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A NEW BURROWING FROG FROM HISPANIOLA WITH COMMENTS ON THE *INOPTATUS* GROUP OF THE GENUS *ELEUTHERODACTYLUS* (ANURA: LEPTODACTYLIDAE)

S. BLAIR HEDGES¹ AND RICHARD THOMAS²

¹*Department of Zoology, University of Maryland,
College Park, MD 20742, USA*

²*Department of Biology, University of Puerto Rico,
Río Piedras, PR 00931, USA*

ABSTRACT: *Eleutherodactylus parapelates* is described from the Massif de la Hotte of the Haitian Tiburon Peninsula. It is a large burrowing species that vocalizes from enclosed underground chambers and is most similar to *E. hypostenor* and *E. ruthae*. Together, these three species form a subgroup within the *inoptatus* group, which now contains six large Hispaniolan *Eleutherodactylus*.

Key words: Amphibia; Anura; Leptodactylidae; *Eleutherodactylus parapelates*; Systematics; Hispaniola

THE island of Hispaniola harbors an exceptionally rich terrestrial frog fauna, with 49 described species of *Eleutherodactylus* (Henderson and Schwartz, 1984). Many of those species are restricted in range, and thus the number at any one site is much lower, usually fewer than eight. However, some areas in the "South Island" of Hispaniola, which includes the Sierra de Bao-ruco, the Massif de la Selle, and the Massif de la Hotte, have an unusually high local diversity of *Eleutherodactylus*. Twenty species are now known from the vicinity of Castillon, a small Haitian village on the north slope of the Massif de la Hotte (Schwartz, 1973, 1976; our recent collections). One reason for such remarkable local diversity is that Castillon is situated at an intermediate elevation (950 m) where a montane fauna reaches its lower limits and a lowland fauna reaches its upper limits (Schwartz, 1973).

On a four-day visit to Castillon in 1971, R. Thomas secured 19 species of *Eleutherodactylus*, seven of which were undescribed. Six of those species have since been described (Schwartz, 1973, 1976), and additional material of the seventh species

(initially identified as *E. hypostenor* by Schwartz, 1973) collected by us in 1984 now confirms its distinctiveness.

In the account below, the following abbreviations are used: AMNH (American Museum of Natural History, New York), ASFS (Albert Schwartz Field Series), E-N (distance between nostril and eye), EYE (horizontal diameter of eye), HW (greatest width of head), IOD (interorbital distance), MCZ (Museum of Comparative Zoology, Harvard University), SHL (shank length), SVL (snout-vent length), THL (thigh length), TYM (horizontal diameter of tympanum), UF (Florida State Museum, University of Florida), USNM (United States National Museum of Natural History, Smithsonian Institution).

Eleutherodactylus parapelates sp. nov.
Figs. 1c, 2

Eleutherodactylus hypostenor: Schwartz, 1965, p. 498 (part, specimens from Haiti).

Holotype.—USNM 257716, an adult male from 0.1 km N Castillon [7.9 km S, 0.3 km E Marché Léon (airline distance)];

