INTRAGENERIC RELATIONSHIPS OF MAINLAND *ELEUTHERODACTYLUS* II. A REVIEW OF THE *ELEUTHERODACTYLUS SULCATUS* GROUP

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Resumen

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Se tratan nueve especies dentro del grupo *Eleutherodactylus sulcatus*, incluyendo una nueva especie que se describen. Las ranas de este grupo se encuentran en los bosques nublados de Colombia y Ecuador como en tierras bajas del occidente de la cuenca amazónica (Brasil, Colombia, Ecuador, y Perú) y sobre la frontera de Colombia y Panamá. De un análisis cladístico (basado en morfología craneal), resulta un cladograma casi completamente resuelto. Las especies de los bosques nublados forman un clado dentro del grupo de especies. Todas las parejas de especies hermanas son alopátricas pero alguna paralogía biogeográfica sugiere que la diversificación inicial andina antecede la geografía andina actual.

Palabras claves: Amphibia, Leptodactylidae, biogeografía, cladística, osteología.

Abstract

Nine species are recognized in the *Eleutherodactylus sulcatus* group, including one species described as new. Frogs of this species group are distributed in cloud forests of Colombia and Ecuador as well as at lower elevations in the western Amazon basin (Brasil, Colombia, Ecuador, and Peru) and along the frontier between Colombia and Panama. A cladistic analysis (based on cranial morphology) results in a nearly fully resolved cladogram. The cloud forest species form a clade within the species group. All pairs of sister species are allopatric but some biogeographic paralogy suggests that initial andean diversification of this clade antedates the present Andean geography.

Key words: Amphibia, Leptodactylidae, biogeography, cladistics, osteology.

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Introduction

Two decades ago, **Lynch** (1975) reviewed the "broad-headed" eleutherodactylines, then characterized by the possession of heads about 50% as wide as SVL and by the presence of cranial crests, and recognized nine species in two genera (*Amblyphrynus* with two species and the remainder in one species group of *Eleutherodactylus*). The most significant subsequent study was that of **Lynch** (1986a) who argued that those nine species do not form a monophyletic group but belong to two very different groups with four species (*E. biporcatus*, *E. bufoniformis*, *E. maussi*, and *E. necerus*) being assigned to the subgenus *Craugastor* and the remaining species to the *sulcatus* group of *Eleutherodactylus*. The nominate species of the *sulcatus* group are *E. cadenai* Lynch, *E. cerastes* Lynch, *E. cornutus* (Jiménez de la Espada), *E. helonotus* (Lynch), *E. ingeri* (Cochran and Goin), *E. laticorpus* Myers and Lynch, *E. ruizi* Lynch, *E. sernai* Rivero, and *E. sulcatus* (Cope). *Eleutherodactylus sulcatus* is distributed in the Amazon Basin of western Brasil, southern Colombia, and eastern Ecuador and Peru and *E. laticorpus* occurs on the low serranía separating Colombia and Panama whereas the other species are cloud forest species distributed in the Andes of Colombia and Ecuador. Species descriptions are available for all but one taxon in **Lynch** (1975, 1981, 1986b), **Myers & Lynch** (1997), and **Rivero** (1984); one new species is named herein. Four generic names were proposed for broad-headed taxa (*Strabomantis* Peters, *Limnophys* Jiménez de la Espada, *Ctenocranius* Melin, and *Amblyphrynus* Cochran and Goin). *Strabomantis* is a synonym of the subgenus *Craugastor* Cope and the other three generic names apply to species of the *sulcatus* group. *Ctenocranius* is an objective synonym of *Limnophys* (**Myers**, 1962).

