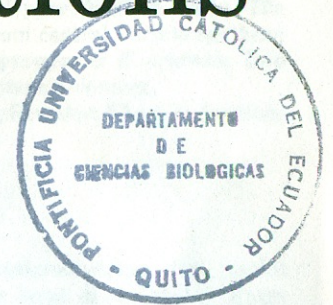


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**Intragenetic Relationships of Mainland
Eleutherodactylus (Leptodactylidae).
I. A Review of the Frogs Assigned to the
Eleutherodactylus discoidalis Species Group**

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ABSTRACT

The narrow-disked frogs previously assigned to the *Eleutherodactylus discoidalis* "group" do not form a monophyletic group and are separated as three species groups. The *dolops* Group (*E. babax* new species and *E. dolops*) occurs at moderate elevations in Colombia and Ecuador. The *nigrovittatus* Group (*E. elassodiscus*, *E. latens* new species, *E. mantipus*, and *E. nigrovittatus*) includes three Andean species in Colombia and Ecuador and one species (*E. nigrovittatus*) found in the Upper Amazon Basin. The *discoidalis* group (*E. cruralis* and *E. discoidalis*) occurs from central Peru to northern Argentina. *Eleutherodactylus granulatus* is considered a synonym of *E. cruralis*. Two new species (*E. babax* and *E. latens*) are described from western Colombia.

Key words: Amphibia; Anura; Leptodactylidae; Colombia; Ecuador; *Eleutherodactylus*; Systematics.

INTRODUCTION

To persons not acquainted with frogs of the genus *Eleutherodactylus*, most species are initially misidentified as treefrogs (because they have large digital disks). Frogs of the family Leptodactylidae are predominantly terrestrial, with the marked exception of *Eleutherodactylus* (mostly climbers and many species are arboreal). While many (perhaps even most) species of *Eleutherodactylus* have enlarged disks on at least some of their fingers and toes, it is no means constant. Many (but not all) of the terrestrial species are large, toad-like forms, especially in the forested lowlands and cloudforests.

This paper concerns several species of smaller, terrestrial, *Eleutherodactylus* found in wet forests of South America (at low and moderate altitudes) and which have narrow digits (Fig. 1). For more than a decade, I have termed these frogs members of the *Eleutherodactylus discoidalis* Group. I am not aware of any synapomorphy peculiar to these frogs and do not here claim that the group is monophyletic. Nevertheless, it seems appropriate to treat these species as if the group were monophyletic because the morphologies of several species have been influential in many of my published arguments about *Eleutherodactylus* and its evolution (Lynch, 1971, 1975a, 1975b, 1976, 1986a).

The recognition of the *discoidalis* Group dates from Lynch (1976) who included five nominate species and who suggested that the group was "... annectant between the *binotatus* and *fitzingeri* groups." The species included in the group were *E. cruralis* (Boulenger) from Bolivia, *E. discoidalis* (Peracca) from northern Argentina, *E. elassodiscus* Lynch from Andean Ecuador, *E. granulatus* (Boulenger) from Peru, and *E. nigrovittatus* (Anderson) from eastern (lowland) Ecuador. Subsequently, *E. dolops* Lynch and Duellman from Andean Ecuador and *E. mantipus* (Boulenger) from Andean Colombia were assigned to the group. In addition to these, two undescribed taxa are added in the present paper (both from Andean Colombia).

As mentioned above, the group is probably not monophyletic. As used in the past, the group has been defined rather than diagnosed. Lynch (1976) recognized the group on the basis of a unique combination of traits (several of which are apparently plesiomorphic): skin of venter smooth; first finger longer than second; head narrow (HW < 45% SVL); no cranial crests; unguis flap of digit not indented; digits not expanded (= lacking disks); and toes lacking webbing. Additionally, Lynch (1976: 9-10) noted some heterogeneity within the group as evidenced by the presence of pointed digital disks in *E. elassodiscus* and *E. nigrovittatus* in contrast to the apically rounded digit disks in the three southern species (Argentina, Bolivia, and southern Peru). He also pointed out that the southern species resembled a Brazilian species (*E. octavioi* of the *binotatus* Group) in having large outer metatarsal tubercles (Fig. 2).

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published position (see references cited above) could be summarized visually with the following linear arrangement:

Ischnocnema — *binotatus* — *discoidalis* — "*fitzingeri*"
Group Group "group"

In order to remove any ambiguities from the literature, I want to explicitly identify the implications in many of my earlier comments about frogs of the *discoidalis* Group. That arrangement supposes that *Ischnocnema*¹ (or frogs substantially like species now placed in that genus) are phylogenetically more primitive than (or perhaps ancestral to) frogs placed in the genus *Eleutherodactylus*. Furthermore, this position supposes that among the many and varied species of the genus *Eleutherodactylus*, those species placed in the *binotatus* Group are the most like species of *Ischnocnema*. This position further suggests that a complex of species (the *fitzingeri* group of Lynch, 1976, and Lynch and Myers, 1983) now divided between the subgenus *Craugastor* and the *conspicillatus* Group (Lynch, 1986a) is advanced to (and/or derived from) the frogs identified as members of the *discoidalis* Group.

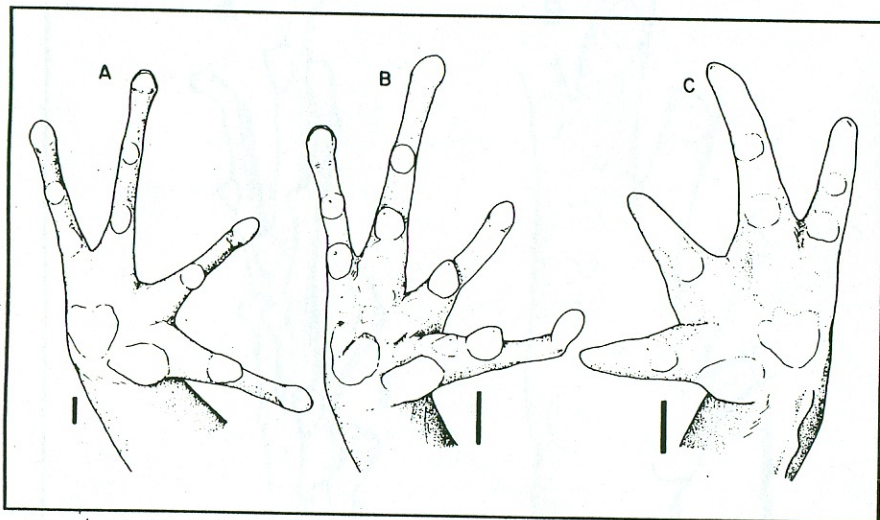


Fig. 1. Palmar views of hands of *Eleutherodactylus*: (A) *E. babax*, ICNMHN 7920; (B) *E. cruralis*, AMNH 91579; (C) *E. latens*, ICNMHN 6346. Scales equal 1 mm.

¹ Savage (1987:47) appeared to relate *Ischnocnema* and the Mexican genus *Tomodactylus* as sister groups. However, his published cladogram is not supported by his data—the two genera do not share any synapomorphies. In fact, it appears that the only similarity between the two genera is they share many plesiomorphies of the non-*Craugastor* lineages. My failure to make comparisons here with the Mexican frogs in the genera *Syrrhophus* and *Tomodactylus* derives from the absence of evidence suggesting relationships. Savage's (1987) proposal is an interesting one but, until the polarity of the *M. depressor mandibulae* character states has been evaluated, should not be taken as a corroborated hypothesis.

While frogs of the *discoidalis* Group are rather similar to one another, that similarity is phenetic and unspecified. The primary objective of the present study is to provide a database for future interpretation of many of the opinions I have expressed about the evolution of frogs of the genus *Eleutherodactylus*, because frogs of the *discoidalis* Group served as models of "primitive" *Eleutherodactylus*. In order to satisfy the primary objective, comparable descriptions complete with anatomical detail are required. At the same time, evaluation of the species of this group would allow me to resolve its status (i.e., is it monophyletic and, if not, what monophyletic subsets can be identified?).

MATERIALS AND METHODS

Terminology and measurements follow Lynch and Duellman (1980) except that the nomenclature of expansions of digits follows Savage (1987). In measuring head length, I use two measurements. The most precise is not a measure of head length but is rather the chord of head length (i.e., the distance from the tip of the snout to the posterior end of the mandible). Most authors call this measurement "head length." Head length, as used here and in many of my papers for the past decade, refers to an estimate of the distance from the tip of the snout to the posterior end of the occiput (approximated by a line drawn between the corners of the jaws). Skeletal preparations were made for each species as either dry skulls (large species) or as cleared and stained specimens (smaller species). The following abbreviations for measurements are used throughout the text: E-N (eye to nostril distance), HW (greatest head width), IOD (interorbital distance), and SVL (snout-vent length). Abbreviations for museum specimens follow those provided by Leviton et al (1985) except that Leviton et al did not include the collection of Colombia's INDERENA (Instituto Nacional de Recursos Naturales y del Ambiente, Bogotá) research laboratory (IND). They use two additional letters to denote the collection of amphibians (IND-AN).

TAXONOMIC ACCOUNTS

Modern descriptions and illustrations are available for four species from northwestern South America, as follows: *E. dolops* (Lynch and Duellman, 1980), *E. elassodiscus* (Lynch, 1973a), *E. mantipus* (Lynch, 1973b), and *E. nigrovittatus* (Andersson, 1945; Lynch, 1980). Cei (1980) provided illustrations for *E. discoidalis* but the other two southern species have not been treated since early in this century.

The Southern (Northern Argentina–Southern Peru) Taxa

Around the turn of the century, three names were applied to small eleutherodactyline frogs from northwestern Argentina, Bolivia, and southern Peru. Peracca (1895) named *Hylodes discoidalis* from Tucumán, Argentina, Boulenger (1902) named *Hylodes cruralis* from La Paz, Bolivia, and Boulenger (1903) named *Hylodes granulatus* from southern Peru. In his descriptions, Boulenger did not make comparisons among the three taxa. These names were not associated together until Lynch (1973a) compared them with *E. elassodiscus*. Later (Lynch, 1976), he placed them in the *discoidalis* group. Aside from Cei's (1980) recent description of *E. discoidalis*, the published accounts of these taxa reflect the needs of the turn of the century. Cei's description is certainly adequate in detail for a faunal region but it is not adequate for comparisons among taxa outside of Argentina.