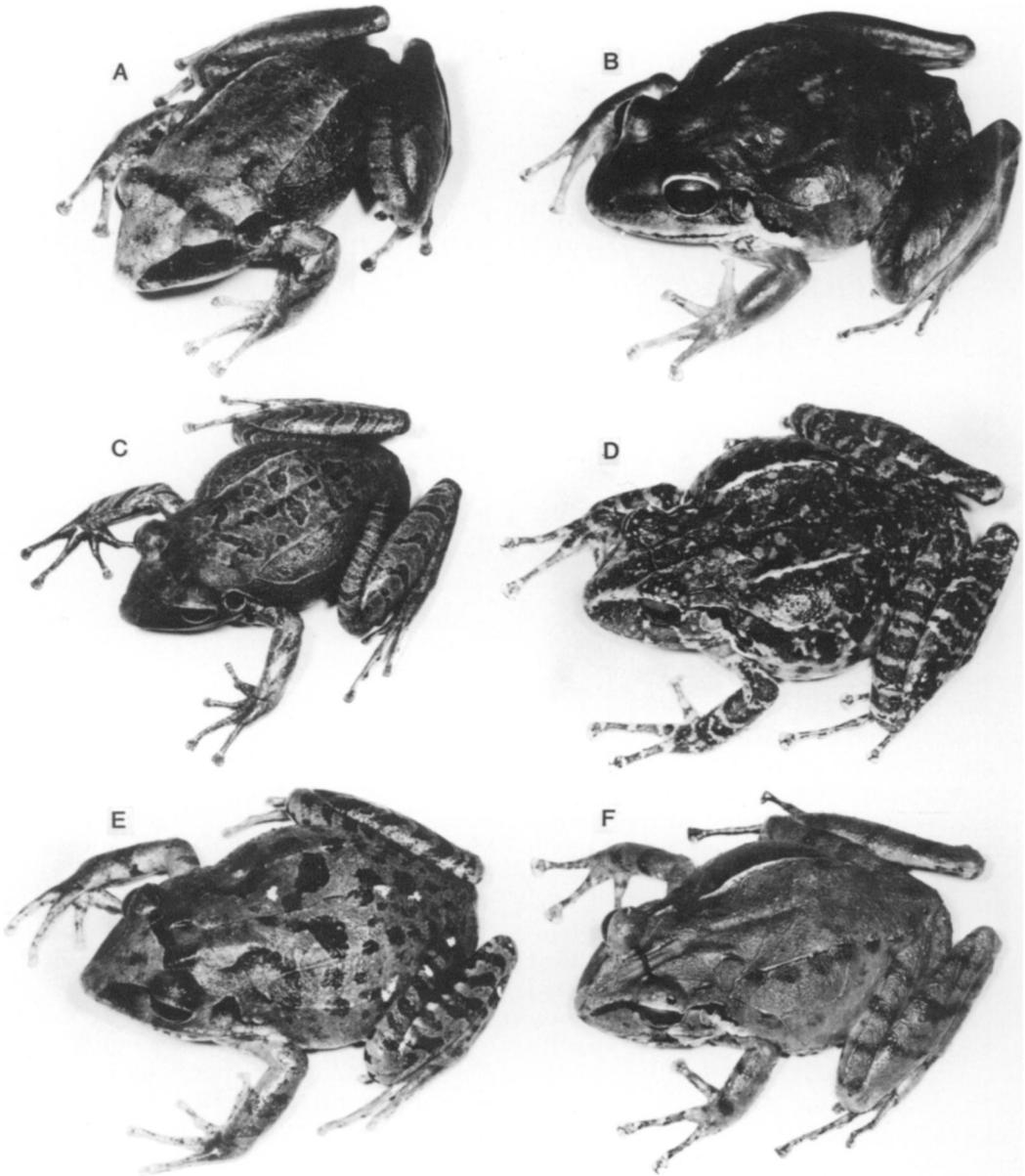


FIG. 1.—The *inoptatus* group of *Eleutherodactylus*: (A) *E. hypostenor* (USNM 257732, male, 50 mm SVL), (B) *E. inoptatus* (USNM 257769, male, 68 mm SVL), (C) *E. parapelates* (USNM 257727, male, 52 mm SVL), (D) *E. nortoni* (USNM 257745, male, 60 mm SVL), (E) *E. ruthae* (USNM 257753, male, 50 mm SVL), (F) *E. chlorophenax* (USNM 257730, female, 77 mm SVL). From color transparencies by SBH.

18°28'07" N, 74°06'58" W], Dépt. de la Grande Anse (formerly the Dépt. du Sud, Appendix I), Haiti, 960 m, collected by Richard Thomas and S. Blair Hedges on 2 November 1984.

Paratypes.—USNM 257717–26, paratypes; USNM 257727, 0.5 km S Castillon [8.5 km S, 0.3 km E Marché Léon (airline distance); 18°27'48" N, 74°06'58" W], 980 m; ASFS V24424, vicinity of Cas-

tillon [8.0 km S, 0.3 km E Marché Léon (airline distance); 18°28'04" N, 74°06'58" W], 950 m; USNM 257728, 1.3 km N Castillon [6.5 km S, 0.1 km E Marché Léon (airline distance); 18°28'50" N, 74°07'03" W], 1050 m; MCZ 36511, mountains 25 mi (40.2 km) N Les Cayes; all in Dépt. de la Grande Anse, Haiti.

Associated specimens (immature and poorly preserved).—AMNH 44074, 44079, 25 mi (40.2 km) N Les Cayes, Dépt. de la Grande Anse, Haiti.

Diagnosis.—An *Eleutherodactylus* of the *inoptatus* group (sensu Schwartz, 1965, 1976), most similar to *E. hypostenor* Schwartz and *E. ruthae* Noble in appearance (large size, protruding snout, chevronate shank bars) and habits (burrowing) but has electrophoretic differences, a unique advertisement call, and a relatively longer head and smaller tympanum (see comparisons for other differences).

Description.—The following description is based on all 15 adult males (holotype and paratypes; females unknown): head as broad as body, as wide as long; HW/SVL 0.380–0.419 (\bar{x} = 0.400); snout subacuminate in dorsal view, protruding in lateral profile, overhanging lower jaw; E–N/EYE 0.855–0.983 (\bar{x} = 0.939); nostrils protuberant and directed laterally; canthus rostralis well defined, straight, and parallel for anterior $\frac{1}{3}$, straight and angled outward for posterior $\frac{2}{3}$; tip of snout with tough, cornified skin, similar in texture to a subarticular tubercle; loreal region slightly concave, sloping to lips; lips not flared; IOD less than width of upper eyelid, space flat (no cranial crests); 1–3 low nonconical tubercles on posterior end of upper eyelids; supratympanic fold prominent, obscuring upper edge of tympanum and then curving ventrally to above insertion of forelimb; a ridge or cluster of large tubercles posterior to angle of jaw; tympanum round and with distinct annulus, non-tuberculate, separated from eye by a distance equal to about $\frac{1}{3}$ – $\frac{1}{2}$ tympanum length, TYM/HW 0.157–0.187 (\bar{x} = 0.170); choanae large and rounded; vomerine odontophores prominent, in straight or slightly curved (2 mm long) rows, oblique in outline, each bearing 10–17 (\bar{x} = 13.9) odontoids; tongue large, ovoid, slightly notched behind, equal

to about $\frac{1}{2}$ the floor of the mouth in area, posterior $\frac{1}{3}$ free; vocal slits posterolateral to tongue; internal median subgular vocal sac with lateral, pouch-like extensions.