Frogs of the *sulcatus* group are markedly different from what most people expect of an *Eleutherodactylus* because they are relatively large frogs (adult females 40.0-70.0 mm SVL), whose habitus is robust or stocky, having large, broad, heads and short hindlegs. The coloration is somber (browns or grays with some black and rust pigmentation dorsally) and the skin of the dorsum is beset with conical and subconical tubercles, often coalescing with sharp ridges. The first finger is longer than the second and the fifth toe is shorter than the third. Some species lack digital pads (and discs) on the fingers. These frogs are usually found motionless in the leaf litter although some limited observations suggest that they actively move about the forest floor during the night. Initially (**Lynch**, 1986a), the *sulcatus* group was defined on the basis of a combination of characteristics: broad heads, cranial crests present, "S" condition of the mandibular ramus of the trigeminal nerve. None of these features qualifies as a synapomorphy except in the most *ad hoc* of ways (broad heads and cranial crests are probably derived conditions). However, unlike frogs of the *biporcatus* and *bufoniformis* groups (subgenus *Craugastor*), the broad-headed taxa of the *sulcatus* group have the posterior part of the *pars facialis* of the maxilla deepened (Fig. 1B). The plesiomorphic condition is seen in members of the *biporcatus* and *bufoniformis* groups (frogs of the subgenus *Craugastor* having broad heads) as well as in all other *Eleutherodactylus*.

The objectives of the present paper are to summarize additional data for these frogs, to provide a cladogram for the *sulcatus* group, and to present an hypothesis concerning its relationships within the genus *Eleutherodactylus*.

Material and Methods

The primary focus of this paper is to utilize osteological features as evidence of relationships. Skeletons and

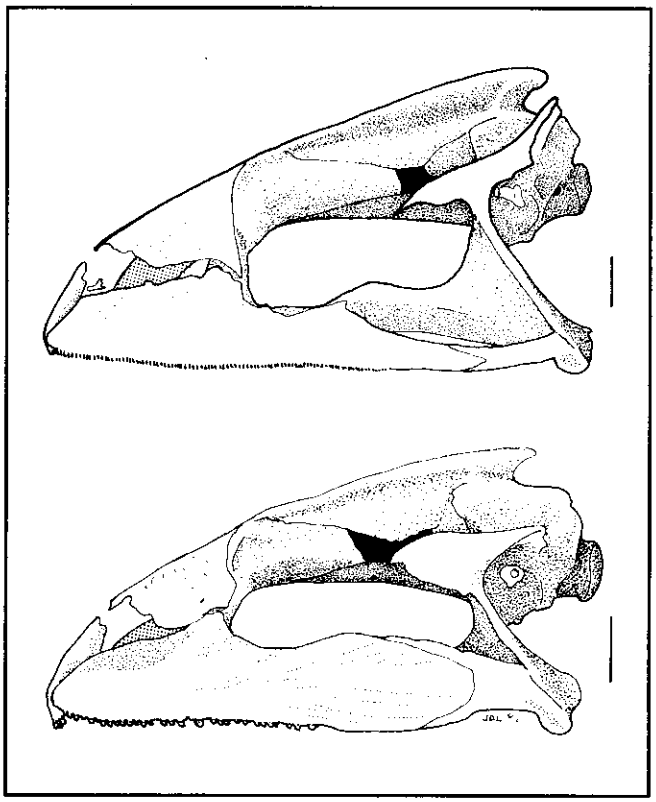

Figure 1. Lateral views of crania of (top) *Eleutherodactylus biporcatus* (KU 113679) and (bottom) *E. cerastes* (ICNMHN 14096) illustrating differences in depth of the posterior part of the *pars facialis* of the maxilla. Scales equals 2 mm.