I consider the three names as applying to two species and provide descriptions of each of those below:

Hylodes discoidalis Peracca, 1895:124 [Syntypes. — BMNH 1947.2. 15.63-65 (formerly 94.12.31.2-4), MZUT "several," Tucumán, Argentina].

Diagnosis. — 1) skin of dorsum shagreened and with a few other tubercles, that of venter smooth; no dorsolateral folds; 2) tympanum distinct, its length 1/2 to 2/3 eye length; 3) snout subacuminata in dorsal view, rounded in lateral profile; canthus rostralis distinct; 4) upper eyelid usually narrower than IOD; no cranial crests; 5) vomerine odontophores between choanae, low, oval; 6) males with vocal slits and nuptial thumb pads; 7) first finger longer than second; outer fingers bearing truncate discs; 8) fingers lacking lateral keels; 9) no ulnar tubercles; 10) no folds or tubercles on tarsus or heel; 11) two metatarsal tubercles, inner oval, 1½ to 2 times size of round outer; supernumerary plantar tubercles pungent; 12) toes with narrow lateral keels; toe discs round, smaller than those of fingers; 13) brown with darker markings; throat and chest brown with small cream spots (or not), other ventral surfaces densely stippled with brown; posterior surfaces of thighs dark brown; 14) adults moderate in size, males 26.8-27.6 (\bar{x} = 27.2, N = 4) mm, females 34.0-39.4 (\bar{x} = 35.7, N = 6) mm SVL.

Eleutherodactylus discoidalis is distinctive among species of the genus in having the vomerine odontophores between the choanae (rather than between and posterior to the choanae). Furthermore, its long slender digits in combination with the smooth skin on the venter and long first finger set it apart from all other eleutherodactyline frogs except *E. cruralis*, some species of the *binotatus* Group, and the genus *Ischnocnema*. The superficial resemblance to frogs of the genus *Ischnocnema* is enhanced by the presence of pungent supernumerary plantar tubercles. Within the *discoidalis* group, *E. discoidalis* is most similar to *E. cruralis* but the similarity is not taken as evidence of relationship (the similarities appear to all be common possession of plesiomorphic states). The two are most easily differentiated because *E. discoidalis* has white nuptial pads (absent in *E. cruralis*). In addition, the vomerine odontophores of *E. discoidalis* lie much farther anterior than those of other species of the genus.

Description. — Head as wide as or slightly wider than body, wider than long; HW 32.7-40.3 (\bar{x} = 35.4, N = 21) % SVL; snout subacuminata in dorsal view, rounded in lateral profile (snout deep, top of snout essentially parallel with border of lip when viewed from side); E-N in males 90.9-109.1 (\bar{x} = 99.0, N = 8) % eye length, in females 88.8-112.8 (\bar{x} = 104.6 ± 2.5, N = 10) %; nostrils weakly protuberant, directed laterally

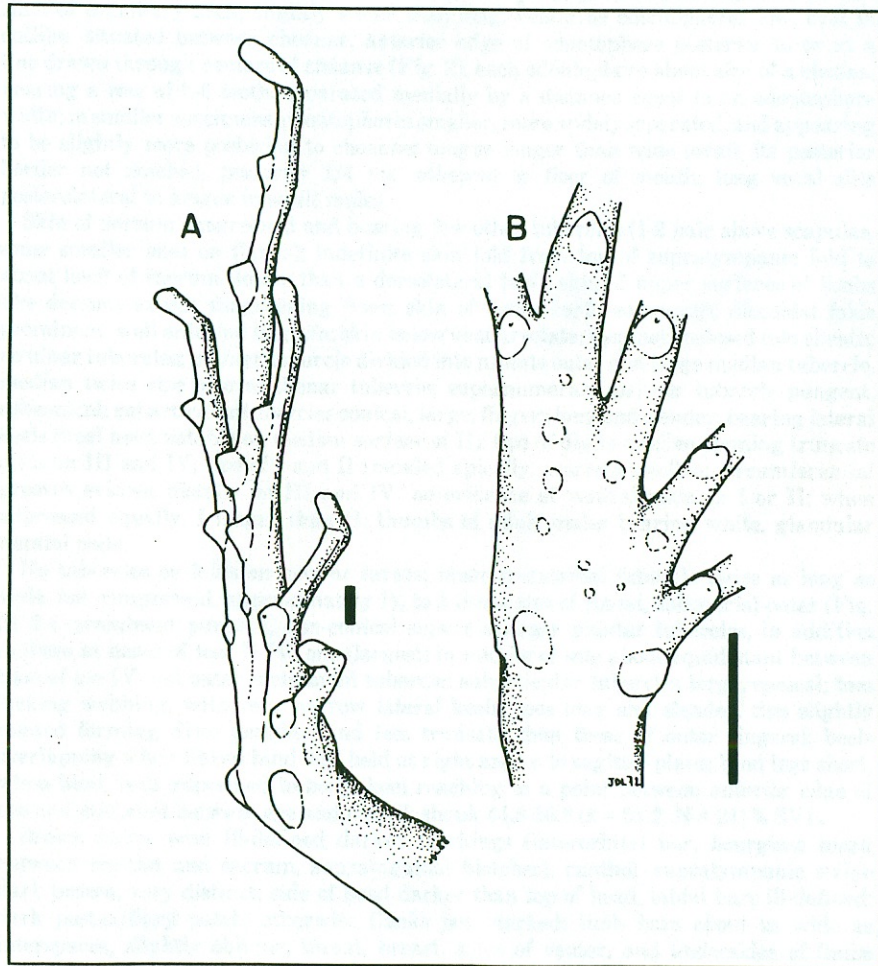


Fig. 2. (A) Ventromedial view of right hind foot of *Eleutherodactylus discoidalis*, TNHC 37885; small arrows point to supernumerary tubercles, large arrow to conical subarticular tubercle. (B) Plantar surface of foot of *E. cruralis*, BMNH 1904.10.29.103. Scales equal 1 mm.

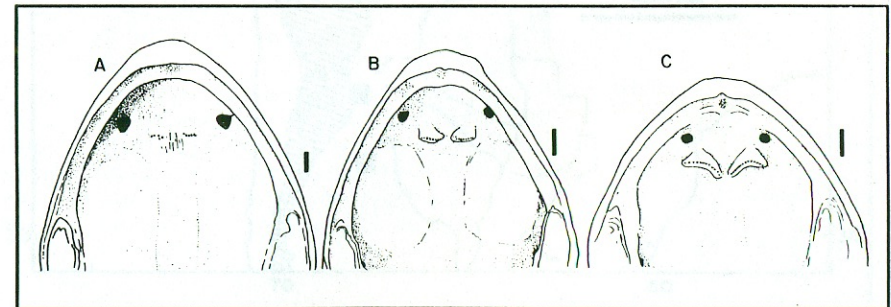


Fig. 3. Palates of *Eleutherodactylus*: (A) *E. discoidalis*, TNHC 37085; (B) *E. cruralis*, AMNH 91579; (C) *E. latens*, ICNMHN 6346. Scale equals 1 mm.

...ly dorsolaterally in large females); canthus rostralis distinct, its edge rounded, straight; loreal region very slightly concave, sloping abruptly to lips; lips weakly flared in large females; upper eyelid width 73.3-100.0 (\bar{x} = 88.2, N = 15) % IOD, bearing a few non-pungent tubercles on posterior one-third; no cranial crests; tympanum distinct, superficial, only the uppermost edge of annulus concealed by supratympanic fold; supratympanic fold prominent, ending in a subconical tubercle dorsal to insertion of forearm; tympanum virtually round, its length 46.7-64.1 (\bar{x} = 54.8, N = 19) % eye length, separated from eye by a distance of less than one-half its diameter; postrictal tubercles large, subconical; skin on rest of dorsal surfaces of head finely shagreened to smooth with low tubercles scattered on occiput; choanae small (Fig. 3), not concealed by palatal shelf of maxillary arch, slightly wider than long; vomerine odontophores low, oval in outline, situated between choanae, anterior edge of odontophore posterior to or at a line drawn through centers of choanae (Fig. 3); each odontophore about size of a choana, bearing a row of 3-6 teeth, separated medially by a distance equal to an odontophore width; in smaller specimens, odontophores smaller, more widely separated, and appearing to be slightly more posterior to choanae; tongue longer than wide (oval), its posterior border not notched, posterior 1/4 not adherent to floor of mouth; long vocal slits posterolateral to tongue in adult males.

Skin of dorsum shagreened and bearing few other tubercles (1-2 pair above scapulae, some smaller ones on flanks); indefinite skin fold from top of supratympanic fold to about level of sacrum (lower than a dorsolateral fold); skin of upper surfaces of limbs like dorsum except shagreening finer; skin of lower surfaces smooth; discoidal folds prominent, well anterior to groin; skin below vent areolate; vent not enclosed into sheath; no ulnar tubercles; palmar tubercle divided into minute outer and large median tubercle, median twice size of oval thenar tubercle; supernumerary palmar tubercle pungent, subconical; subarticular tubercles conical, large; fingers long and slender, bearing lateral keels (keel most notable on median surface of II); tips of digits swollen forming truncate discs on III and IV; tips of I and II rounded apically, scarcely swollen; circumferential grooves distally on III and IV, no evidence of ventral pads on I or II; when adpressed equally, I longer than II; thumbs of adult males bearing white, glandular nuptial pads.

No tubercles or folds on heel or tarsus; inner metatarsal tubercle twice as long as wide, not compressed, approximately 1½ to 2 times size of round, subconical outer (Fig. 2); 2-4 prominent pungent, non-conical supernumerary plantar tubercles, in addition to those at bases of toes II-IV, one (largest) in middle of sole about equidistant between base of toe IV and outer metatarsal tubercle; subarticular tubercles large, conical; toes lacking webbing, with very narrow lateral keels; toes long and slender, tips slightly dilated forming discs (smaller and less truncate than those of outer fingers); heels overlapping when flexed hind legs held at right angles to sagittal plane; hind legs short, when hind limb adpressed to body, heel reaching to a point between anterior edge of eye and midpoint between eye and nostril; shank 44.8-56.8 (\bar{x} = 51.2, N = 21) % SVL.

Brown above with ill-defined darker markings (interorbital bar, hourglass mark between occiput and sacrum, suprainguinal blotches); canthal-supratympanic stripe dark brown, very distinct; side of head darker than top of head, labial bars ill-defined; dark postaxillary patch, otherwise flanks not marked; limb bars about as wide as interspaces, slightly oblique; throat, breast, sides of venter, and undersides of limbs densely stippled with brown; center of belly not pigmented; posterior surfaces of thighs dark brown.