Skin of dorsum smooth anteriorly, tuberculate posteriorly and laterally; dorsolateral fold extending to above the groin; an additional, less prominent lateral fold (series of tubercles) connecting with the dorsolateral fold anteriorly and extending diagonally and ventrally for about $\frac{1}{3}$ the length of the dorsolateral fold; skin of throat smooth; skin of belly smooth anteriorly and coarsely areolate posteriorly; lateral and posterior discoidal folds; dorsal and ventral surface of forelimb and ventral surface of shank smooth; anterior dorsal surface of thigh and dorsal surface of shank finely shagreened; posterior dorsal and ventral surface of thigh coarsely areolate.

Ulnar tubercles absent or forming a low ridge along forearm; thenar tubercle oval (conical in some individuals), $\frac{1}{2}$ as large as bifid palmar tubercle, both elevated; one supernumerary tubercle at base of each finger and several on palmar surface, all distinct and nearly conical; subarticular tubercles prominent, conical, and angled outward; all fingers expanded at tips, fingers III–IV more than fingers I–II; oval shaped pad present on ventral surface of digital tip ["pad" is used here sensu Lynch and Myers, 1983 (i.e., specialized area of epithelium on ventral surface of the digital tip); "disc" is not used here, because it connotes a circular shape to structures (digital tips and pads) that are often not circular], "U-shaped" circumferal groove distinct and surrounding $\frac{3}{4}$ of pad margin (distal); largest pad (III) $\frac{1}{2}$ – $\frac{2}{3}$ TYM, smallest (I) $\frac{1}{3}$ TYM; fingers with indistinct lateral ridges; first finger slightly longer than second when fingers adpressed; fingers long and slender, III–IV–I–II in order of decreasing length.

Heel and outer edge of tarsus lacking tubercles; inner metatarsal tubercle elongate and greatly enlarged, length 2–3 times width; outer metatarsal tubercle conical and elevated, $\frac{1}{3}$ size of inner; supernumerary plantar tubercles conical and distinct; subarticular tubercles conical, very prominent, and angled outward; toes relatively long, unwebbed, with lateral ridges

and slightly expanded tips; toe tips rounded; toe pads transversely oval, slightly smaller than finger pads, "U-shaped" circumferal groove bordering distal $\frac{3}{4}$ of pad; hind limbs long and slender; heels overlap when flexed legs are held at right angles to sagittal plane; THL/SVL 0.484–0.550 (\bar{x} = 0.524); SHL/SVL 0.563–0.666 (\bar{x} = 0.600).

In preservative, dorsal ground color gray; irregular dorsal spots darker gray forming a more or less bilaterally symmetrical pattern; dorsolateral folds white in some individuals; a dark gray interorbital triangle or band and an indistinct dark gray patch on snout usually present; lores dark gray; tip of snout without pigment; distinctive black stripe below white supratympanic fold; tympanic membrane mostly clear but with dark brown pigment in center and black above; tympanic ring white; forelimbs with narrow, dark gray bars, usually one chevron on each forearm; groin region white, cream, or light gray with heavy black (or dark brown) mottling or reticulations, often extending along anterior surface of thigh and ventrolateral surface of body; dorsal surface of thigh with parallel, dark gray bars, posterior surface black with light gray mottling or reticulations; shank with distinctive dark gray chevrons; anterior dorsal surface of foot with narrow dark gray bars or chevrons, posterior edge black or dark brown; nearly all dorsal markings with narrow white outline; ventral surface white or cream with moderate to heavy black (or brown) mottling; chin, and underside of forearm, shank, and foot darkest (solid black or dark brown in some individuals); lack of mottling in pectoral region of some giving effect of pale transverse band.

In life, dorsal ground colors dark brown to pale brown (almost tan) with darker spotting; dorsolateral folds light; loreal region slightly darker than ground color; supratympanic markings black; crural chevrons dark brown with light (buff) edges; ventrolateral surface of the body, concealed areas of the groin, posterior region of the thigh, and some of the ventral shank areas blue-gray with black reticulations [one individual (USNM 257717) with or-

ange in the ventral shank region]; ventral surface off-white with black marbling, less contrasting on the undersides of the limbs; plantar surfaces black; unpatterned iris; pupillary opening large, filling almost all of the visible part of the eye.

Measurements of the holotype.—An adult male weighing 9.43 g (live) and with the following measurements (mm; in preservative): SVL 50.5, HL 20.6, HW 20.6, TYM 3.5, EYE 6.7, E–N 6.0, naris–snout 3.0, IOD 6.0, naris–naris 5.0, eye–mouth 2.3, THL 25.6, SHL 29.3, tarsal length 16.3, foot length 22.4, third fingertip width 1.7, fourth toetip width 1.4 (toe IV of right foot is deformed), HW/SVL 0.408, and SHL/SVL 0.580.

Etymology.—The name is from the Greek (*para*, meaning "near", and *pelates*, meaning "neighbor") in allusion to its close morphological resemblance and presumed relationship to *E. hypostenor* and *E. ruthae*. Not coincidentally, this name is also appropriate, since most of the known specimens were collected within a very small area, often calling 1 m or less apart. Calling males of the other two burrowing species are normally separated by considerably greater distances.

