753, 20.9 mm SVL), (C) *E. eileenae* (USNM 309754, 26.9 mm SVL), (D) *E. guantanamera* (USNM 309744, 28.4 mm SVL), (E) *E. ionthus* (USNM 309757, 26.5 mm SVL), and (F) *E. leberi* (USNM 309758, 30.5 mm SVL).

that is not wider than the body (distinctly wider than the body in *E. melacara*).

Description.—Head wider than body, width greater than length; snout semicircular in dorsal view, but with pointed tip (between nares), acuminate in lateral view, overhanging lower jaw; nostrils weakly protuberant, directed dorsolaterally and

slightly forward; canthus rostralis rounded, slightly concave in dorsal view; loreal region slightly concave, sloping gradually; lips not flared; upper eyelid bearing a few (or no) small rounded tubercles; interorbital space without tubercles (occasionally one or two small rounded tubercles present); supratympanic fold weakly defined

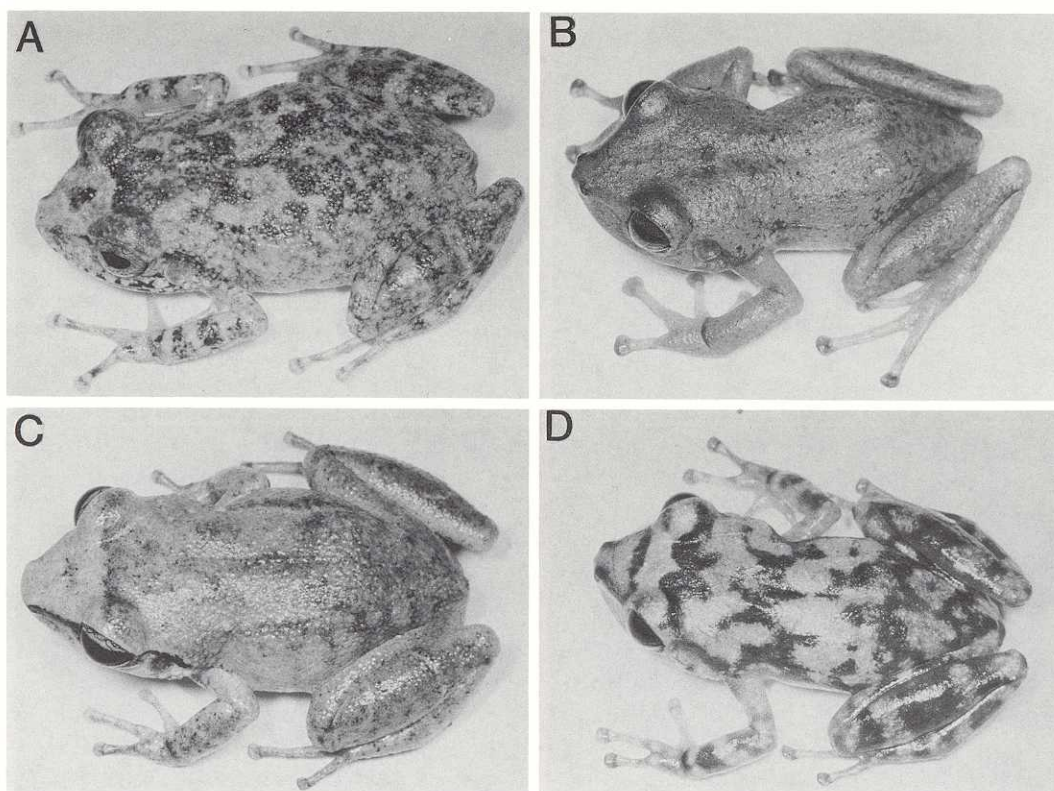


FIG. 2.—Four species of Cuban *Eleutherodactylus*: (A) *E. mariposa* (USNM 309749, 30.9 mm SVL), (B) *E. melacara* (USNM 309736, 30.9 mm SVL), (C) *E. ronaldi* (USNM 309760, 24.1 mm SVL), and (D) *E. varians* (USNM 309761, 27.0 mm SVL).

(one or two swollen areas), concealing upper edge of tympanic annulus; tympanum moderate-sized, round, separated from eye by a distance equal to its own diameter; several enlarged, subconical, postrictal tubercles; choanae small, round, not (or partially) concealed by palatal shelf of maxillary arch when roof of mouth is viewed from above; vomerine odontophores medial and posterior to choanae, each about the same size as a choana, oval, separated widely at midline; tongue longer than wide, posterior edge without notch, posterior one-fourth to one-third not adherent to floor of mouth; males with vocal slits; vocal sac median subgular.

Skin of dorsum weakly tuberculate, without dorsolateral folds; skin of flanks similar to dorsum; skin of venter moderately areolate, with discoidal folds (evident posteriorly in some individuals); anal opening not (or just barely) extended in sheath; no supra-axillary, inguinal, or post-

femoral glandular areas present, although two individuals have large interorbital glandular areas, and one of those has a very large and swollen post-tympanic glandular area; ulnar tubercles absent; palmar tubercle bifid or divided, about the same size or smaller than thenar; thenar tubercle oval, elevated; several moderate-sized, subconical supernumerary palmar tubercles; subarticular tubercles of fingers oval and conical, angled outward; well-defined lateral ridge on fingers; all fingers with expanded tips, III and IV more than I and II; fingertips rounded; oblong pad on ventral surface of fingertip; circumferential groove bordering distal two-thirds of finger pad; width of largest pad (III) three-fourths to same size as TYM; first finger shorter than second when adpressed; heel tubercles absent or small and subconical; no row of tubercles along outer edge of tarsus; metatarsal tubercles elevated, inner (oval) 3–4 times as large as outer (subcon-