In life, *E. discoidalis* is tan-brown to brown with darker brown to black markings. The ventral surfaces are gray to grayish brown. The concealed surfaces of the hind limbs are light brown with a slight orange wash to the groin and behind the knee. The undersides of the limbs are flesh-colored. The iris is chocolate brown. Cei (1980:312)

described the throat as reddish with white spots and the venter as bright yellowish. The syntypes examined (BMNH 1947.2.15.63-65) have a dark throat with distinct cream spots. This distinctive ventral coloration is seen in some (not all) specimens from the mountains west of Tucumán but, is not seen in material from Jujuy Province.

Distribution. — *E. discoidalis* is known from moderate elevations (960-1550 m) on the eastern flanks of the Andes in northern Argentina (Fig. 4). Cei's (1987:249-50) report of *E. cruralis* from Jujuy Province was based on an earlier opinion I held about the material from Prov. Jujuy.

Eleutherodactylus cruralis (Boulenger)

Hylodes cruralis Boulenger, 1902:396 [Holotype, BMNH 1947.2.15.70 (formerly 1901.8.2.44), La Paz, Bolivia, 4000 m].

Hylodes granulatus Boulenger, 1903:553 [Holotype, BMNH 1947.2.15.72 (formerly 1902.11.28.15), Santo Domingo, Carabaya, S.E. Peru, 600 feet]. **New Synonymy.**

Diagnosis. — 1) skin of dorsum smooth to finely areolate with few to many small tubercles, that of venter smooth; no dorsolateral folds; 2) tympanum distinct, its length 2/5 to 3/5 eye length; 3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis distinct; 4) upper eyelid about as wide as IOD; no cranial crests; 5) vomerine odontophores oval to oblique, prominent, posterior to choanae; 6) males with vocal slits; no nuptial pad on thumb; 7) first finger longer than second; truncate discs

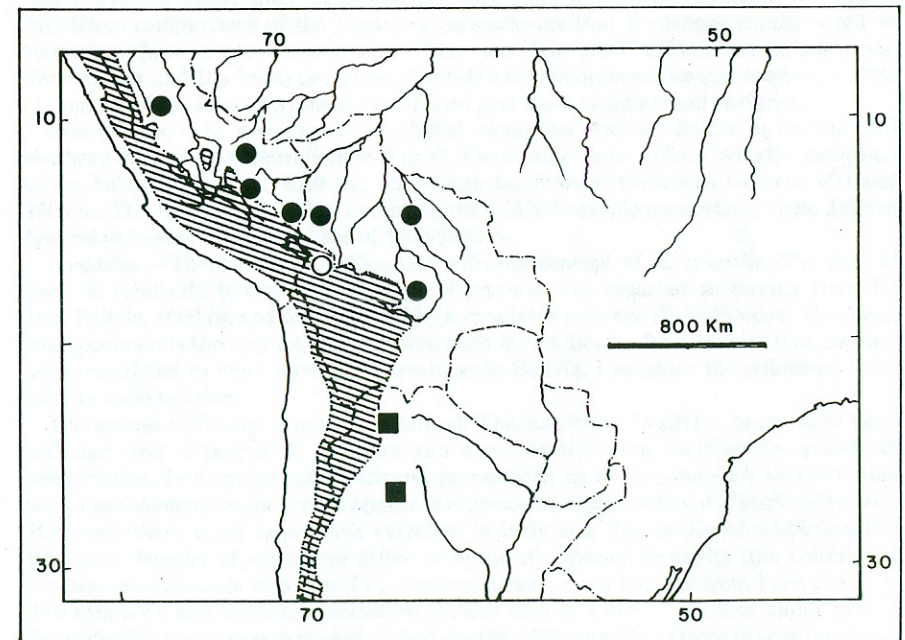


Fig. 4. Distributions of *Eleutherodactylus cruralis* (circles) and *E. discoidalis* (squares). Hatched area 3000 m and above. Open circle is type-locality of *E. cruralis* (probably in error, see text).

on fingers III and IV; 8) no lateral keels on fingers; 9) no ulnar tubercles; 10) no tubercles on heel or tarsus; 11) two metatarsal tubercles, inner oval, slightly larger than round outer; 12) toes lacking lateral keels; toe discs truncate, small; 13) brown above with darker brown markings; throat and chest brown with white spots; posterior surfaces of thighs brown; 14) adults moderate-sized, males 22.9-30.9 ($\bar{x} = 26.3 \pm 0.7$, $N = 12$), females 26.4-38.8 ($\bar{x} = 32.7 \pm 1.3$, $N = 13$) mm SVL.

Description. — Head as broad as (or slightly broader than) body, wider than long; HW 34.9-41.0 ($\bar{x} = 38.6$, $N = 34$) % SVL; snout subacuminate in dorsal view, rounded in lateral profile (Fig. 5); E-N 80.0-103.0 ($\bar{x} = 90.3 \pm 1.7$, $N = 11$) % eye length in males, 86.5-105.0 ($\bar{x} = 94.3 \pm 2.9$, $N = 7$) % in females; canthus rostralis distinct, edge rounded, straight; loreal region concave, sloping abruptly to lips; lips not flared (except weakly in large females); nostrils protuberant, directed laterally; upper eyelid width 80.4-115.6 ($\bar{x} = 97.5 \pm 3.4$, $N = 12$) % IOD in males, 79.3-125.0 ($\bar{x} = 104.9 \pm 3.6$, $N = 16$) % in females; no enlarged tubercles on upper eyelids; interorbital space flat; supratympanic fold distinct, concealing upper edge of tympanum; tympanum round in males, higher than long in females, superficial, separated from eye by a distance equal 1/2 to 2/3 tympanum length; tympanum length 40.0-57.7 ($\bar{x} = 46.4 \pm 1.6$, $N = 11$) %, eye length in males, 40.0-55.6 ($\bar{x} = 47.4 \pm 2.0$, $N = 8$) % in females; postorbital tubercles large, prominent; choanae small to moderate-sized, not concealed by palatal shelf of maxillary arch; vomerine odontophores large, oblique, situated median and posterior to choanae (Fig. 3), bearing teeth in a transverse row slanting posteriorly near midline; odontophores narrowly separated from one another, each bearing a row of up to 8 or 10 teeth (as few as 3); tongue slightly longer than wide, its posterior border with a shallow notch, posterior 1/3 not adherent to floor of mouth; males with short vocal slits posterolateral to tongue.

Skin of dorsal surfaces smooth to finely shagreened with few to numerous small tubercles (more extensive on anterior portions of body than posterior); occasional individuals coarsely tuberculate above; no dorsolateral folds; skin of ventral surfaces smooth; discoidal folds prominent; skin around vent coarsely areolate; no ulnar tubercles; two palmar tubercles, inner largest, larger than oval thenar tubercle; several supernumerary palmar tubercles; subarticular tubercles conical; digital discs of fingers

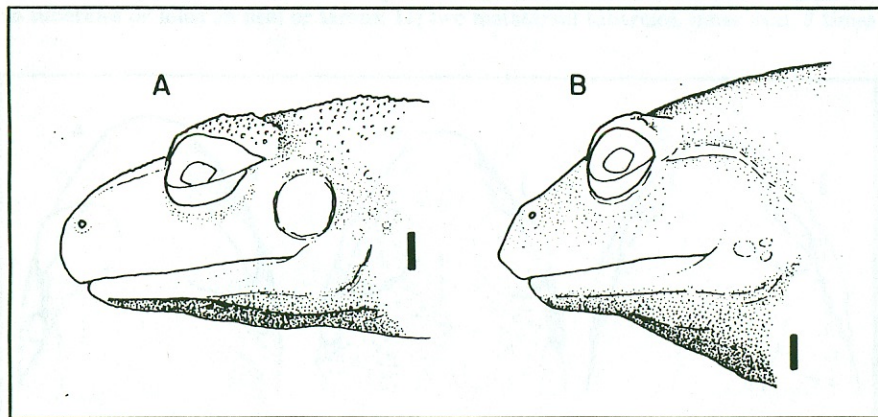


Fig. 5. Profiles of heads of *Eleutherodactylus*: (A) *E. cruralis*, AMNH 91579; (B) *E. latens*, ICNMHN 6346. Scale equals 1 mm.

III-IV truncate, of I-II round, slightly wider than digits; circumferential grooves on outer fingers only; first finger much longer than second (Fig. 1); fingers lacking lateral fringes or keels.

Heel and tarsus lacking tubercles or folds; inner metatarsal tubercle longer than wide, slightly larger than round, elevated outer; low but distinct supernumerary plantar tubercles; subarticular tubercles conical; toes lacking lateral fringes or keels; discs on toes II-V truncate; circumferential grooves present but ventral pads not distinct; toes long and slender; shank 51.6-63.4 ($\bar{x} = 57.1$, $N = 34$) % SVL.

Pale brown above with dark brown markings (interorbital bar, scapular W, blotch on sacrum, inguinal spots); scapular W continuing onto flanks as dark postaxillary mark; canthal-supratympanic stripe poorly-defined, lips barred (face dark, obscuring markings), some white spots along upper lip; limbs barred, bars oblique on shanks, as broad as interspaces; flanks pale brown; posterior surfaces of thighs uniform pale brown aside from a few tiny cream flecks; anal triangle brown; throat and breast brown with white spots, rest of venter (and undersides of hind legs) yellowish-cream speckled with brown.

In life, *E. cruralis* was described as dorsum dull brown to olive-tan with dark brown and orange-tan markings; throat gray; chest grayish-yellow; remaining venter dull yellow; groin salmon; concealed surfaces of legs orange-brown; iris dull bronze heavily flecked with black (W. E. Duellman field notes).

Remarks. — Boulenger (1903) made no comparisons when describing *granulosus* but I surmise that he distinguished *cruralis* and *granulosus* as a result of errors of observation in his description of *cruralis* (Boulenger, 1902). Boulenger (1902) reported that the first finger was not longer than the second and that there was a web rudiment in *cruralis*. My direct comparisons of the holotypes persuade me that Boulenger simply erred in reporting those traits for *cruralis*. There are few other differences between the descriptions and the holotypes (sizes of vomerine odontophores, tongue notches, widths of upper eyelids, sizes of tympana) and I interpret these as individual variation.