Comparisons.—*Eleutherodactylus parapelates* (maximum SVL = 52 mm) resembles the five other *inoptatus* group species (Fig. 1) in being moderately large and having a relatively long first finger. It is sympatric at Castillon with *E. chlorophenax* (77 mm), *E. inoptatus* (88 mm), and *E. nortoni* (66 mm), but is smaller, has a different dorsal pattern, and lacks a prominent spinelike tubercle on the upper eyelid present in those species. Additionally, *E. chlorophenax* and *E. nortoni* have larger digital pads and are often green (some *E. chlorophenax* are tan); *E. inoptatus* has a more rounded snout and canthus rostralis, and is usually brown or tan (never green). Also, *E. chlorophenax*, *E. inoptatus*, and *E. nortoni* do not have a tough, cornified patch of skin on the tip of their snouts like *E. parapelates*.

The two species that could be most easily confused with *E. parapelates* are *E. ruthae* and *E. hypostenor*. All three species are about the same size (50 mm SVL),

usually have a patch of cornified skin at the tip of their snouts, and have chevronate shank bars. The dark mottled venter of *E. parapelates* (Fig. 2) distinguishes it from *E. hypostenor*, which has a white or cream venter with little or no dark pigment. Also, as in *E. ruthae*, the first finger is slightly longer than the second in nearly all specimens of *E. parapelates*, the reverse being true in *E. hypostenor*. In *E. ruthae*, the chevronate shank bars are wider and fewer in number than in *E. parapelates* or *E. hypostenor*. A combination of measurements (Table 1) will also distinguish *E. parapelates* from *E. hypostenor* and South Island *E. ruthae*: it differs from both in having a relatively longer head and a smaller tympanum; from *E. hypostenor*, it differs in having a shorter thigh, a narrower thigh and shank, a longer first finger, a shorter second finger, smaller digital pads, and fewer vomerine odontoids; from *E. ruthae*, it differs in having a longer thigh and shank, a longer second finger, and larger digital pads.

The known distributions of the three burrowing species are allopatric or parapatric: no more than one species has been taken at a single locality. *Eleutherodactylus parapelates* and *E. ruthae* may be sympatric on the eastern slopes of the Massif de la Hotte (Fig. 3). The *E. parapelates* locality 40.2 km N Les Cayes is only 8 km from the nearest *E. ruthae* locality (Marceline), yet none of the specimens from those localities shows any evidence of intergradation. The known range of *E. hypostenor* (Fig. 3) includes the Sierra de Baoruco and the extreme southeastern portion of the Massif de la Selle, thus leaving a gap of 230 km between the westernmost *E. hypostenor* locality and the easternmost *E. parapelates* locality.

Natural history.—Castillon is a small village on the north slope of the Massif de la Hotte, absent from topographic maps but located 8.0 km S, 0.3 km E Marché Léon (airline distance). It is reached by a primitive road heading east from Marché Léon for a short distance and then going south through Bois Sec and Rampe des Lions. Castillon is situated on a narrow ridge but in a topographic dip between



FIG. 2.—Venter of *Eleutherodactylus parapelates* (USNM 257728, paratype).

two hills. The road is impassable from this point on, although a trail continues south and then east, eventually leading to Pic Macaya. Schwartz (1973) gave a brief description of the region surrounding Castillon from an account of Thomas' 1971 visit. In November 1984, considerably more forest had been destroyed, and all that remained of the natural vegetation were some small, isolated patches of forest, usually on nearly vertical slopes.

The single 1971 specimen (ASFS V24424) was collected on 21 June by RT as it was sitting on herbaceous vegetation, about 1 m above the ground along a road cut. One individual obtained in 1984 (USNM 257728) was native-collected and has no natural history data associated with it. We unearthed the remaining 12 specimens in our 1984 series from shallow underground chambers; with one exception, no external openings were apparent. The exceptional frog was calling from an open cavity beneath a mat of dead vegetation. All were calling in the early morning (0100–0500 h) of 2 November 1984. One individual (USNM 257727) was vocalizing

TABLE 1.—Measurements (in mm) of *Eleutherodactylus hypostenor*, *E. parapelates*, and South Island *E. ruthae*. Values are means \pm 3 SE (*n*); significant difference ($P < 0.01$) from *hypostenor*, *parapelates*, and *ruthae* indicated by h, p, and r, respectively.

	<i>hypostenor</i>	<i>parapelates</i>	South Island <i>ruthae</i>
Adult SVL	48.4 \pm 1.04 (53)	48.9 \pm 1.31 (15)	50.4 \pm 1.80 (10)
Head length	19.8 \pm 0.35 (52)	19.6 \pm 0.50 (15)	19.6 \pm 0.80 (10)
Head width	20.4 \pm 0.42 (52) p	19.6 \pm 0.53 (15) h, r	20.7 \pm 0.72 (10) p
Tympanum	3.53 \pm 0.077 (53) p	3.32 \pm 0.147 (15) h, r	3.61 \pm 0.170 (10) p
Thigh length	26.6 \pm 0.46 (53) p, r	25.6 \pm 0.83 (15) h, r	23.0 \pm 1.14 (10) h, p
Thigh width	10.0 \pm 0.34 (52) p, r	8.04 \pm 0.332 (15) h	8.80 \pm 0.891 (10) h, p
Shank length	30.1 \pm 0.59 (53) r	29.4 \pm 0.72 (15) r	24.9 \pm 0.75 (10) h, p
Shank width	7.85 \pm 0.290 (52) p, r	6.29 \pm 0.287 (15) h	6.34 \pm 0.708 (10) h
Finger I length	7.21 \pm 0.266 (37) p, r	7.69 \pm 0.291 (14) h	7.80 \pm 0.407 (10) h
Finger II length	7.82 \pm 0.243 (37) p, r	7.34 \pm 0.354 (15) h, r	6.75 \pm 0.356 (10) h, p
Fingertip (III) width	2.18 \pm 0.078 (50) p, r	1.79 \pm 0.150 (15) h, r	1.33 \pm 0.261 (10) h, p
Toetip (IV) width	2.05 \pm 0.075 (49) p, r	1.71 \pm 0.143 (15) h, r	1.16 \pm 0.246 (10) h, p
Number of vomerine odontoids (right row)	17.9 \pm 1.16 (44) p, r	13.9 \pm 1.80 (15) h	13.3 \pm 1.22 (9) h