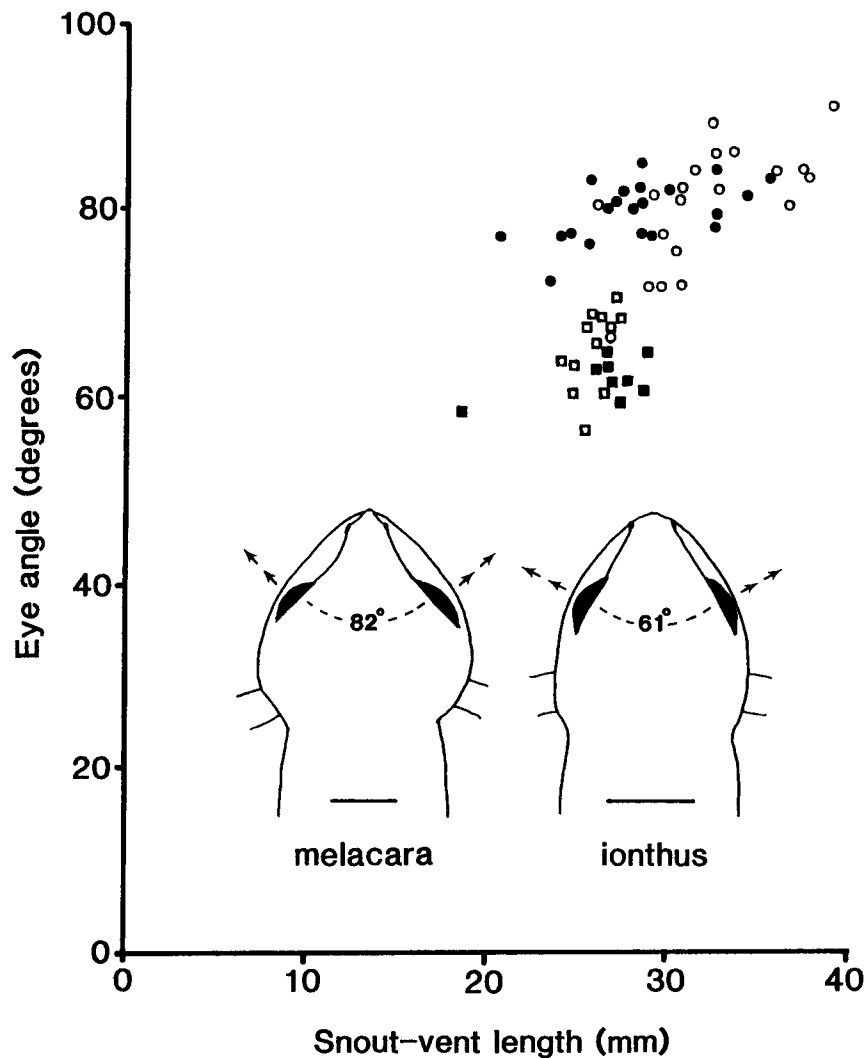


FIG. 3.—Eye angle versus snout-vent length in four species of *Eleutherodactylus*: *E. ionthus* (open squares), *E. guantanamera* (open circles), *E. melacara* (closed circles), and *E. varians* (closed squares). Inset illustrates the difference in eye orientation for *E. melacara* (holotype) versus *E. ionthus* (holotype) (bar = 5 mm).

ical); numerous small, low, supernumerary plantar tubercles; subarticular tubercles of toes oval and subconical or conical; toes unwebbed or with slight basal webbing; well-defined lateral ridge on toes; all toes with expanded tips; toetips rounded; oblong 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, 1989).

In preservative, dorsal ground color tan, with light brown flecks and distinctly

darker brown anteriorly; no dorsal body markings; flanks darker posteriorly (to groin); no groin markings; forearm with faint light band in some individuals; small, dark fold of skin around wrist (defines hand), and one individual with circular area of black pigment on hand (dorsal surface); concealed portions of thigh and shank uniformly dark brown (darker than dorsal surface of limbs); no canthal bar; post-ocular/supratympanic bar dark brown (not sharply defined); light interocular bar in most individuals, although usually faint, followed posteriorly by a round, dark area

centrally located on back of head; ventral ground color tan, with small brown flecks uniformly distributed across entire ventral surface [one individual with circular patch (2 mm) of black pigment on chest]; glandular areas (where present) yellowish; testicular and ovarian peritoneum unpigmented; two hatchlings and a small juvenile (10 mm) are darker than the adult frogs, otherwise similarly patterned.

In life, dorsal ground color greenish-brown with no distinct pattern (unicolor), although head dark brown immediately after removal from bromeliad; faint brown supratympanic bar; iris dark brown below, bronze above; faint trace of two pale shank bars; no thigh markings, although concealed surfaces of thighs purplish; pale venter with no markings, except for some light brown flecks on chin; glandular areas (if present) yellowish-orange and very distinct (color notes for USNM 309733–35).

Measurements (Table 1).—The live masses of two adult males (27.1 and 28.4 mm SVL) were 1.20 and 1.42 g. Three adult females (28.8, 30.9, and 32.9 mm SVL) weighed 1.48, 2.00, 2.26 g, respectively.

Etymology.—From the Greek; *mela*, dark, and *cara*, head; a noun in apposition referring to the differential head/body coloration of this species.

Natural history.—All but one specimen of *E. melacara* were collected during the day in arboreal bromeliads 2–4 m above the ground. The single exception (USNM 309739), a female, was on a leaf at night, about 2 m above the ground. The localities are in cloud forest on Pico Turquino. Some parts of the forest in this region are undisturbed, but many areas near the trail have been partially cut-over, facilitating bromeliad growth. Most of the specimens were taken from a single large clump of bromeliads about 4 m high in a dead (but standing), exposed tree. This locality was located on Estribo Turquino, a narrow ridge extending several kilometers due north of Pico Turquino. A detailed description of the Pico Turquino region and route of ascent is given elsewhere (Schwartz and Hedges, 1991).

Some unusually large eggs were found in the clump of bromeliads, along with adults and hatchlings. Clutch size ap-

peared to be small (5–10), but because of the close proximity of the bromeliads and adults, it was not possible to distinguish discrete clutches.