Distribution. — *E. cruralis* is distributed along the Andean flanks in central and southern Peru and northern Bolivia (Fig. 4). The samples from Bolivia, with the exception of the holotype (La Paz, 4000 m), come from localities at elevations between 400 and 1000 m. The Peruvian samples, excepting the AMNH sample purportedly from Juliaca (see below), come from elevations of 1330-2900 m.

Remarks. — There are two difficulties with my concept of *E. cruralis*. The first of these is relatively trivial. The holotype of *cruralis* was reported as coming from La Paz, Bolivia, 4000 m, and was collected by a reputable collector (P. O. Simons). However, this specimen is the only one known from such high altitudes for a species that appears to be restricted to more moderate elevations in Bolivia. I consider the published type-locality to be in error.

The second difficulty is more substantial. The specimens available to me have been collected over a period of 75 years and show considerable variation in quality of preservation. In terms of color patterns, proportions, dentition, and such tuberculation as can be detected, the specimens appear to represent a single species of *Eleutherodactylus*. However, there is an impressive variation in body size (for an *Eleutherodactylus*) in that some females of equal size differ in terms of apparent maturity (the holotype of *Hylodes granulosus* is 26.8 mm SVL whereas other gravid females from Peru are 35.1-38.8 mm SVL and there are immature females 30.5-32.7 mm SVL). The 'small' gravid female is the same size as three gravid females (26.4-27.1 mm SVL) from Bolivia (localities are only 400-1000 m elevation there). In the Bolivian samples, there is an immature female 27.0 mm SVL. The smallest gravid females (26.4-26.8 mm SVL) I am assigning to *E. cruralis* are about the size of the large males. If this is correct, this species is the first species of mainland *Eleutherodactylus* known in which marked sexual di-

phism in body size has not been found. Additional material is needed to resolve the question because the available samples are spread across an elevational gradient of as much as 2500 m and along a considerable geographic gradient as well. The most northern specimen available (AMNH 91579) is an immature male (no vocal slits) and is much larger (24.4 mm SVL) than the smallest mature male (22.9 mm SVL) from Bolivia (UMMZ 66609). The largest single sample available (AMNH 6060-73) is of only modest use because its locality data probably are incorrect ("Juliaca," a high elevation site to which specimens probably were shipped; the collection probably was made in the mining district of Santo Domingo 2000 m lower on the slopes. C. W. Myers, pers. comm.).

New Species from Colombia

Field work in Colombia in the past decade has resulted in the acquisition of specimens of two frog species that could be assigned to Lynch's (1976) *discoidalis* group. One is a smaller version of *Eleutherodactylus dolops* and the other is similar to *E. mantipus*.

Eleutherodactylus babax New Species

Holotype. — ICNMHN 13592, an adult male from "Finca La Planada," 5 km by road from caserío Chucunés, Municipio de Ricuarte, Departamento de Nariño, Colombia, 1970 m, obtained by Pedro M. Ruiz, 23 November 1982.

Paratypes. — IND-AN 1439-40, Reserva Natural La Planada, El Ondón, 1700 m; IND-AN 1458-59, 1468-69, 1641-42, PAB 170-71, Reserva Natural La Planada, 7 km S Chucunés, 1780 m (Depto. de Nariño, Colombia).

Diagnosis. — 1) skin on back bearing low warts, that of venter smooth; dorsolateral folds present, incomplete; 2) tympanum distinct, 26-35% eye length; 3) snout subacuminate in dorsal view, rounded to truncate in lateral profile; canthus rostralis sharp; snout short; 4) upper eyelid broader than IOD, not bearing pungent warts; no cranial crests; 5) vomerine odontophores, prominent, triangular in outline; 6) males with vocal slits; 7) first finger much longer than second; digital discs scarcely expanded, bearing ventral pads on all fingers; 8) no lateral fringes on fingers; 9) no ulnar tubercles or folds; 10) no tubercles or folds on heel or tarsus; 11) two metatarsal tubercles, inner oval, 3 times

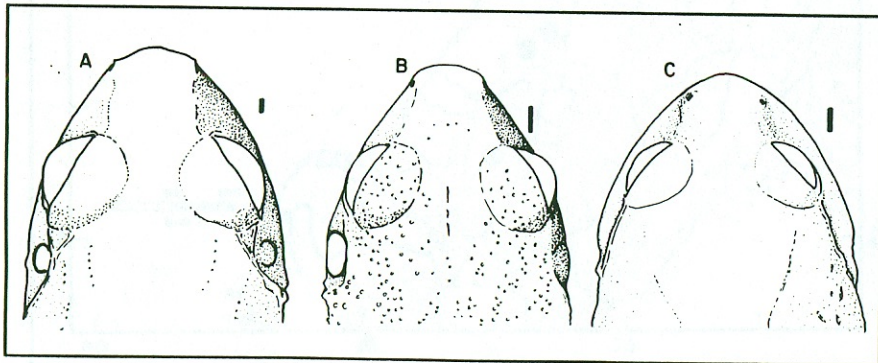


Fig. 6. Dorsal views of heads of *Eleutherodactylus*: (A) *E. babax*, ICNMHN 7920; (B) *E. cruralis*, AMNH 91579; (C) *E. latens*, ICNMHN 6346. Scale equals 1 mm.

size of rounded outer; no supernumerary plantar tubercles; 12) toes lacking lateral fringes and webbing; toes discs larger than those of fingers; 13) brown with darker brown blotches; posterior surfaces of thighs brown with cream flecks; throat and chest brown, venter cream; venter and concealed limb surfaces salmon in life; 14) adults large, one male 42.4 mm SVL, two females 46.8-48.7 mm SVL (but see remarks).

Eleutherodactylus babax is most similar to *E. dolops*, the only other larger species of the group. Each has relatively small outer metatarsal tubercles and narrow interorbital spaces. Unlike *E. dolops* (skin pustulate), *E. babax* has flattened warts on the posterior parts of the back and has dorsolateral folds. The digital disks of the hand of *E. babax* are scarcely expanded (obvious, albeit small, in *E. dolops*). The brown throat and chest of *E. babax* and the salmon colors in life also serve to distinguish it from *E. dolops* (throat and chest cream with brown spots or reticulation; in life, venter creamy yellow to pinkish tan).

Description. — Head as wide as body, wider than long; HW 37.7% SVL in one male, 39.1-43.1 (\bar{x} = 41.3, N = 10) % SVL in females; snout subacuminate to subovoid in dorsal view, angularly rounded in lateral profile; E-N 69.8% eye length in male, 71.0-87.0 (\bar{x} = 77.2, N = 10) % in females; no fleshy protuberance on snout of breeding male; nostrils protuberant, directed laterally; canthus rostralis distinct, slightly convex to straight; internarial space large (greater than E-N or IOD) (Fig. 6); loreal region slightly concave, sloping abruptly to lip; lips not flared; upper eyelid width 92.1% IOD in male, 100.0-137.1 (\bar{x} = 124.0, N = 10) % in females; numerous, small, non-pungent tubercles on upper eyelids; no cranial crests; tympanum distinct (only uppermost edge obscured by supratympanic fold), round in males (its length 34.9% eye length), higher than long in females (its length 27.5-32.8 [\bar{x} = 30.1, N = 10] % eye length); tympanum separated from eye by distance at least equal to length of tympanum; postriectal tubercles fused to form short ridge; choanae oval, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and slightly posterior to choanae, elevated, triangular in outline, bearing 10-14 teeth in a transverse row, separated on midline by a space equal to 1/3 an odontophore width; odontophores much larger than choanae; tongue longer than wide, its posterior border round, posterior 1/3 not adherent to floor of mouth; male with short vocal slits lateral to free portion of tongue.

Skin of head relatively smooth, that of back coarsely granular (low, flattened warts); some warts forming ridges (two dorsolateral folds on each side of body extending from shoulder to above groin, lower fold longer and apparently homologous to single dorsolateral fold seen in many other *Eleutherodactylus*); flanks weakly areolate or smooth; upper and lower surfaces of limbs smooth; skin of throat bearing longitudinal wrinkles in male, otherwise ventral surfaces smooth; discoidal folds well anterior to groin; no anal sheath or tubercles; skin below vent granular; no ulnar tubercles; palmar tubercle bifid, outer portion less distinct than larger median portion; thenar tubercle oval; no supernumerary palmar tubercles; subarticular tubercles longer than wide, non-conical; no lateral keels on fingers; fingers long and slender, first finger much longer than second (Fig. 1); tips of all fingers weakly swollen, but only III and IV bearing ventral pads (circumferential grooves evident). No nuptial pad on thumb of breeding male.

No tubercles or folds on heel or tarsus; inner metatarsal tubercle elevated, its length $2\frac{1}{2}$ to 3 times its width, 2-3 times size of round, subconical outer; no supernumerary plantar tubercles; subarticular tubercles longer than wide, non-conical (but more pungent than those of fingers); no webbing or lateral keels on toes; toes long and slender, bearing narrow discs (apically rounded) with circumferential grooves evident distally; digital discs of toes larger than those of outer fingers; heels of flexed hind legs overlapping; shank 57.6% SVL in male, 57.9-65.4 (\bar{x} = 62.2, N = 10) % in females.

Dorsum gray to brown with darker brown spots and stripes, edged with pale gray or not; limbs brown with darker brown bars, bars on shank oblique; posterior surfaces

Thighs brown with cream flecks; groin brown with small cream spots; no canthal-supratympanic stripe; lip bars dark brown, edged ventrally with cream; throat and chest brown with cream spots; lower venter and undersides of thighs cream; ventral surfaces of shanks brown with large cream spots; anal triangle obscure.

In life, *E. babax* is yellowish-olive to reddish-brown above with dark brown markings (outlined in greenish-cream or not); flanks, anterior and posterior surfaces of thighs, concealed surfaces of shanks, feet, and forearm dull orange to salmon; brown spots on flanks; brown reticulation on concealed surfaces of thighs; throat and chest brown; salmon spots on chest; venter and undersides of thighs salmon; iris bronze above with dark brown spots and brown horizontal streak, black below.

Measurements of holotype in mm. — SVL 42.4; shank 24.4; HW 16.0; head length 13.7; chord of head length 15.9; upper eyelid width 3.5; IOD 3.8; tympanum length 2.2; eye length 6.3; E-N 4.4.