next to a well-used trail 0.5 km S Castillon, and we collected the others in a small coffee grove on a hill 0.1 km N Castillon and immediately west of the road. Most frogs were in a relatively small area with distances between individuals of about 1 m (see notes below on call site and vocalization).

Electrophoresis.—One particularly useful feature of electrophoretic data is the general association between genetic distance and taxonomic level. In intraspecific studies, 98% of genetic distances (Nei, 1972) fall below 0.16 whereas 97% of interspecific genetic distances are above this value (Thorpe, 1982). Ignoring frequency differences, a genetic distance (D) of 0.16 corresponds to about 15% of the loci examined having "fixed differences" (no shared alleles).

Although *E. parapelates* can be distinguished morphologically from *E. ruthae* and *E. hypostenor*, it is similar enough to those two species that its specific status might be questioned. We therefore examined those three species using starch gel electrophoresis of 30 loci (see Hedges, 1986, for general methodology). Five individuals of *E. parapelates* (USNM 257717–20, 257727), five *E. hypostenor* (USNM 257733–37), and three *E. ruthae* (USNM 257750–52) were compared.

The following loci were monomorphic: Acon-1, Acp, Ck, Cr, Dpep, Glud, Gsr-1,

Icd-2, Me, Pgm, Pt-3, Pk, and Xdh. There were fixed differences at nine loci (Acon-2, Ak, Aat-1, Aat-2, Gpi, Icd-1, Ldh-2, Mdh-1, Pt-2) between *E. parapelates* and *E. hypostenor* and frequency differences at three other loci (Gpd, Lgl, and Mpi) resulting in a D of 0.36. There were 11 fixed differences between *E. parapelates* and *E. ruthae* (Acon-2, Adh, Apep, Aat-1, Aat-2, Gpi, Icd-1, Ldh-2, Mdh-2, Pt-1, and Pt-2) and frequency differences at five other loci (Gpd, Ldh-1, Lgl, Mdh-1, and Mpi) for a D of 0.51. Seven fixed differences (Ak, Adh, Apep, Gpi, Mdh-1, Mdh-2, and Pt-1) and five frequency differences (Acon-2, Ldh-1, Lgl, Mpi, and Pt-2) were found between *E. hypostenor* and *E. ruthae* ($D = 0.36$). Modified Nei's D 's (Hillis, 1984) are virtually identical to standard Nei's D 's for all three comparisons. Thus, all three species are separated by a considerable genetic distance, well within the range of species-level differences in other groups.

DISCUSSION

The *inoptatus* group of *Eleutherodactylus* (Schwartz, 1965, 1976) is restricted to the island of Hispaniola and contains six fairly large and robust species: *chlorophenax*, *hypostenor*, *inoptatus*, *nortoni*, *parapelates*, and *ruthae*. Lynch (1971) found that in the two species he examined osteologically (*inoptatus* and *ruthae*), there was no fusion between the frontoparietal

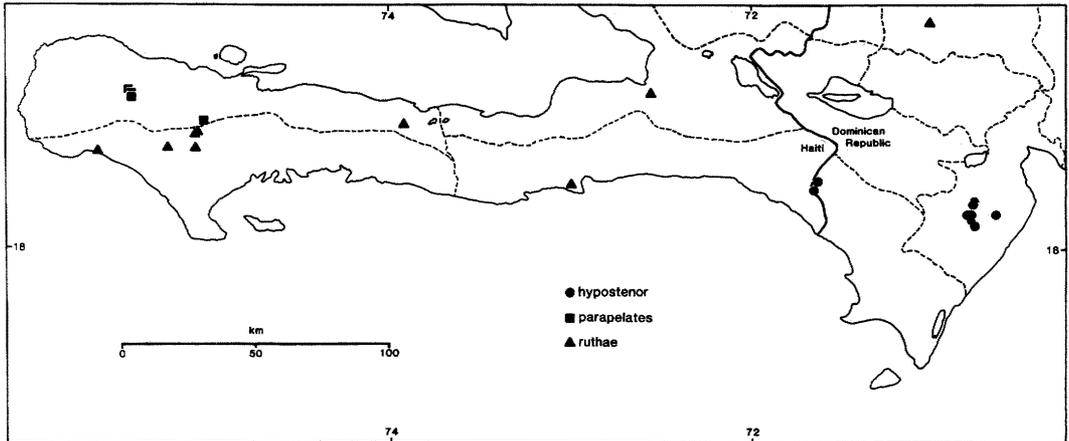


FIG. 3.—Southern Hispaniola, showing locality records for *Eleutherodactylus ruthae* (entire distribution not shown), *E. hypostenor*, and *E. parapelates*. Dashed lines indicate political subdivisions within Haiti and the Dominican Republic.

and prootic bones, apparently a unique condition among West Indian *Eleutherodactylus*. Also, *inoptatus* group species have relatively long first fingers, and in three (*inoptatus*, *parapelates*, and *ruthae*), the first finger is longer than the second. This trait is moderately common among South American species but is not found in other West Indian *Eleutherodactylus* (Lynch, 1976).