Eleutherodactylus melacara exhibits an interesting color change associated with its bromeliad-dwelling habits. All specimens taken from bromeliads had a distinctive dark brown snout that graded into a paler (tan) posterior body coloration. Within about 0.5 h, the dark anterior coloration disappeared and the entire animal became uniform tan or light brown (Fig. 2B). Several observations suggest that this color change is related to the occupation of a bromeliad rather than light conditions. For example, a uniformly-colored individual was placed in a clear plastic bag with a bromeliad. After it rested in the bromeliad for about 1 h, it was removed and found to have a dark snout. About 0.5 h after removal, the dark snout coloration had disappeared. In another bag containing several individuals and one bromeliad, the frogs inside the bromeliad had dark snouts whereas those outside the bromeliad were uniform in coloration. The single specimen captured outside of a bromeliad (on a leaf at night) was uniform tan. Such observations of behavioral color change suggest that dark anterior coloration in bromeliad-dwelling frogs is related to their unique lifestyle.

The call of *E. melacara* consists of a series of 14–22 hollow “tock’s” (Table 2). The call recorded at Pico Cardero was similar to the call that we heard throughout the Pico Turquino region, which includes the peak itself (1974 m), Pico Cuba camp (1720 m), Pico Cardero (1230 m), and down to about 850 m on the SW slope (2 km N La Esmajagua). The large number of notes per call and the widely-spaced intervals between calls clearly distinguishes *E. melacara* from all other species of *Eleutherodactylus* in Cuba (Table 2). Our conclusion that *E. melacara* and *E. ionthus* are sympatric in the vicinity of Pico Cardero is based on vocalization only, although specimens of *E. ionthus* (MCZ 22060–65) have been found only a few kilometers away on the south coast.

Several calls of *E. melacara* were traced to arboreal bromeliads 4 m or more above the ground, but no individuals were cap-

TABLE 2.—Call variation in 10 species of Cuban *Eleutherodactylus* (one individual recorded at each locality). Shown are means \pm 2 SE and range (parentheses).

Species	Calls analyzed	Notes/call	Dominant frequency (Khz)	Call duration (msec)	Calls/min
<i>E. auriculatus</i>					
Soroa	10	1	3.89 \pm 0.01 (3.88–3.92)	8.02 \pm 0.55 (6.6–8.9)	779.1 \pm 8.54 (759–800)
<i>E. bartonsmithi</i>					
Boca de Yumurí	8	5.38 \pm 1.13 (3–7)	3.00 \pm 0.01 (2.96–3.02)	526 \pm 107.2 (293–693)	9.85 \pm 2.49 (6.2–15.0)
<i>E. eileenae</i>					
Soroa	1	2	1.83/3.12	177	48
<i>E. guantanamera</i>					
Isabelica	10	3.5 \pm 0.33 (3–4)	2.41 \pm 0.01 (2.40–2.44)	440 \pm 40 (380–530)	22.3 \pm 1.39 (20.0–26.7)
La Tagua	6	5.18 \pm 0.89 (3–7)	2.57 \pm 0.18 (2.56–2.59)	706 \pm 6.11 (700–710)	33.3 \pm 11.2 (20–60)
Cañyón Maya	9	5.3 \pm 1.73 (2–10)	2.60	610 \pm 180 (250–1080)	44.8 \pm 3.52 (34.3–61.5)
Baracoa	10	3.7 \pm 0.43 (3–5)	2.72 \pm 0.008 (2.68–2.72)	380 \pm 42 (300–510)	24.6 \pm 3.16 (19.2–45.8)
El Yunque	6	4.0 \pm 0.52 (3–5)	2.56 \pm 0.03 (2.56–2.57)	400 \pm 54 (290–500)	28.6 \pm 1.99 (24.9–31.4)
<i>E. ionthus</i>					
Pico Cardero	10	1.8 \pm 0.27 (1–2)	2.45 \pm 0.03 (2.36–2.52)	290 \pm 62 (110–400)	23.1 \pm 1.51 (18.9–25.9)
Yerba de Guinea	10	2.1 \pm 0.36 (2–3)	2.80 \pm 0.01 (2.78–2.82)	260 \pm 38.9 (210–387)	52.5 \pm 2.3 (47–58)
<i>E. leberi</i>					
La Tabla	10	1	2.02 \pm 0.01 (2.00–2.04)	137 \pm 5.8 (125–156)	60.4 \pm 2.88 (53–66)
<i>E. mariposa</i>					
La Tagua	8	1	2.71 \pm 0.02 (2.84–2.86)	54 \pm 2.14 (51–61)	224 \pm 4.07 (217–236)
<i>E. melacara</i>					
Pico Cardero	8	18.5 \pm 1.96 (14–22)	2.24 \pm 0.02 (2.20–2.28)	1440 \pm 160 (1090–1730)	2.56 \pm 0.7 (1.13–4.05)
<i>E. ronaldi</i>					
8 km S Baracoa	10	1	3.77 \pm 0.01 (3.75–3.79)	21.3 \pm 0.91 (19.5–23.6)	385 \pm 14.5 (343–405)
<i>E. varians</i>					
Soroa	10	1.7 \pm 0.60 (1–4)	2.68 \pm 0.10 (2.65–2.71)	169 \pm 64.5 (92–440)	37.2 \pm 4.51 (27–47)

tured while calling. However, one frog of this species was seen (by headlamp) in an exposed position near the distal end of a bromeliad leaf several meters high in a tree at night.

Distribution.—Known only from the region of Pico Turquino (Fig. 4). The highest point on Pico Turquino (and in Cuba), Pico Real (1974 m), is the upper altitudinal limit of this species, and 850 m (voice rec-

ord approximately 2 km N La Esmajagua) on the SW slope is the lower altitudinal limit. The specimen of "*E. eileenae*" from Cueva del Aura, Pico Turquino, re-identified as an immature female *E. ionthus* (UMMZ 80910) by Valdes (1988) is neither *E. melacara* nor *E. ionthus* but is an adult female (enlarged ova) of *E. ronaldi*.