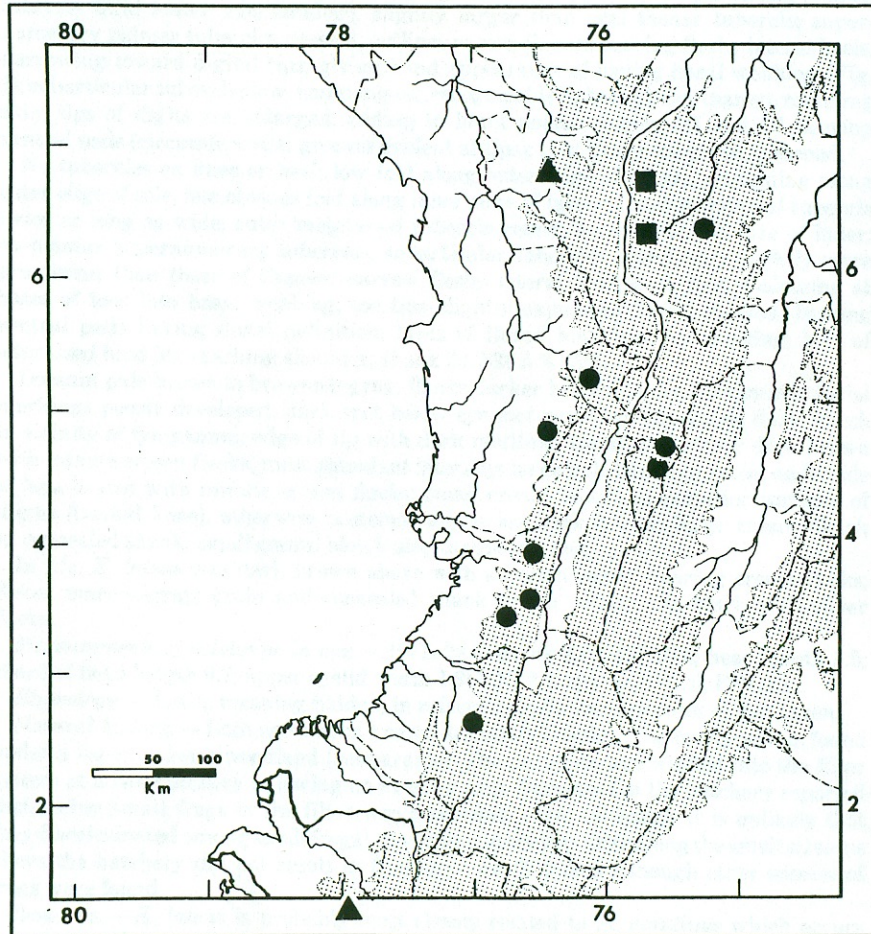


Fig. 7. Map of western Colombia showing distribution of *Eleutherodactylus babax* (triangles), *E. latens* (squares), and *E. mantipus* (circles). Areas above 1500 m stippled.

Etymology. — Greek, a babbler; used as a noun in apposition.

Natural history. — All females from the vicinity of the type-locality were obtained in dense forest at night where they were found sitting on the forest floor. The holotype was collected during the day while it was calling in a bush. Pedro Ruiz described the call as high pitched (“cheep, cheep, cheep”) and noted that many were heard calling in November in dense vegetation.

At the type-locality, females measuring 36.9-40.2 mm SVL (N = 4) are juveniles (oviducts straight, not convoluted) whereas those measuring 43.6-46.6 mm SVL (N = 4) exhibit some convolution to the oviduct as well as slightly enlarged ova.

Remarks. — Two specimens are referred to *E. babax* even though they are small. ICNMHN 16595 and 16597 were collected in northwestern Colombia [Departamento Antioquia, Municipio de Frontino, Nutibara-La Blanquita rd, km 16.5-18.0, 1900-1940 m]. ICNMHN 16597 is a male 34.7 mm SVL but lacks vocal slits; initially, I presumed that it was immature. ICNMHN 16595 is an adult female but is only 41.5 mm SVL. These two frogs differ from topotypic *E. babax* in that all fingers bear circumferential grooves (rather than only the outer fingers) and may have more pointed finger tips (difficult to assess, owing to some desiccation).

A recently collected specimen (ICNMHN 20713, juvenile female, 36.0 mm SVL, Colombia: Cauca: Municipio El Tambo, vereda La Playa, Rio San Joaquin, 1200-1500 m [not mapped on Fig. 7]) is like the topotypes in size. This specimen was collected at a finca (La Playa or La Primavera) on the trail from El Tambo to the Rio San Micay. This locality may be the same site called “El Tambo, La Costa” by Kurt Von Schneidern who obtained specimens of *E. mantipus* there.

Eleutherodactylus latens New Species

Holotype. — ICNMHN 6346, an adult female from Boqueron, Serranía Las Valdías, Municipio de Medellín, Departamento de Antioquia, Colombia, 2800-3000 m, obtained by Pedro M. Ruiz on 9 Agosto 1978.

Paratype. — ICNMHN 8610, from El Yermal, 6 km N Belmira, Municipio Belmira, Departamento de Antioquia, Colombia, 2720 m.

Diagnosis. — 1) skin of dorsum smooth except for low warts on lower back, that of venter smooth, dorsolateral folds incomplete; 2) tympanum concealed; 3) snout round in dorsal view, sloping in lateral profile; canthus rostralis rounded; 4) upper eyelid narrower than IOD; no cranial crests; 5) vomerine odontophores large, arched; 6) males not known; 7) first finger longer than second; fingers lacking discs, ventral pads evident on outer fingers; 8) fingers bearing fleshy lateral keels; 9) ulnar fold present; 10) no heel tubercles; indefinite inner and outer tarsal folds; 11) two metatarsal tubercles, inner oval, twice size of round outer; no supernumerary plantar tubercles; 12) toes with fleshy lateral fringes; toe tips with slightly expanded discs; 13) dorsum brown, darker laterally; venter dark brown with pale flecks; cream blotch in groin; 14) adults small, two adult females 27.1-28.5 mm SVL.

Eleutherodactylus latens is similar to *E. mantipus* and *E. nigrovittatus* in habitus (all small frogs with broad, arched vomerine odontophores and very broad interorbital spaces) but is distinguished most easily by virtue of having a concealed tympanum (Fig. 5), by having lateral keels/fringes on the digits, by having ulnar folds, and by virtue of having low inner and outer tarsal folds.

Description. — Head narrower than body, wider than long; HW 37.2-38.4 % SVL; snout round in dorsal view, sloping in lateral profile; E-N 67.9-75.0 % eye length; nostrils slightly protuberant, directed dorsolaterally; canthus rostralis rounded, concave (Fig. 6); loreal region concave, sloping gradually to lips; lips weakly flared; upper eyelid narrow, its width 48.2-67.9 % IOD; upper eyelid bearing 2-3 small, non-pungent tubercles; no

cranial crests; tympanum concealed beneath skin; supratympanic fold distinct; postri-
 tubercles small; skin on face spiculate, that on rest of head finely granular; choanae
 round, not concealed by palatal shelf of maxillary arch; vomerine odontophores large,
 posterior to choanae, width of each odontophore about 4 times width of a choana, arched,
 bearing a row of 8-11 teeth (Fig. 5); odontophores separated by a distance equalling
 one-half width of a choana; tongue longer than wide, its posterior border not notched,
 posterior 2/5 not adherent to floor of mouth.

Skin of dorsum essentially smooth except for low flat warts (especially evident on
 lower back); low occipital folds reaching level of scapulae; dorsolateral folds extending
 from temporal region to a point midway between sacrum and groin; flanks more warty
 than dorsum, warts low, elongate; skin of throat and venter smooth; discoidal folds not
 evident; no anal sheath; ulnar fold present, reaching from elbow to posterolateral edge
 of palmar tubercle; some portions of ulnar fold higher than others, giving impression
 of three elongate subconical warts (less pungent in holotype than in paratype); palmar
 tubercle bifid (outer lobe smaller), slightly larger than oval thenar tubercle; super-
 numerary palmar tubercles present, outlines vague; fingers bearing fleshy lateral keels,
 narrowing toward digital tips, giving hand appearance of having basal webbing (Fig.
 1); subarticular tubercles low, non-pungent, recognizable by being paler than surrounding
 skin; tips of digits not enlarged, ending in blunt points; fingers III and IV bearing
 ventral pads (circumferential grooves evident at tips); first finger longer than second.

No tubercles on knee or heel; low fold along outer edge of tarsus, continuing along
 outer edge of sole, less obvious fold along inner edge of tarsus; inner metatarsal tubercle
 twice as long as wide; outer metatarsal tubercle round, non-conical, 1/2 size of inner;
 no plantar supernumerary tubercles; subarticular tubercles round, only slightly more
 prominent than those of fingers; narrow fleshy lateral fringes on toes, coalescing at
 bases of toes into basal webbing; toe tips slightly expanded, feebly pointed, bearing
 ventral pads having distal definition; heels of flexed hind legs not meeting; heel of
 adpressed hind leg reaching shoulder; shank 34.7-36.5 % SVL.

Dorsum pale brown to brownish-gray, flanks darker brown; limbs dark brown; facial
 markings poorly developed, dark spot below eye (not reaching lip), vague dark blotch
 in vicinity of tympanum; edge of lip with dark mottling; throat and venter dark brown
 with minute cream flecks, most abundant laterally; large pale blotch in groin; underside
 of legs brown with minute cream flecks; small cream blotch on posterior surfaces of
 thighs (behind knee), otherwise posterior thighs are dark brown; large cream blotch
 on concealed shank; small cream blotch atop tarsus and foot.

In life, *E. latens* was dark brown above with a brown venter bearing cream flecks;
 throat maroon-gray; groin and concealed shank lemon yellow; iris black with silver
 flecks.

Measurements of holotype in mm. — SVL 28.5; shank 9.9; HW 10.6; head length 8.5;
 chord of head length 9.7; upper eyelid width 1.9; IOD 2.8; eye length 2.8; E-N 2.1.

Etymology. — Latin, meaning hidden, in reference to the secretiveness of this taxon.

Natural history. — Both specimens known are adult females. The holotype was found
 under a log in a dense woodland (subparamo). The paratype was washed into the filter
 system at a fish hatchery following an evening rain. Personnel at the hatchery reported
 that seeing small frogs in the filter was a common event (although it is unlikely that
 they discriminated among small frogs). Searching in the leaf litter along the small streams
 above the hatchery did not result in finding more *E. latens* although other species of
 frogs were found.

Remarks. — *E. latens* is probably most closely related to *E. mantipus* which occurs
 at somewhat lower elevations from central Antioquia south in western Colombia.