Variation in vocal sac structure, calling site and vocalization have also been useful in characterizing species in this group (Schwartz, 1965, 1976, 1984). Below, we discuss these features of the *inoptatus* group and comment on the presumed relationships of the species.

Vocal Sacs

Schwartz (1965) considered the vocal sac an important character in distinguishing the *inoptatus* group from the *auriculatus* group of West Indian *Eleutherodactylus*. He recorded no vocal sac in *E. hypostenor* and *E. inoptatus*; *E. ruthae* was considered to have a "double vocal sac." Members of the *auriculatus* group apparently have single subgular vocal sacs (Schwartz, 1965).

We have examined the six species of the *inoptatus* group and found, upon dissection, that all possess internal, median, subgular vocal sacs (terminology of Liu,

1935). The deflated vocal sac normally occupies the posterior one-half of the gular region: slightly more in *E. inoptatus*, slightly less in *E. hypostenor* and *E. parapelates*. In *E. ruthae*, the lateral ends of the vocal sac extend into a postmandibular/preaxillary space and probably form accessory pouches when inflated. A tendency toward this lateral extension of the vocal sac is also found in *E. hypostenor* and *E. parapelates*, but it is not so well developed as in *E. ruthae*.

None of the six species was closely observed while vocalizing, and therefore it is not known how much of the skin is distended when the vocal sac is inflated. There is little external evidence of the vocal sac in *E. chlorophenax*, *E. inoptatus*, and *E. nortoni*. In the three burrowing species, external evidence of a vocal sac can be seen on some preserved specimens as slightly distended or loose (but not folded) skin in the gular and preaxillary regions, the best examples being MCZ 43188 (*ruthae*) and ASFS V30219 (*hypostenor*). Without knowledge of the internal anatomy, these two species would appear to have a "double" vocal sac, as Schwartz (1965) suggested for *E. ruthae*. However, since even in *E. ruthae* the vocal sac is a continuous structure with no noticeable median constriction, it comes under the category of median subgular, rather than

paired subgular vocal sac (Duellman and Trueb, 1986:92; Liu, 1935). Lateral extensions of the vocal sac in the three burrowing species probably represent adaptations for underground vocalization. They may function in transmitting sound upwards and through the roof of the chamber more efficiently than a normal, ventrally oriented subgular vocal sac. On the other hand, it may simply be a response to space limitations: the lateral extensions could help to distribute the inflated vocal sac more evenly within the cavity.

Calling Sites

Eleutherodactylus inoptatus calls from a variety of places, ranging from the surface of the ground to at least 6 m high in trees. Our experience with this abundant species leads to no generalization as to preferential call site. Even in undisturbed forest in the *haitises* of northeastern Dominican Republic, we found many individuals calling on bare ground, as well as in trees. Individuals sometimes call from moderate concealment—cavities in rocks or sites partly covered by vegetation. *Eleutherodactylus nortoni*, however, seems to prefer arboreal call sites. Schwartz (1976) found this species on vines or branches in trees up to 3 m above the ground, although one was calling from an open cavity in the ground. Our experience with this species confirms its preference for arboreal call sites: we have found it in trees, shrubs, and on limestone rocks. One individual was calling from within a large clump of moss and decayed vegetation, about 3 m high in a tree. Surprisingly, another calling male was unearthed from a shallow underground cavity with no apparent external opening. We collected a single male of *E. chlorophenax* as it was calling within a tangle of vines several meters above the base of a small sinkhole.

Male *E. hypostenor*, *E. parapelates*, and *E. ruthae* call almost exclusively from shallow underground chambers. These cavities have no apparent external openings and are about 1–3 cm below the surface, usually in loose soil. The cornified and unpigmented patch of skin on the snout, and the large, conical, subarticular

tubercles in these species strongly suggest that they burrow head-first and construct their own chambers. Females apparently come to the burrows to mate and deposit their eggs, because hatchlings have been found in an enclosed chamber (*E. ruthae*; Schwartz, 1965). Several calling males of *E. ruthae* were found aboveground (Schwartz, 1965), although this is apparently an unusual call site. One of us (SBH) heard an *E. parapelates* that seemed to be calling from 3 m high in a very spiny citrus tree, but it was never seen or collected. Although the enlarged digital pads of *E. hypostenor* and *E. parapelates* suggest arboreal habits, the calling site preferences in these two species and in *E. ruthae* are decidedly subterranean.