For the second new species, also a bromeliad specialist, we propose the name:

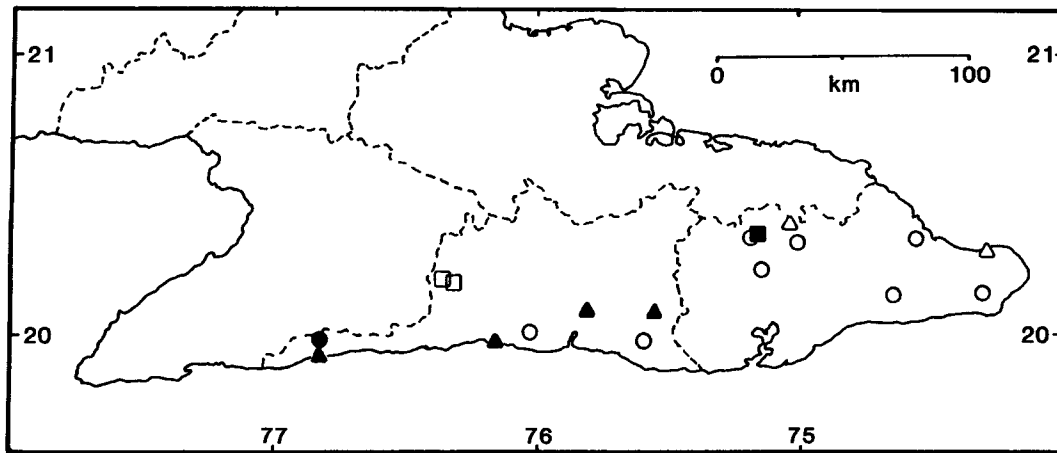


FIG. 4.—Distributions of six species of *Eleutherodactylus* in eastern Cuba: *E. bartonsmithi* (open triangles), *E. ionthus* (closed triangles), *E. lebert* (open squares), *E. mariposa* (closed square), *E. melacara* (closed circle), and *E. guantanamera* (open circles). Dashed lines indicate provincial boundaries.

Eleutherodactylus guantanamera sp. nov.
Fig. 1D

Holotype.—MNHNCU 589, an adult female, collected at El Molino (7 km W Palenque), Guantánamo Prov., Cuba, 405 m, on 21 June 1990, by S. Blair Hedges. Original number USNMFS 191062.

Paratypes.—Guantánamo Prov.: MNHNCU 590, USNM 309742–43, paratopotypes; USNM 309744, 5.4 km WSW La Tagua; MCZ 3117, Monte Líbano, El Perú; MCZ 22104–09, mountains north of Imias, 909–1212 m; MCZ 22160–61, upper Ovan-do River, 303–606 m; MCZ 22066–69, El Yunque de Baracoa, 303–545 m. Santiago de Cuba Prov.: MCZ 21929–33, Gran Piedra Range, 606–909 m; USNM 309740–41, Isabelica (Gran Piedra); MCZ 22139, Cobre Range, Sierra Maestra, 909–1152 m.

Diagnosis.—*Eleutherodactylus guantanamera* can be distinguished from other members of the subgenus *Eleutherodactylus* on Cuba by its larger size (26.5–32.8 mm SVL, males; 32.1–37.3 mm SVL, females), flattened body, short snout with concave canthus rostralis, brown and usually unpatterned dorsum, 4–5 note call, and 28 chromosomes. The only species that require comparison are *E. ionthus* and *E. melacara*. Both occur in eastern Cuba and are similar in that they have a flattened body and a relatively uniform dorsal coloration (tan or brown). *E. ionthus* is a smaller species (24.7–27.0 mm SVL, males;

females unknown), has a head as wide as the body (much wider than body in *E. guantanamera*), a straight canthus rostralis (not concave: Fig. 3), a more typical (lateral) eye orientation (56–70° versus 66–86° in *guantanamera*), a two-note call, and 26 chromosomes.

Closer comparison is required for *E. melacara*, which is very similar to *E. guantanamera*. Both species show the morphological adaptations seen in bromeliad-dwelling frogs: flattened body, short snout, wide head, forward eye orientation, and uniform coloration. The two major differences between these two species are the call, which has considerably more notes (14–22) in *E. melacara* and is lower in frequency than the 4–5 note call of *E. guantanamera*, and chromosome number (28 versus 24 in *melacara*). *Eleutherodactylus guantanamera* is slightly larger in size than *E. melacara*, has a smooth dorsum (not weakly tuberculate), and has a longer snout and narrower head [EN/HW = 29.1–32.8 (males); 28.5–31.4 (females) versus 26.8–28.5 (males) and 26.2–28.7 (females) in *melacara*]. Also, the dorsal coloration of *E. guantanamera* is brown, and the concealed surfaces of the hind limbs are not darker than the rest of the dorsum. In *E. melacara*, the dorsum is tan and the concealed surfaces of the hind limbs are uniformly dark brown.

Description.—Head wider than body, width greater than length; snout semicir-

cular in dorsal view, acuminate in lateral view, overhanging lower jaw; nostrils weakly protuberant, directed dorsolaterally and slightly forward; canthus rostralis rounded, slightly concave in dorsal view; loreal region slightly concave, sloping gradually; lips not flared; upper eyelid smooth; interorbital space without tubercles; supratympanic fold weakly defined (one or two swollen areas), concealing upper edge of tympanic annulus; tympanum moderate-sized, round, separated from eye by a distance equal to its own diameter; several enlarged, subconical, postrictal tubercles; choana small, round, not (or partially) concealed by palatal shelf of maxillary arch when roof of mouth is viewed from above; vomerine odontophores medial and posterior to choanae, each about the same size as a choana, oval, separated widely at midline; tongue longer than wide, posterior edge without notch, posterior one-fourth to one-third not adherent to floor of mouth; males with vocal slits; vocal sac median subgular and evident externally.