Described Species

Recent summaries are available for *E. dolops* and *E. elassodiscus* (Lynch and Duellman,
 1980) and for *E. nigrovittatus* (Lynch, 1980) and no significant additional information
 has been found for those species. *Eleutherodactylus mantipus* is less well documented
 in the literature. Lynch (1973b) provided a detailed description of the holotype but there
 are now many specimens known from western Colombia (Fig. 7). A revised diagnosis
 is presented below:

Eleutherodactylus mantipus (Boulenger)

Diagnosis. — 1) skin of dorsum smooth with scattered small warts, that of venter smooth;
 dorsolateral folds present; 2) tympanum visible, superficial, 1/3-3/5 eye length; 3) snout
 subacuminate in dorsal view, round in lateral profile; canthus rostralis round; 4) upper
 eyelid width narrower than IOD; no cranial crests; 5) vomerine odontophores long, arched,
 posterior to choanae; 6) males lacking vocal slits; nuptial pads present in males; males
 with fleshy ridge along upper lip in breeding condition; 7) first finger longer than second;
 fingers lacking disks and pads; 8) fingers lacking lateral fringes; 9) no ulnar tubercles
 or fold; 10) outer edge of tarsus bearing series of small tubercles; no tubercles on heel
 or inner edge of tarsus; 11) two metatarsal tubercles, inner oval, 2-3 times size of round
 outer; no supernumerary plantar tubercles; 12) no fringes on toes; toes with narrow
 disks and ventral pads; 13) brown above and below (venter somewhat paler); posterior
 surfaces of thighs brown with cream flecks; 14) adults moderate-sized, males 23.6-26.3
 ($\bar{x} = 24.7 \pm 0.3$, $N = 8$) mm, females 28.2-33.7 ($\bar{x} = 30.2 \pm 0.4$, $N = 16$) mm SVL.

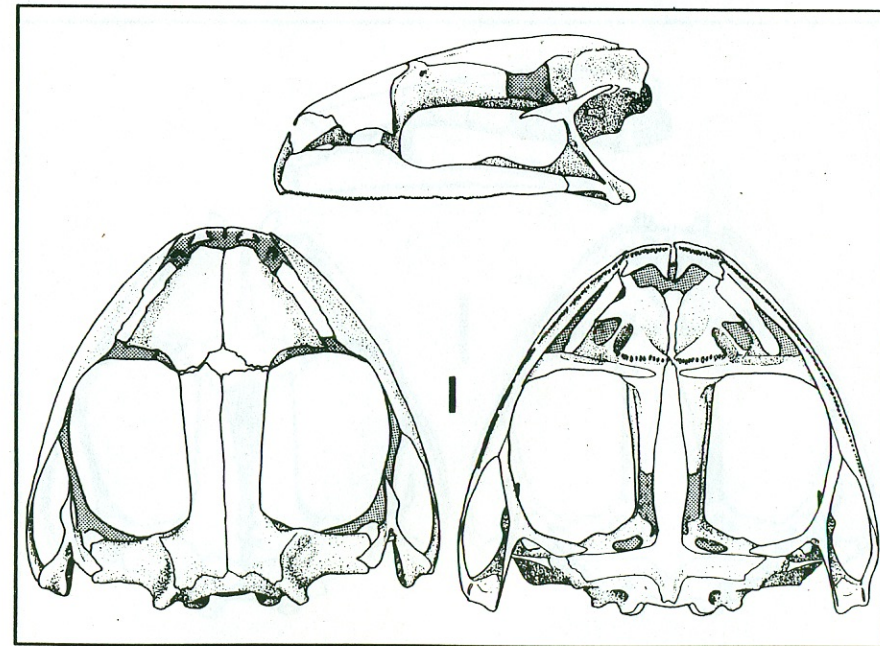


Fig. 8. Cranium of *Eleutherodactylus dolops*, KU 165866. Scale equals 2 mm.

Proportions. — Males (N = 12): HW 38.9-46.6 ($\bar{x} = 42.1 \pm 0.5$) % SVL; upper eyelid 50.0-78.6 ($\bar{x} = 67.5 \pm 2.5$) % IOD; tympanum length 32.7-58.6 ($\bar{x} = 40.7 \pm 2.1$) % eye length; E-N 79.3-96.4 ($\bar{x} = 88.0 \pm 1.8$) % eye length; shank 46.0-52.1 ($\bar{x} = 48.7 \pm 0.5$) % SVL. Females (N = 16): HW 40.8-45.0 ($\bar{x} = 42.9 \pm 0.3$) % SVL; upper eyelid 52.6-80.6 ($\bar{x} = 65.1 \pm 1.9$) % IOD; tympanum length 37.1-45.7 ($\bar{x} = 40.8 \pm 0.7$) % eye length; E-N 75.6-94.4 ($\bar{x} = 85.4 \pm 1.4$) % eye length; shank 45.1-50.3 ($\bar{x} = 48.1 \pm 0.3$) % SVL.

In life, *E. mantipus* is dark brown to gray with darker markings on the limbs and dorsum. Suprainguinal spots, if visible, are black. The upper arm may be more pale than the rest of the dorsal surfaces. The ventral surfaces are brown to dark gray (throat darkest) with or without white flecks. The posterior surfaces of the thighs are black with white flecks. The postrectal tubercles (ridge) are orange. The iris is bronze with black flecks.

Distribution. — Cloud forests (1490-2100 m) of the Cordillera Central and Cordillera Occidental of Colombia (Fig. 7). The distribution area appears to be discontinuous with one part found on the western flanks of the Cordillera Central of Colombia from the Los Nevados region north to the Medellin region (south and east of the Rio Medellin) and the other on the western flanks of the Cordillera Occidental from the headwaters of the Rio San Juan south to the Farallones de Cali. A single record is available from the eastern flanks of the Cordillera Occidental (UV 7019, from the Bosque San Antonio, near Dapa, Depto. Valle del Cauca). There are two records from slightly south of the Farallones de Cali (Depto. Cauca) but the locality data are imprecise and the specimens are not well-preserved. To the north and west of the Rio Medellin in Depto. Antioquia, at comparable altitudes, one finds *E. latens* (Fig. 7).

OSTEOLOGY AND CRANIAL ANATOMY

At least one specimen of each species was dissected in order to determine the disposition of the mandibular ramus of the trigeminal nerve relative to the jaw adductors. In every case, the mandibular ramus passed lateral to the *Musculus levator posterior mandibulae subexternus* (condition "S" of Starrett, 1968).

There is considerable heterogeneity among the skulls of the species now placed in the *discoidalis* Group. This heterogeneity may well signal that the group is paraphyletic. In anticipation of recognition below of the various components of the *discoidalis* group as three species groups, the treatment of crania will be subdivided into accounts for three subgroups.

Subgroup I (*babax* and *dolops*) (Fig. 8)

The skulls of these two species differ most obviously from those of the other subgroups in the apparent sizes of the nasal bones (Fig. 8). The nasals of these two species are large and in broad median contact. Furthermore, the nasals are either in broad contact with the anterior ends of the frontoparietals or are very narrowly separated from the frontoparietals. The nasals are made to seem even larger by the fact that the braincase is relatively narrow (contrast with frogs of the *nigrovittatus* subgroup, Fig. 10-11). The edges of the frontoparietals are approximately parallel (or they are slightly broader anteriorly than posteriorly). The cristae paroticae are broad and narrow, contributing to the impression of a narrow central region to the skull with a massive nasal region. The frontoparietals are not fused to the prootics.

The palatal shelf of the premaxilla is relatively narrow (in comparison with frogs of the *nigrovittatus* subgroup). The vomers are large and relatively narrowly separated.

The odontophores are triangular in outline and lie posteromedial to the choanal opening. The alae and cultriform process of the parasphenoid are long and slender and lie perpendicular to one another. The anterior end of the cultriform process is pointed and reaches to between the palatine bones. The distal ends of the parasphenoid alae are "overlapped" by the median rami of the pterygoids. The maxillae do not bear obvious processes in the area of contact with the pterygoids.

The *pars facialis* of the maxilla is only modestly deep. The quadratojugals are comparatively slender. The otic and zygomatic rami of the squamosals are approximately equal in length. The ascending process of the squamosal is directed anterodorsally at an angle of 50-55 degrees. The skulls of these two species are moderately elevated (skull height 41-44 % skull length). The posterior portion of the skull is more elevated than the anterior portion in each species but the greater elevation is most obvious in *dolops*.

Subgroup II (*cruralis* and *discoidalis*) (Fig. 9)

The nasals in these two species are similar in size and in terms of the articulations with adjacent bones. The anteromedial portions of the nasals are closely approximated and as one proceeds caudad, there is greater space between the nasal bones. The nasal bones are widely separated from the frontoparietals exposing much of the sphenethmoid. The braincase does not appear as wide as in *babax* or *dolops* but the braincase of *discoidalis* appears to be broader than that of *cruralis*. A relatively large, albeit narrow, fontanelle is exposed between the frontoparietals in *discoidalis* (Fig. 9) whereas the frontoparietals in *cruralis* conceal the fontanelle. The cristae paroticae are more stocky in these species

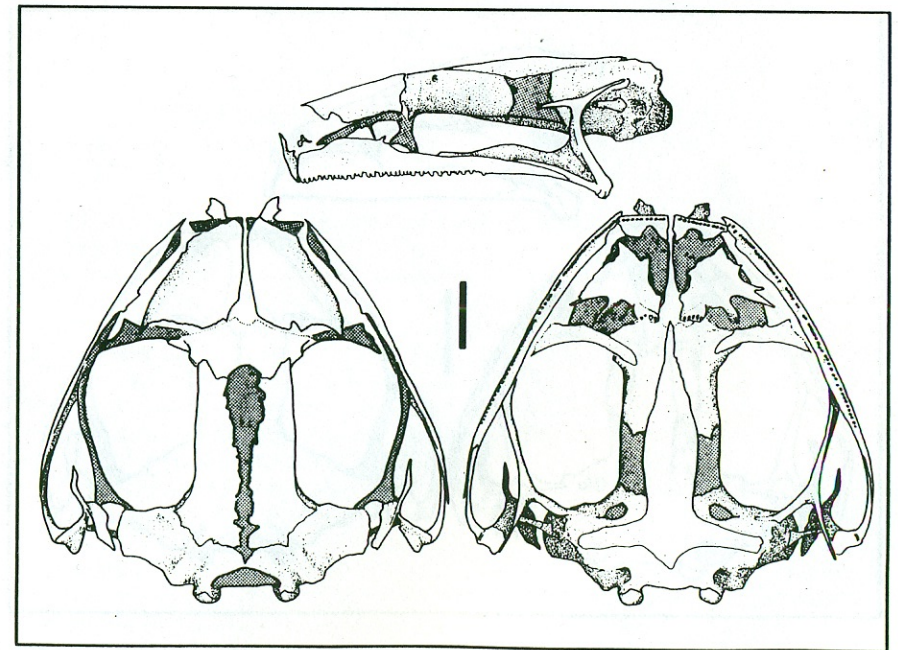


Fig. 9. Cranium of *Eleutherodactylus discoidalis*, KU 206433. Scale equals 2 mm.

in the former subgroup and the epiotic eminences are less prominent. The frontoparietals and prootics are fused in *cruralis* (but not in *discoidalis*), but the fusion is secondary because traces of sutures are apparent.