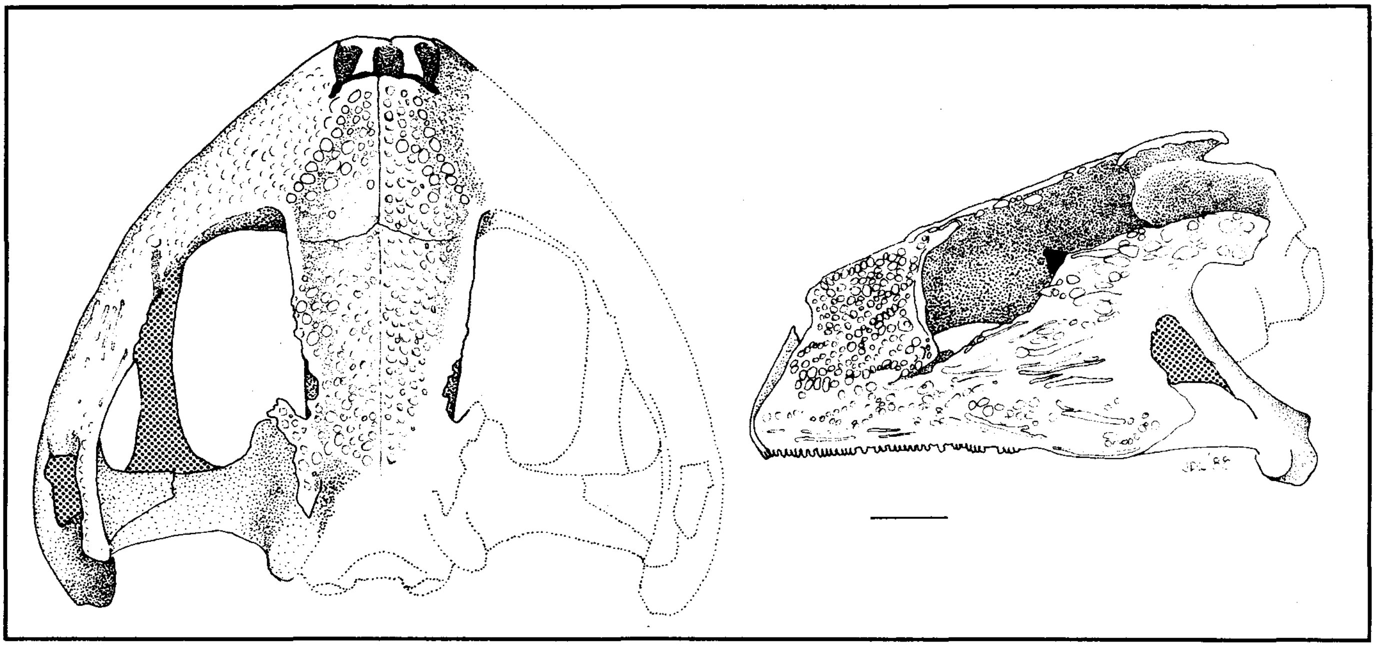

Figure 2. Dorsal and lateral views of cranium of *Eleutherodactylus cadenai* (ICNMHN 13731). Those parts of the cranium obscured by tissue are indicated by dotted lines. Scales equal 2 mm.

crania were prepared in one of two ways: as doubly stained cleared specimens, following **Dingerkus & Uhler** (1978), or as dry crania, prepared by flensing and then erosion of soft tissues in weak chlorox followed by 12 hr of washing in cold water. Osteological data were obtained as well by reflecting the skin of the head to expose the frontoparietals, nasals, and squamosals. Character polarization was accomplished by use of a strict out-group method,[2] using approximately 290 other species of *Eleutherodactylus* as the out-group (200 listed in **Lynch**, 1996) and by reference to juvenile specimens (an ontogenetic criterion). The following abbreviations are used in the text: E-N (distance from nostril to eye), HW (greatest head width), IOD (interorbital distance), and SVL (snout-vent length). Means are reported ± 1 standard error of the mean. Three hundred and eighty-eight specimens were examined and are identified by the appropriate symbolic code for the museum collection (Appendix 1).

Accounts of Species

Eleutherodactylus cadenai Lynch

Eleutherodactylus cadenai Lynch, 1986b:504 [Holotype. ICNMHN 13731, adult female, Alto de Río Cuevas, carretera Nutibara-La Blanquita, corregimiento de Murrí, Municipio de Frontino, Departamento de Antioquia, Colombia, 1900 m.].