Skin of dorsum smooth, without dorso-lateral folds; skin of flanks similar to dorsum; skin of venter moderately areolate, with discoidal folds; anal opening not extended in sheath; no supra-axillary, inguinal, or postfemoral glandular areas present; ulnar tubercles absent; palmar tubercle bifid or divided, about the same size or smaller than thenar; thenar tubercle oval, elevated; several moderate-sized, subconical supernumerary palmar tubercles; subarticular tubercles of fingers oval and conical, angled outward; well-defined lateral ridge on fingers; all fingers with expanded tips, III and IV more than I and II; fingertips rounded; oblong pad on ventral surface of fingertip; circumferential groove bordering distal two-thirds of finger pad; width of largest pad (III) three-fourths to same size as TYM; first finger shorter than second when adpressed; heel tubercles absent; no row of tubercles along outer edge of tarsus; metatarsal tubercles elevated, inner (oval) 3–4 times as large as outer (subconical); numerous small, low, supernumerary plantar tubercles; subarticular tubercles of toes oval and subconical or conical; toes unwebbed or with slight basal webbing; well-defined lateral ridge on toes; all toes with expanded tips; toetips round-

ed; oblong 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, 1989).

In preservative, dorsal ground color uniform dark brown (tan in older specimens), with light brown flecks and distinctly darker brown anteriorly; usually no dorsal body markings except for occasional tan mottling; no groin markings; forearm with faint pale band in some individuals; small dark fold of skin around wrist (defines hand); concealed portions of thigh and shank same as dorsum; no distinct canthal bar, although a faint indication in some individuals; post-ocular/supratympanic bar dark brown (not sharply defined); pale interocular bar in most individuals (e.g., holotype), although usually faint, followed posteriorly by a round, dark area centrally located on back of head; ventral ground color tan, with small brown flecks uniformly distributed across entire ventral surface; testicular and ovarian peritoneum unpigmented.

In life, dorsal ground color yellowish-brown with no distinct pattern (unicolor), although anterior region darker brown in some individuals (as in *E. melacara*), and occasional darker brown markings on dorsum and flanks; faint brown supratympanic bar; iris grayish-bronze; faint trace of two pale shank bars; no thigh markings; pale venter with no distinct markings.

Measurements (Table 1).—The live masses of two adult males were 2.12 and 2.13 g.

Etymology.—From Spanish (a noun in apposition); after the classic song of the same name written by Joseito Fernández, with the *versos sencillos* of José Martí; in allusion to the distribution of this species, almost entirely within Guantánamo Province, Cuba. Coincidentally, the even-pitched, five-syllable Guan-tán-a-mer-a of the chorus bears a resemblance to the call of this species, which averages 4–5 notes and is constant in frequency.

Natural history.—The frogs at Isabelica (Gran Piedra) were calling from leaves of small trees, and the individual recorded at Baracoa was vocalizing on the top of a banana leaf 3 m above the ground. All

other individuals heard or recorded appeared to be calling from bromeliads high in trees. The specimens from 5.4 km WSW La Tagua were taken from bromeliads during the day. Two large adult females from Gran Piedra Range, MCZ 21932–33, contain nine and five very large (3 mm) ova, respectively, confirming that this species has an unusually large investment per offspring (small clutch size/large eggs) for an *Eleutherodactylus*. By comparison, similar-sized females of the arboreal Hispaniolan species *E. armstrongi* have a clutch size of about 40 (S. B. Hedges, unpublished data).

Distribution.—Known only from upland areas in the southern half of eastern Cuba (Fig. 4), from the Cobre Range (Santiago de Cuba Prov.) to El Yunque de Baracoa and the Meseta de Maisi (Guantánamo Prov.). Gran Piedra (1150 m) is the upper altitudinal record for this species, and the lowest elevations are at El Yunque de Baracoa (300–545 m), although it was heard calling 8 km S Baracoa, 60 m (because of possible confusion with *E. ionthus*, undocumented voice records for these eastern populations should be treated with caution).

For the distinctive new species from the Meseta del Guaso, we propose the name:

Eleutherodactylus mariposa sp. nov.

Fig. 2A

Holotype.—MNHNCU 591, an adult male, collected at 5.4 km WSW La Tagua, Meseta del Guaso, Cuba, 720 m, on 17 June 1990, by S. Blair Hedges and Richard Thomas. Original number USNMFS 190919.

Paratypes.—KU 217777–78, MNHNCU 592–95, USNM 309745–49, paratopotypes (same data as holotype).

Diagnosis.—The largest member of subgenus *Eleutherodactylus* on Cuba (29.8–36.1 mm SVL, males; females unknown). It can be distinguished from all other species by its distinctive dorsal pattern feature (a large papilionaceous blotch), a stout-bodied habitus, a tuberculate dorsum, leg barring, lip markings, absence of glandular areas, advertisement call (a continuous series of muffled “mee”s), and chromosome number ($2N = 22$). *E. guantanamera*, *E. ionthus*, and *E. melacara* are

smaller species with a flattened habitus and have an unpatterned dorsum. *Eleutherodactylus bartonsmithi* is also mottled, but it is much smaller (17.6–20.9 mm SVL) and lacks the middorsal blotch. *Eleutherodactylus leberi* is mottled and may have middorsal blotches, but they are never well-defined. It is smaller (27.7–32.4 mm SVL) than *E. mariposa*, has limb markings that are barely discernable (bold in *mariposa*), lacks lip markings (present in *mariposa*), has a more acuminate snout (more rounded in *mariposa*), has lores that drop abruptly to lips (slope in *mariposa*), a flattened habitus (stout-bodied in *mariposa*), and a very different call.

Eleutherodactylus mariposa bears a superficial resemblance to two Cuban species of the subgenus *Euhyas*, *Eleutherodactylus pezopetrus* and *E. sierramaestrae*, both of which are large, have a tuberculate dorsum, enlarged digital tips, and a mottled dorsum with a central blotch or blotches (in *E. sierramaestrae*). However, both can be readily separated from *E. mariposa* by their smooth venters, long vomerine odontophores, and absence of an external vocal sac in adult males.