The palatal shelf of the premaxilla is relatively deep and is dissected. The alary processes of the premaxillae of *discoidalis* are directed very slightly anterodorsally whereas those of *cruralis* are directed slightly posterodorsally (as in most species of *Eleutherodactylus*). The vomers are smaller than those of frogs in subgroup I and they are more widely separated medially. The vomers of *cruralis* are very much like those of *babax* or *dolops* except that there is less bone anteromedially, the odontophores are smaller, and the odontophores lie less posteriorly in *cruralis*. The odontophores in *discoidalis* are low structures that lie relatively anteriorly (relative to the location of the choanae). Contrasting the positioning of the vomers of *discoidalis* with those in other species leads to the idea that the vomers of *discoidalis* are rotated some 30 degrees (contrast Fig. 9 and 8). The alae and cultriform processes of the parasphenoid are less slender and shorter than in frogs of subgroup I. The cultriform processes are long (as in subgroup I), separating the palatine bones but, they are broader in the region of mid-orbit. The parasphenoid alae are not perpendicular to the cultriform process (deflected slightly posteriorly). Their shortness (or the slight posterior deflection) results in little or no "overlap" between the alae and the median rami of the pterygoids even though the median rami are long and slender. The maxilla does not bear an enlarged flange at the point of contact with the pterygoid.

The *para facialis* of the maxilla is not deep and the quadratojugals are slender bones. The otic ramus of the squamosal is longer than the zygomatic ramus. Both rami are slender. The ascending process of the squamosal is more vertical in these species than in those of subgroup I and forms an angle with the maxillary arch of 60-70 degrees. The skulls of *cruralis* and *discoidalis* appear to be flatter than those of other species of this group. The skulls are very moderately elevated (posterior height 33-40 % skull length) but the posterior part of the skull is only slightly more elevated than is the anterior portion of the skull.

Subgroup III (*elassodiscus*, *latens*, *mantipus*, and *nigrovittatus*)
(Figs. 10-11)

The nasal bones in these species appear to be small. The bones are shaped much like those of the frogs in subgroup II (separated medially but more closely approximated anteriorly than posteriorly) in three species (*elassodiscus*, *mantipus*, and *nigrovittatus*) but in *latens* the nasals have more rounded medial borders so that the anterior portions are not more closely approximated than the posterior portions. The nasals are widely separated from the frontoparietals in *elassodiscus* and *mantipus* but the nasals either contact the frontoparietals at a single point by way of a posterior flange (*nigrovittatus*) or are narrowly separated from the frontoparietals (*latens*). The nasals in *latens* are rounded posteriorly (as in *mantipus*) but are less separated from the frontoparietals than are those of *mantipus* (Fig. 8). In all four species, the anterior ends of the frontoparietals are transverse. In each of these species, the braincase appears relatively broad. The braincase appears to be shortest in *latens* and *nigrovittatus*. The lateral margins of the braincase are approximately parallel in *elassodiscus* and *latens* with a slight swelling of the braincase at mid-orbit. The swelling is more apparent in *nigrovittatus* (Fig. 11) than in *elassodiscus* or *latens*. In *mantipus*, the braincase is somewhat wider anteriorly than posteriorly. The cristae paroticae are short and thick in all four species and are more robust than those in *cruralis* and *discoidalis* (subgroup II). The epiotic eminences are relatively prominent. The frontoparietals and prootics are fused but the sutures are partially visible in most specimens.

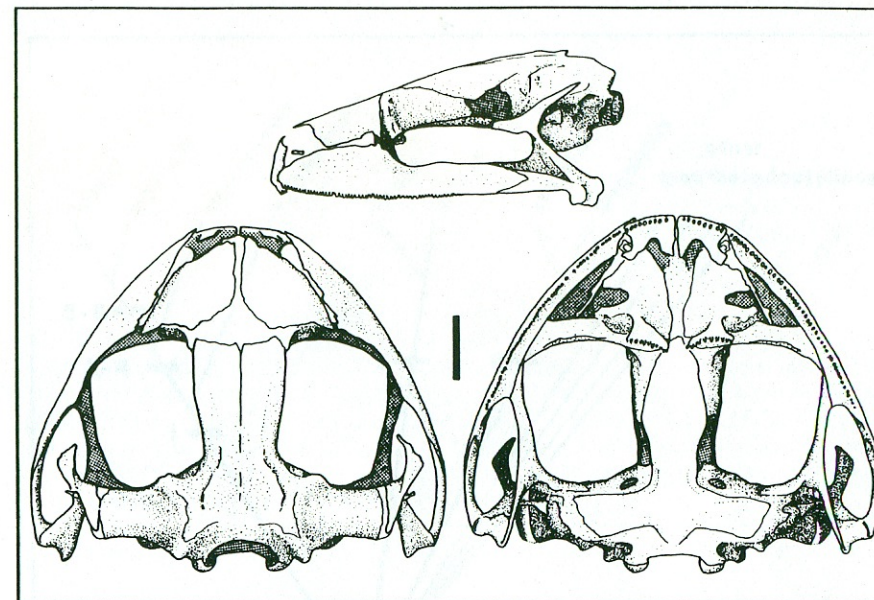


Fig. 10. Cranium of *Eleutherodactylus mantipus*, KU 211060. Scale equals 2 mm.

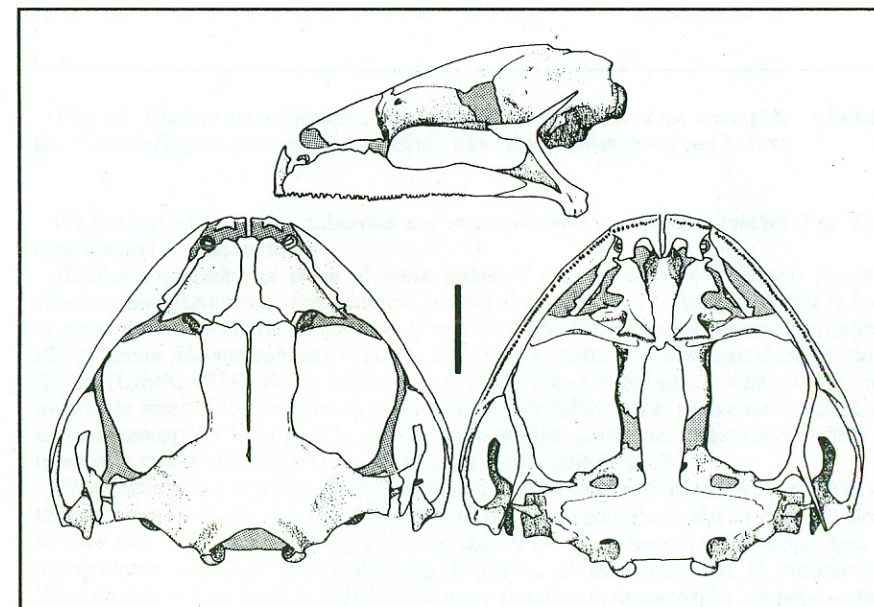


Fig. 11. Cranium of *Eleutherodactylus nigrovittatus*, USNM 222807. Scale equals 2 mm.

In all four species, the palatal shelf of the premaxilla is broad and deeply dissected. The vomers are longer than wide and are separated medially. The odontophores are prominent structures and lie well posteromedial to the choanae. The odontophores appear to be displaced laterally in *elassodiscus* whereas in the other three species the odontophores are relatively narrowly separated and even become arch-like in *latens* and *mantipus*. In each of these species, the odontophores overlay the median portions of the palatines. The alae and cultriform processes of the parasphenoids are relatively short and stocky. The cultriform process is not pointed anteriorly and extends to just between the palatines (in *latens* and *mantipus* the median ends of the vomerine odontophores overlay the anterior end of the cultriform process). The parasphenoid alae are deflected slightly posteriad. The median rami of the pterygoids "overlap" the parasphenoid alae in all four species (the overlap is broad only in *latens*), but the pterygoid rami contact the prootic well anteriorly of the parasphenoid alae in *nigrovittatus* whereas the bones are closely approximated in the other three species. In all four species, the maxilla bears a prominent flange at the point of contact between the maxilla and pterygoid.

The *pars facialis* of the maxilla is moderately deep in each species and the quadratojugal is relatively stocky in *elassodiscus*, *mantipus*, and *nigrovittatus*. In *latens*, the quadratojugal is greatly enlarged. In each species, the otic ramus of the squamosal is longer than the zygomatic ramus. In all except *latens*, the anterior tip of the zygomatic ramus points toward the nasal bones, whereas in *latens* the tip points toward the posterior third of the maxilla. The zygomatic ramus of the squamosal in *latens* is expanded ventrally. The ascending process of the squamosal is inclined anteriorly at an angle of 45-50 degrees. The skulls of each of the frogs in this subgroup are depressed anteriorly (much greater elevation posteriorly than anteriorly). The flattening of the snout is most pronounced in *latens* and least evident in *elassodiscus*. The skulls are moderately elevated (skull height 43-47 % skull length) in *elassodiscus*, *mantipus*, and *nigrovittatus*.

RELATIONSHIPS

My previous studies of these frogs are of limited value because, although characters were used to define groups, no distinction was made between derived and primitive character states. Perusing the claims made in the literature, no character emerges that serves as a synapomorphy for the group. In the absence of such a synapomorphy, no defensible claim of monophyly for the *discoidalis* Group (*sensu* Lynch, 1976, or Lynch and Duellman, 1980) can be made.