Vocalizations

We have heard the calls of all six species in the *inoptatus* group and have recorded all but the call of *E. chlorophenax* (Fig. 4). The vocalizations of these six species are similar in that they are low in dominant frequency and rapidly pulsed, resulting in a vibratory or raspy sound. *Eleutherodactylus chlorophenax*, *E. hypostenor*, *E. inoptatus*, and *E. nortoni* have single-note calls. Schwartz (1976) described the call of *E. nortoni* as comprising multiple “notes,” here referred to as “pulses” within a single note, the difference apparently being a matter of terminology rather than call structure (A. Schwartz, personal communication). Of the four species with single notes, *E. inoptatus* differs in having an “urrr” call that is constant in frequency. The calls of *E. chlorophenax*, *E. hypostenor*, and *E. nortoni* all rise in frequency and sound very similar: “urrrp,” or “wherp,” as Schwartz (1965, 1984) described for *E. hypostenor*.

Our knowledge of the vocal abilities of *E. chlorophenax* derives from a single calling male (USNM 257729) collected near Plaines Formon, Dépt. du Sud, Haiti. Because the call was so similar to that of *E. nortoni* (calling abundantly in the immediate vicinity), we assumed it was that species and failed to make a recording before collecting it. Although the call of *E. hypostenor* sounds similar to that of *E.*

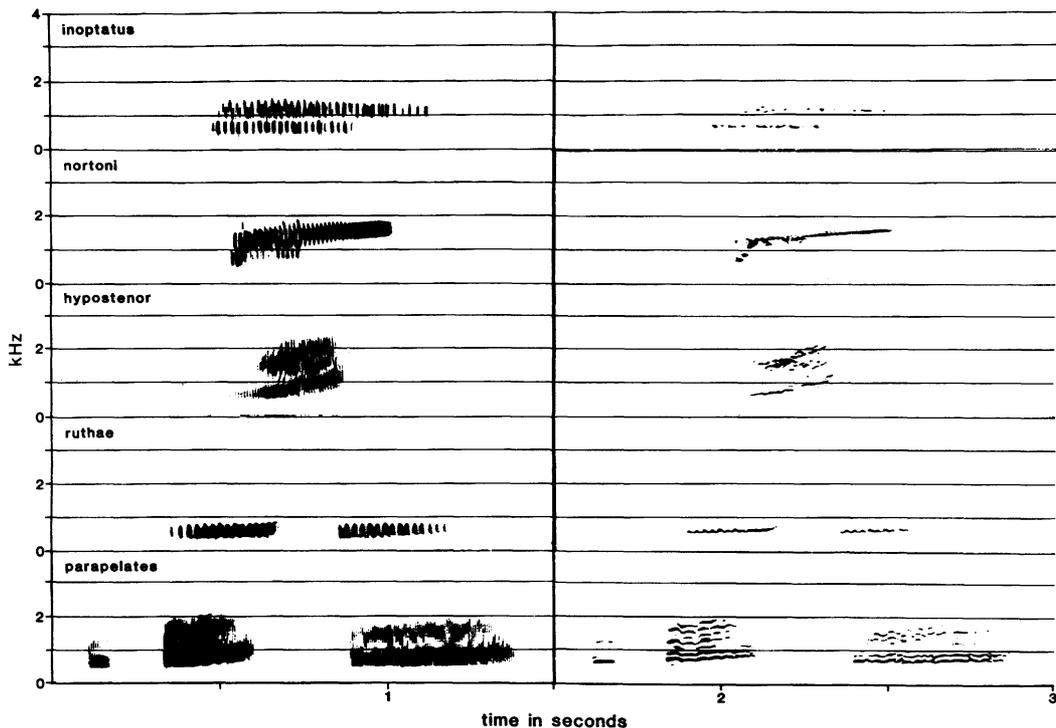


FIG. 4.—Audiospectrograms of five species in the *inoptatus* group of *Eleutherodactylus*: *E. inoptatus* (Dominican Republic: Barahona Prov., not collected), *E. nortoni* (Haiti: Dépt. du Sud, USNM 257745), *E. hypostenor* (Dominican Republic: Barahona Prov., USNM 257738), *E. ruthae* (Haiti: Dépt. du Sud, USNM 257753), *E. parapelates* (Haiti: Dépt. de la Grand'Anse, USNM 257727). Two calls are shown for each species: 300 Hz filter (left), and 45 Hz filter (right).

nortoni, it is shorter in duration and has a different structure (Fig. 4).

Schwartz (1965) described the call of *E. ruthae* as a two-note pair of "grunts" or a 5–8 note series of ascending brrrp's (*E. r. ruthae*); a three note series of "whoop"s (*E. r. aporostegus*); a four note series of "whoop"s with the last two trilled (*E. r. tyathrous*); and a 5–8 note series of "wherp"s, each with a slight ascending inflection (*E. r. bothroboans*). We heard and collected *E. ruthae* from near Les Platons (1000 m) on the southern slope of the Massif de la Hotte and only 12 km airline distance from the type locality of *E. r. aporostegus*. The four individuals collected at this locality gave a two-note "urrr-urrr" call, constant in frequency (Fig. 4). Except for being unusually tuberculate, they otherwise appear to be morphologically identical to *E. r. aporostegus*, which has a three-note call. The extreme geo-

graphic variation in the call of *E. ruthae*, unparalleled in the genus, suggests that *E. ruthae* may be a composite of several species. Schwartz (1965) cited *E. pantoni* of Jamaica as being another case of considerable intraspecific call variation. However, electrophoretic data on *E. pantoni* obtained by one of us (SBH) and call data (Crombie, 1986) indicate that at least two species are involved there. Additional distributional and natural history data, as well as biochemical and chromosome analysis, may help to resolve this question in *E. ruthae*.