Description.—Head as wide as body, width equal to length; snout subacuminate to rounded in dorsal view, subacuminate in lateral view, overhanging lower jaw; nostrils moderately protuberant, directed laterally; canthus rostralis moderately sharp, straight in dorsal view; loreal region flat, sloping to lips; lips not flared; upper eyelid bearing small, rounded tubercles; interorbital space with low, flat tubercles; supratympanic fold weakly defined, concealing upper edge of tympanic annulus; tympanum large, round, separated from eye by a distance less than its own diameter; several postrictal tubercles, enlarged, subconical; choanae moderate-sized, round, partially concealed by palatal shelf of maxillary arch when roof of mouth is viewed from below; vomerine odontophores medial and posterior to choanae, each larger than a choana, straight and angled postero-medially, separated moderately at midline; tongue longer than wide, posterior edge without notch, posterior one-third not adherent to floor of mouth; males with vocal slits and vocal sac; vocal sac median subgular and externally visible.

Skin of dorsum weakly to moderately tuberculate, without dorsolateral folds, skin of flanks slightly more tuberculate; skin of venter strongly areolate, with discoidal folds; anal opening not extended in sheath; no glandular areas present; ulnar tubercles absent; palmar tubercle single or bifid, larger than thenar, thenar tubercle oval, low; several small, low, supernumerary tubercles; subarticular tubercles of fingers round and subconical; weak lateral ridge on fingers; 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) one-half to three-fourths tympanum; first finger shorter than second when adpressed; heel tubercles absent; no tubercles along outer edge of tarsus; metatarsal tubercles elevated, inner (elongate) twice size of outer (subconical); numerous low supernumerary tubercles on plantar surface; subarticular tubercles of toes round and subconical; toes unwebbed; weak lateral ridge on toes; all toes with expanded tips; toetips rounded; semicircular pad on ventral surface of toetip; circumferential groove bordering distal two-thirds of toe pad; heels just touch when flexed legs are held at right angles to sagittal plane; liver shape "auriculatus-type" (Hedges, 1989).

In preservative, dorsal ground color light gray, with darker gray mottling; a large light gray papilionaceous middorsal blotch, dark gray interocular bar with two posterior lobes; snout light gray with a central dark spot; distinct upper and lower lip markings (bars); wide, dark limb markings separated by narrow pale bars; concealed portions of hind limbs mottled like dorsum; belly unpigmented, with some dark flecks; undersides of limbs mottled; testicular peritoneum black.

In life, dorsal ground color pale, with greenish-gray mottling; tympanum purple; reddish flecks on top of snout; iris gray; flanks slightly yellowish, limbs with slight purplish hue.

Measurements (Table 1).—Live mass 2.13–3.12 (\bar{x} = 2.63) g.

Natural history.—The type series was collected at night in thick secondary growth next to a coffee grove (*cafetale*) on the Meseta del Guaso. All individuals were

calling, mostly from horizontal sites 2–3 m high on vines and small trees growing on jagged limestone rock. One frog was calling from a vertical position on the trunk of a large tree and another was calling from within the folds of a dead leaf 3 m high in a tree. The whistle-like "warm-up" call of this species is similar to that of *E. varians*, *E. ionthus*, and *E. guantanamera*. *Eleutherodactylus guantanamera* was calling from bromeliads high in the surrounding trees, and several individuals of that species were taken from bromeliads during the day. Other species of *Eleutherodactylus* encountered at that locality were *E. atkinsi*, *E. dimidiatus*, *E. limbatus*, and *E. ricordii*. In addition, *E. auriculatus*, *E. ronaldi*, *E. sierramaestrae*, *E. varleyi*, and an undescribed terrestrial species (Estrada and Hedges, 1991) were found at nearby sites on the Meseta del Guaso and all of these (10 species) should be considered sympatric with *E. mariposa*.

Etymology.—From the Spanish word for butterfly (a noun in apposition); in allusion to the large papilionaceous middorsal blotch in this species.

Distribution.—Known only from the type-locality on the Meseta del Guaso (Fig. 4).

DISCUSSION

Vocalization

Schwartz (1965) summarized available information on vocalization in this group. Our additional collections, recordings, and call analyses provide a more complete picture of call variation in these frogs. Males of all 10 species of the subgenus *Eleutherodactylus* (Figs. 1, 2) vocalize and have externally-visible submandibular vocal sacs, which are often yellow in life. Audiospectrograms for all species are shown in Figs. 5 and 6, and variation in call parameters is summarized in Table 2.

The calls of *E. auriculatus* and *E. ronaldi* are short "tick's", repeated many times or continuously in close, regular intervals (like a ratchet). The calls of *E. barton-smithi* (3–7 notes), *E. guantanamera* (2–10 notes), *E. ionthus* (1–3 notes), *E. melacara* (14–22 notes), and *E. varians* (1–4 notes) are all similar in quality (a series of hollow and slightly metallic "tock's") but