Using other eleutherodactyline frogs as the out-group, some features appear to define monophyletic units within the *discoidalis* Group of Lynch and Duellman (1980). The following are proposed as synapomorphies:

- (1) A large sphenethmoid extending anteriorly to a point anterior to the nasals (Fig. 10-11): *E. elassodiscus*, *E. latens*, *E. mantipus*, and *E. nigrovittatus*.
- (2) Arched vomerine tooth rows (Fig. 3, 10-11): *E. latens*, *E. mantipus*, and *E. nigrovittatus*.
- (3) Tubercles/folds along outer edge of tarsus: *E. latens*, *E. mantipus*, and *E. nigrovittatus*.
- (4) Fleshy supralabial ridge in males (see Lynch, 1980:300): *E. mantipus* and *E. nigrovittatus*; occurrence here predicted for *E. latens*.
- (5) Vomer overlays cultriform process of parasphenoid (Fig. 10): *E. latens* and *E. mantipus*.
- (6) Enlarged quadratojugal and large pterygoid process on maxilla (Fig. 10): *E. latens* and *E. mantipus*.
- (7) Very large nasal bones (Fig. 8): *E. babax* and *E. dolops*.

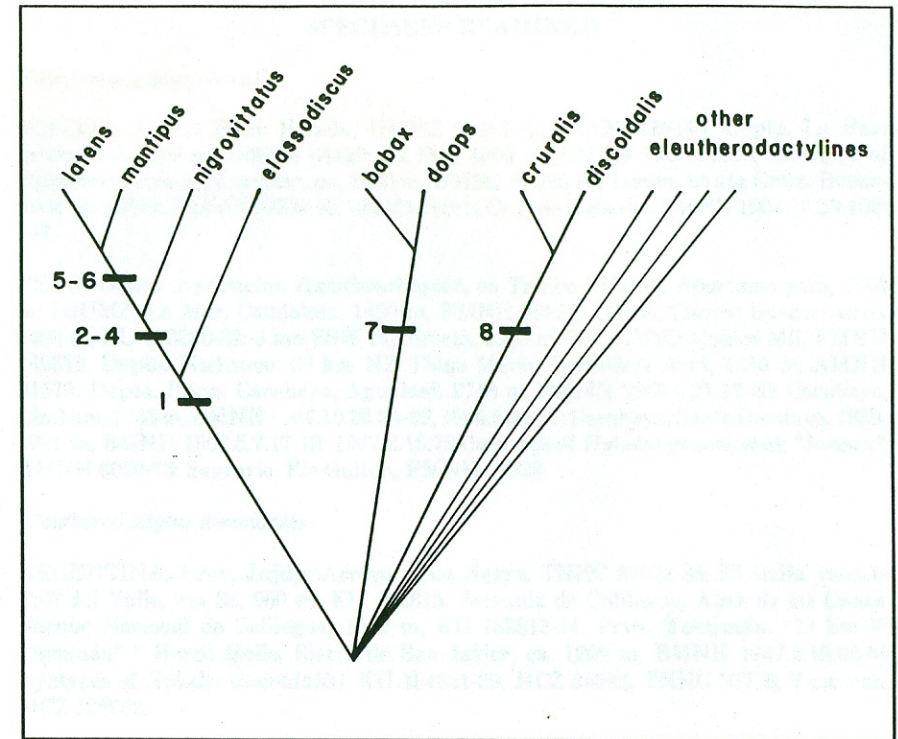


Fig. 12. Cladogram expressing the hypothesis of relationships among the species of the *discoidalis* group (*sensu* Lynch, 1976). Synapomorphies discussed in text.

(8) Conical subarticular tubercles and supernumerary plantar tubercles (Fig. 2): *E. cruralis* and *E. discoidalis*.

Similar expression of some of these putative synapomorphies is known for other eleutherodactyline frogs. For example, a state similar to that termed (1) above is found in some members of the *E. gollmeri* Group (subgenus *Craugastor*) as well as in toads of the genus *Rhamphophryne* (Trueb, 1971) and members of the *Leptodactylus fuscus* Group (Lynch, 1971). Strict adherence to some rules of out-group comparison could invalidate most of the putative synapomorphies identified here. I have used these traits as synapomorphies because I believe that the similar expressions elsewhere reflect our ignorance rather than evidence falsifying my hypothesis (Fig. 12).

These synapomorphies are compatible and specify a set of relationships (Fig. 12) among these species such that three species groups must be recognized: the *discoidalis* Group for the two southern species, the *dolops* Group for *E. babax* and *E. dolops*, and the *nigrovittatus* Group for *E. elassodiscus*, *E. latens*, *E. mantipus*, and *E. nigrovittatus*. Whereas one might quarrel with one or more putative synapomorphy, at present there are no reliable characters which contradict this arrangement.

BIOGEOGRAPHY

The *nigrovittatus* Group is of some biogeographic interest because while three species are Andean (moderate-intermediate altitudes), *E. nigrovittatus* (within the clade) is a species widely distributed in the lowlands of the Upper Amazon basin, providing the sort of evidence Lynch (1987) suggested would be expected if Andean groups had dispersed into the lowlands. The distributional picture seen in another eleutherodactyline clade from northwestern South America, the *E. sulcatus* Group (Lynch, 1981a, 1986b) is markedly distinct. There, the lowland species (*E. sulcatus*) is the sister species to the three highland species.

The only data sets for the Colombian cordilleras are those for these two groups of species and the two cladograms are not congruent. Work in progress on other cloud forest species may enable us to decide which cladogram is the more general (assuming that a general area cladogram is to be found). The *sulcatus* Group is only partially studied (Lynch, 1986b) and contains several other species found in close proximity to the Andes (Lynch, 1986a). The subunit that has been studied is monophyletic within the group and includes species on all three Colombian cordilleras. The *nigrovittatus* Group appears to be complete, at least in terms of lacking a representative on the Cordillera Oriental of Colombia where fieldwork in the past decade has revealed a moderately large eleutherodactyline fauna.

The patterns of distributions seen in the two species groups are similar in that in each case there is a lowland Amazonian species and three Andean species. Further, there is no evidence of sympatry among the species of either clade although the failure to find *E. cadenai* and *E. ruizi* (*sulcatus* Group) sympatric on the western flanks of the Cordillera Occidental of Colombia may be temporary. Sister species are either separated altitudinally (*E. latens* and *E. mantipus*) or occur on separate cordilleras with pronounced geographic separations (most cases). The pair of data sets provides concrete contradictions/corroborations of the opinions voiced by Lynch (1979, 1981b) and Lynch and Duellman (1980:65) to the effect "... that most species ... have their closest allies in adjacent (or the same) altitudinal strata."

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SPECIMENS EXAMINED

Eleutherodactylus cruralis

BOLIVIA: **Depto. Beni:** Huachi, UMMZ 58987 (2), 58988, 135343. **Depto. La Paz:** Ixiamas, ca. 500 m, UMMZ 64120; La Paz, 4000 m, BMNH 1947.2.15.70 (holotype of *Hylodes cruralis*); Tumupasa, ca. 1000 m, UMMZ 58985-86. **Depto. Santa Cruz:** Buenavista, ca. 400 m, UMMZ 66609-10, 135341; Santa Cruz de la Sierra, BMNH 1904.10.29.102-107.

PERU: **Depto. Ayacucho:** Huanhuachayocc, on Tambo-Valle de Apurimac path, 1650 m, LSUMZ; La Mar, Caudalosa, 1400 m, FMNH 39801. **Depto. Cuzco:** Buenos Aires, 2400 m, KU 173230-32; 3 km SSW Pillahuata, 2900 m, KU 173233; Quince Mil, FMNH 140312. **Depto. Huánuco:** 30 km NE Tingo Maria, Cordillera Azul, 1330 m, AMNH 91579. **Depto. Puno:** Carabaya, Agualani, 2743 m, BMNH 1905.5.31.17-20; Carabaya, Limbani, 2743 m, BMNH 1904.10.26.94-99, 1905.5.21.21; Carabaya, Santo Domingo, 1829-1981 m, BMNH 1907.5.7.17-18, 1947.2.15.72 (holotype of *Hylodes granulosis*); "Juliaca", AMNH 6060-73; Sagrao, Rio Guitun, FMNH 40328.

Eleutherodactylus discoidalis

ARGENTINA: **Prov. Jujuy:** Arroyo Agua Negra, TNHC 37078-85; El Indio, road to Tafi del Valle, km 38, 960 m, KU 182815; Serranía de Calilegua, Abra de las Canas, Parque Nacional de Calilegua, 1550 m, KU 182813-14. **Prov. Tucumán,** "13 km W Tucumán" = Horco Molle, Sierra de San Javier, ca. 1200 m, BMNH 1947.2.15.63-65 (syntypes of *Hylodes discoidalis*), KU 154521-29, MCZ 35583, TNHC 36776; Tucumán, MCZ 126692.

Eleutherodactylus mantipus

COLOMBIA: **Depto. Antioquia:** Santa Rita, 1490 m, LACM 47131-33, 47137-38; Represa Santa Rita, 6 km (airline) SSW Alejandria, 1930 m, AMNH 104409. **Depto. Cauca:** Mpio. El Tambo, La Costa, 1000 m, KU 138722; Mpio. El Tambo, Rio Michengue, 800 m, KU 138723. **Depto. Chocó:** Cerro Torrá, 1625-1700 m, UV 6696-99; Cerro Torrá, east slope, 1900-1940 m, UV 6700-06, northeast slope, 1800-1940 m, UV 6707-13; ridge between Rio Negro and Cerro Torrá, 1625 m, UV 6714-15. **Depto. Quindío:** Mpio. Calarcá, vereda San Julian, vic. Hda. Brillante, 2030-2100 m, ICNMHN 9161; Mpio. Finlandia, vereda El Roble, Bosque Resera de Bremen, 2050 m, ICNMHN 9162-73. **Depto. Risaralda:** Mpio. Pueblo Rico, La Selva (Pacific side), 1700 m, FMNH 54371. **Depto. Valle del Cauca:** Mpio. Dagua, [Cerro] San Antonio, 1770 m, BMNH 1947.2.17.46 (holotype), UV 5898, ca. 4 km W San Antonio, LACM 109652; Mpio. Dagua, km 18, Cali-Buenaventura road, 2070 m, KU 143970; Mpio. Dagua, Tokio-Antenna Telecom (S of Quereamal), 2050 m, UV 7426-27; Mpio. Darien, Las Campanas, Lago Calima, 1580 m, ICNMHN 4945-46; UV 5667-83, 5684-93, 5695; Mpio. Yumbo, Dapa, Bosque San Antonio, UV 7019.

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