The call of *E. parapelates* is usually two notes (errk-urrr): the first note rises slightly and the second note is relatively constant in pitch. Calls were often separated by intervals of from 1–10 or more minutes, but the modal interval was distinctly shorter than is typical for the other two burrowing species. One individual (USNM

257727) consistently gave a three-note call (Fig. 4), the first note being very short and immediately followed by the normal two-note call. This individual was also separated from the 12 other calling male *E. parapelates* by 0.6 km.

Menzies and Tyler (1977) noted differences between the calls of burrowing microhylids and those of other microhylid species from New Guinea. In particular, nearly all burrowing species had low frequency (<1 kHz) calls, apparently an adaptation for more effective sound transmission through soil. Although the three burrowing species of the *inoptatus* group (*E. hypostenor*, *E. parapelates*, and *E. ruthae*) also have low frequency calls, they are not any lower in frequency than the other three species in the group.

Relationships

The relationships of the three large species (*E. chlorophenax*, *E. inoptatus*, and *E. nortoni*) to each other or to the rest of the group is unclear. The two South Island endemics, *E. chlorophenax* and *E. nortoni*, both have large digital pads and a similar, rising call. However, *E. chlorophenax* otherwise resembles *E. inoptatus*, the species with which it was initially compared (Schwartz, 1976).

The remaining three species (*E. hypostenor*, *E. parapelates*, and *E. ruthae*) almost certainly form a monophyletic subgroup within the *inoptatus* group. Several characters shared by all three appear to be synapomorphies: chevron-shaped shank bars, protruding snout with cornified skin at tip, and laterally extended vocal sac. Also, there is no sexual dimorphism in body size in at least two of the three species (adult females of *E. parapelates* are unknown), an unusual condition in *Eleutherodactylus* where females are nearly always larger than males (Lynch and Duellman, 1980).

At least two traits present in *E. hypostenor*, *E. parapelates*, and *E. ruthae* (tough, unpigmented snout tip, lack of sexual dimorphism) are found in other burrowing anurans (Menzies and Tyler, 1977) and are probably related to fossorial habits. A reinforced snout tip would be advan-

tageous for head-first burrowing. The relationship between sexual dimorphism in body size and burrowing habits is not as clear. However, if females deposit eggs in chambers that are constructed by males, then it may be advantageous for females to be similar in size to males in order to gain access to the chamber. Unfortunately, very little is known about the natural history of these species to test that hypothesis, except for the finding of hatchlings in an enclosed chamber (Schwartz, 1965).

Within this trio of burrowing species, it is not clear which two are more closely related. In several measurements (Table 1), and in the call (Fig. 4), *E. parapelates* is intermediate between *E. hypostenor* and *E. ruthae*. It is possible that all three became isolated at about the same time due to changing climatic conditions.

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APPENDIX I

Although the junior author and others publishing on the systematics of various Hispaniolan taxa have

for some years used a system of five political *départements* (such as appears on oil company road maps), we are informed by the Haitian Consulate in Washington, D.C., that this is incorrect. Haiti is correctly divided into nine *départements*: Nord Ouest, Nord, Nord Est, l'Artibonite, Centre, l'Ouest, Sud'Est, Sud, and Grande Anse.

APPENDIX II

Specimens Examined

Eleutherodactylus chlorophenax (10). HAITI: Dépt. du Sud, UF 56797, 56799-800, 59252, 61600-03, USNM 257729-30.

Eleutherodactylus hypostenor (61). DOMINICAN REPUBLIC: Barahona Prov., ASFS X9790, X9797-800, V40-49, V23384-99, V30294, V30404-05, V30922, V31304, V31331-32, V31541-44, V31595, V39588, V45026, MCZ 43187 (holotype), 43190, USNM 257731-38; Pedernales Prov., ASFS V30215-19, V39989.

Eleutherodactylus inoptatus (25). DOMINICAN REPUBLIC: Barahona Prov., USNM 257767-71; El Seibo Prov., USNM 257773-76; Pedernales Prov., USNM 257754-59, 257772. HAITI: Dépt. de la Grande Anse, USNM 257760-63; Dépt. de l'Ouest, USNM 257777; Dépt. du Sud, USNM 257778; Dépt. du Sud'Est, USNM 257764-66.

Eleutherodactylus nortoni (11). HAITI: Dépt. de la Grande Anse, USNM 257739; Dépt. de l'Ouest, USNM 257741; Dépt. du Sud, USNM 257740, 257742-49.

Eleutherodactylus ruthae (36). DOMINICAN REPUBLIC: El Seibo Prov., ASFS X9335-36; La Altagracia Prov., ASFS V942, V967-70, V1039, V17441, V29040, V29047, V29303, V35267; Le Vega Prov., ASFS V1946-47, V4197, V4219, V4236, V4238-40, MCZ 43189; San Juan Prov., MCZ 43188. HAITI: Dépt. de la Grande Anse, ASFS V42984; Dépt. de l'Ouest, ASFS V8490, V47099; Dépt. du Sud, ASFS X2713, V20395, V44696, V48961, MCZ 43186, USNM 257750-53; Dépt. du Sud'Est, ASFS 37615.