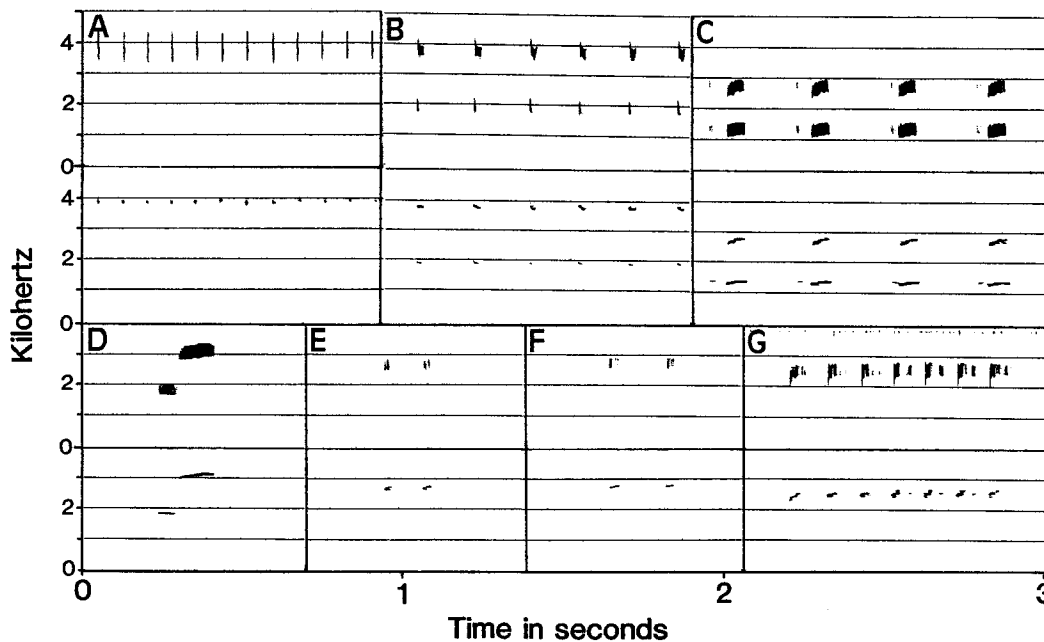


FIG. 5.—Audiospectrograms of seven species of Cuban *Eleutherodactylus* of the subgenus *Eleutherodactylus*. For each call, 300 Hz filter (above) and 45 Hz filter (below): (A) *E. auriculatus* (Pinar del Río Prov., Soroa), (B) *E. ronaldi* (Guantánamo Prov., 8 km S. Baracoa), (C) *E. mariposa* (Guantánamo Prov., 5.4 km WSW La Tagua), (D) *E. eileenae* (Pinar de Río Prov., Soroa), (E) *E. varians* (Pinar del Río, Soroa), (F) *E. ionthus* (Guantánamo Prov., 0.5 km W Yerba de Guinea), and (G) *E. guantanamera* (Guantánamo Prov., 5.4 km WSW La Tagua). Figures A–C are portions of continuous calls; D–G are single, discrete calls.

differ in the number of notes and dominant frequency. The call of *E. eileenae* (a two-note “co-lee”) and *E. leberi* (a single metallic “tenk”) differ from the other eight Cuban species in having two types of notes instead of one. In both species, the first note is lower in pitch than the second, although in *E. leberi*, the two notes are so close together that they sound like a single note. Finally, the call of *E. mariposa* is a single, short, muffled “mee”, repeated many times or continuously in close, regular intervals. The call of this species is unusual in that each note has two components, a lower “note” which is constant in pitch and a higher-pitched note that rises slightly.

All of these species use arboreal calling sites, but some specific preferences are evident. The two bromeliad specialists, *E. guantanamera* and *E. melacara*, usually vocalize from bromeliads in trees, often high (5–10 m) above the ground. Four other tree-dwelling species, *E. bartonsmithi*, *E. eileenae*, *E. ionthus*, and *E. varians*, vocalize from leaves, branches, or some-

times close to the ground on saplings beneath larger trees. With the possible exception of *E. eileenae*, bromeliads also are utilized as occasional calling sites in those species. *Eleutherodactylus leberi* vocalizes from the leaves of aroids (Schwartz, 1965) or small trees (personal observations) in rocky areas. *Eleutherodactylus mariposa* calls from a variety of sites intermediate in height (2–5 m), but it appears to prefer saplings and vines in areas of thick growth. *Eleutherodactylus auriculatus* and *E. ronaldi* both call from the leaves and branches of shrubs <2 m above the ground.

The Bromeliad Ecomorph

Morphological and ecological convergence is common among West Indian *Eleutherodactylus*, and several convergent types, or “ecomorphs”, recently have been named (Hedges, 1989). The bromeliad ecomorph is one of the most clearly defined and consists of species that live exclusively, or nearly so, in bromeliads. Two of the new species described here, *E. guantanamera* and *E. melacara*, are the

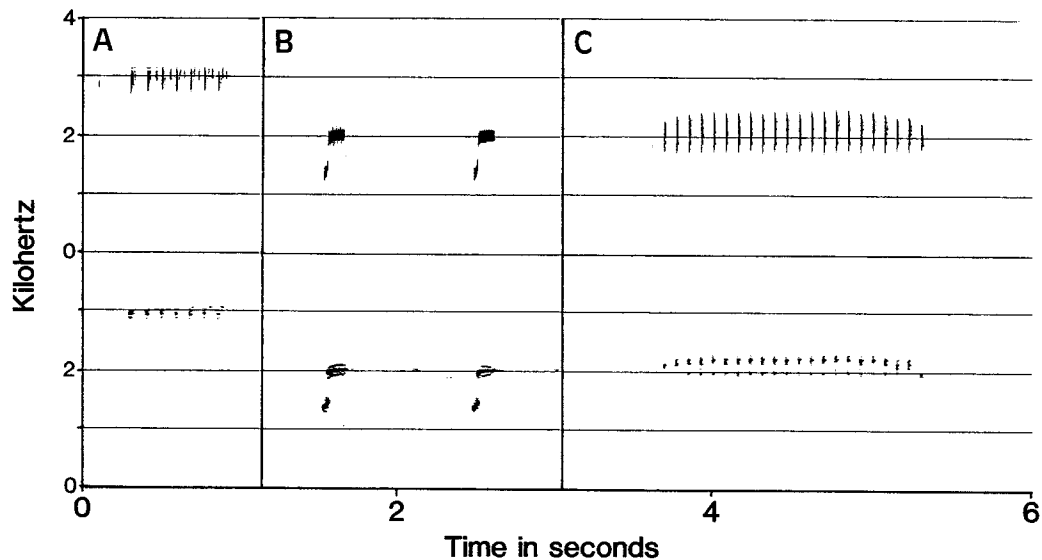


FIG. 6.—Audiospectrograms of three species of Cuban *Eleutherodactylus* of the subgenus *Eleutherodactylus*. For each call, 300 Hz filter (above) and 45 Hz filter (below): (A) *E. bartonsmithi* (Guantánamo Prov., Boca de Yumuri), (B) *E. leberi* (1.5 km WSW La Tabla), and (C) *E. melacara* (Santiago de Cuba Prov., Pico Cardero). One call is shown in A and C; two calls are shown in B.

first representatives of the bromeliad ecomorph known from Cuba. This ecomorph is represented elsewhere in the Greater Antilles by *E. jamaicensis* (Jamaica), *E. auriculatoides*, *E. fowleri*, *E. heminota*, *E. lamprotes*, and several undescribed species (Hispaniola), and *E. gryllus* and *E. jasperii* (Puerto Rico). Some morphological traits usually associated with this lifestyle are (1) a dorsoventrally flattened head and body, (2) a short, rounded (in dorsal profile) head, often with a pointed tip, (3) eyes oriented more forward, (4) short digits, (5) digital fringe, (6) relatively large, rounded digital tips, and (7) a dark snout grading posteriorly into a paler dorsal body color. Body coloration is variable, but most are green, yellow, or brown, and lack a distinct pattern.

Mainland *Eleutherodactylus* specializing in bromeliads (e.g., species in the *celator* and *lacrimosus* assemblies; Lynch and Duellman, 1980; Lynch and Ruíz-Carranza, 1985) also have these traits, as do other bromeliad frogs (e.g., *Hyla bromeliacea*, *H. dendroscarta*, *H. marianae*, *H. wilderi*). This further supports the hypothesis that convergence associated with the bromeliad niche has shaped the morphology of those species. The adaptive advantages

of some of the traits are easy to visualize: a flattened body could facilitate movement between bromeliad leaves, and enlarged digital tips almost certainly aid in climbing. A dark snout may be a way of camouflaging the exposed portion of the frog as it sits (characteristically head-up) between the bromeliad leaves, or it could have evolved as a mechanism for protection from harmful ultraviolet rays (bromeliads usually are exposed to direct sunlight). The association between pad shape and substrate in West Indian *Eleutherodactylus* (Hedges, 1989) suggests a functional relationship, but the details still are unclear.

Relationships

Schwartz (1965) discussed the phylogenetic relationships of the six arboreal species of Cuban *Eleutherodactylus* known at the time. He suggested that (1) *E. auriculatus* and *E. ronaldi* were sister species, (2) *E. bartonsmithi* and *E. varians* were sister species, together forming a sister group with *E. leberi*, and (3) *E. eileenae* represented a third lineage. These groupings were based on body size, call rate, number of notes per call, and coloration. With the addition of four more spe-

cies, along with chromosome and call data, the relationships of the arboreal Cuban *Eleutherodactylus* now can be reexamined.

Chromosome numbers in these species are 18 (*auriculatus*, *bartonsmithi*, *eileenae*, and *varians*), 22 (*mariposa*), 24 (*leberi*, *melacara*), 26 (*ionthus*), and 28 (*guantanamera*). Some members of the subgenus *Eleutherodactylus* on Hispaniola and Puerto Rico have 26 chromosomes, and several species on Hispaniola have 18 chromosomes (Bogart, 1981; Bogart and Hedges, unpublished). The number 24 is known in only one other (unrelated) species (*E. junori* of Jamaica), a member of the subgenus *Euhyas*. Pending more detailed chromosome analyses (underway), variation in chromosome numbers does not support or refute a monophyletic origin for the Cuban species of the subgenus *Eleutherodactylus*.

The calls of nearly all West Indian *Eleutherodactylus* are known (Drewry and Rand, 1983; Hedges, unpublished; Schwartz, 1969; Schwartz and Henderson, 1991). Although no two species have identical calls, the types of calls found in most Cuban arboreal species also are found in Hispaniolan and Puerto Rican members of the subgenus. For example, the two-note "co-lee" of *E. eileenae* (and to a lesser degree, the call of *E. leberi*) is similar to *E. flavescens*, *E. fowleri*, and *E. wetmorei* (Hispaniola), and *E. antillensis*, *E. coqui*, *E. portoricensis*, and *E. schwartzi* (Puerto Rico Bank), and *E. johnstonei*, *E. martincensis*, and *E. urichi* (Lesser Antilles), as noted by Schwartz (1969). Likewise, the short and repetitious "tick" calls of *E. auriculatus* and *E. ronaldi* are quite similar to the calls of *E. abbotti*, *E. audanti*, and *E. haitianus* (Hispaniola), and to a lesser degree, *E. locustus* (Puerto Rico). The call of *E. mariposa* is unlike any other species, although its continuous, evenly-spaced notes resemble the calls of *E. auriculatus* and *E. ronaldi* of Cuba. The hollow, metallic "tock" call of *E. bartonsmithi*, *E. guantanamera*, *E. ionthus*, *E. melacara*, and *E. varians* appears to be unique and suggests that those five species of tree-dwelling frogs form a radiation on Cuba. We refrain from any further discussion of

relationships pending the results of ongoing molecular analyses of these species.

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APPENDIX I

Specimens Examined

Eleutherodactylus auriculatus.—Pinar del Río Prov., Soroa (155 m), USNM 309750-52. *E. barton-smithi*.—Guantánamo Prov., Boca de Yumurí (30-60 m), USNM 309753. *E. eileenae*.—Pinar del Río Prov., Soroa (155 m), USNM 309754-56. *E. ionthus*.—Santiago de Cuba Prov., Coast S Pico Turquino, MCZ 22060-65; 4.2 km W Aserradero, AMNH 63417-18; 8 km S Dos Caminos, AMNH 63416; 10 km E La Maya, AMNH 63414 (holotype), 63413, 63415; 0.5 km W Yerba de Guinea (170 m), USNM 309757. *E. leberti*.—Santiago de Cuba Prov., 1.5 km WSW La Tabla (465 m), USNM 309758. *E. ronaldi*.—Santiago de Cuba Prov., Cueva del Aura, below Pico Turquino, UMMZ 80910; Guantánamo Prov., 8 km S Baracoa (60 m), USNM 309760. *E. varians*.—"Cuba", MCZ 11621 (syntype); Pinar del Río Prov., 12.8 km S Manicaragua, AMNH 61156-58; 4 km W, 8 km N Trinidad, AMNH 61159-61; Camagüey Prov., 8.8 km NE Banao, AMNH 61162-63.