This species remains known only from the holotype. The holotype is an adult female, 40.6 mm SVL, and is thus one of the smaller species of the *sulcatus* group. The species is probably sympatric with *E. cerastes* but collecting data are too few to document sympatry. Subsequent collecting in the vicinity of the type-locality revealed only *E. cerastes*. **Lynch** (1986b) suggested that *E. cadenai* and *E. ingeri* are sister species on the basis of the shared bony cheek (Fig. 2). Although poorly-known, I partially prepared the holotype to reveal some features of the cranium. The bony tubercles on the frontoparietals, nasals, and maxillae are distinctive as is the broad contact between the nasals and maxillae (probably autapomorphies). Other features of the cranium appear to be plesiomorphic (shape

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[2] A strict out-group method requires the initial assumption of monophyly of the in-group. All other taxa, "similar" or not, closely related or not, examined or not, comprise the out-group. The cautious biologist will want to examine more (or all) of the out-group taxa than will the bold biologist but, whether examined or not, any out-group taxon, possessing a particular state, is sufficient to falsify the claim that such and such a character state is derived for the in-group (all states [of a character] seen in both the in-group and the out-group are judged plesiomorphic for the in-group; only a state restricted to the in-group is judged as derived for the in-group).

of the cranial crests, nasal-frontoparietal contact). The other salient features of this species include (1) fingers with small disks and pads, (2) skin of venter smooth, (3) no tarsal fold, (4) one elongate eyelid tubercle, (5) no lateral fringes on the toes, and (6) narrow vomerine odontophores. The distribution of *E. cadenai* and *E. ingeri* is seemingly a biogeographic enigma, especially because the Cordillera Central is occupied by less closely-related species.

Distribution. Known only from the type-locality, in cloud forest at 1900 m on the western flank of the Cordillera Occidental in Departamento de Antioquia, Colombia (Fig. 3).

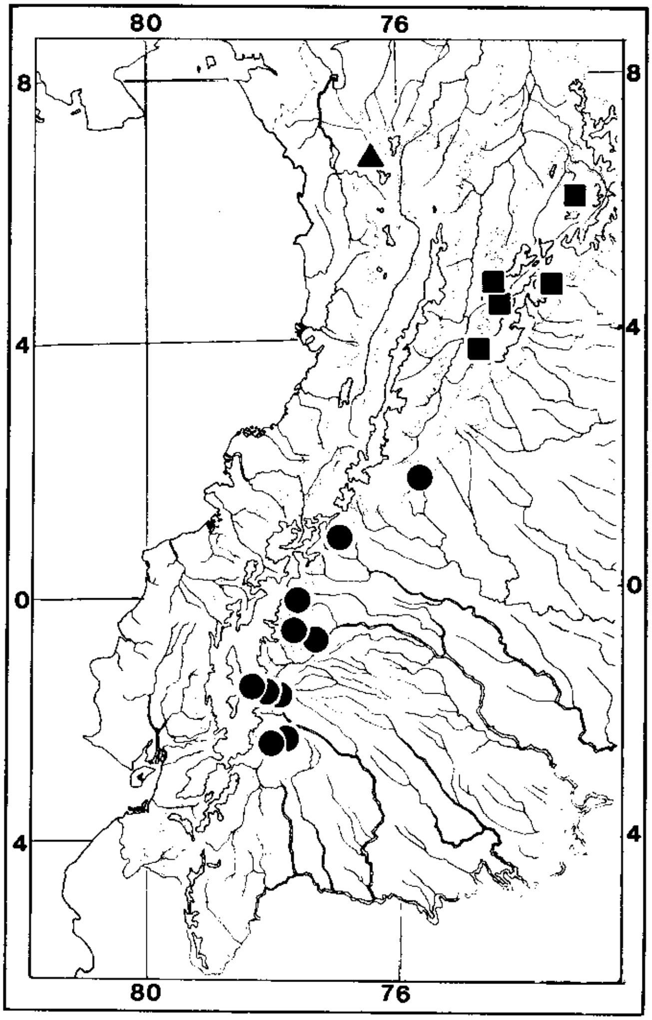

Figure 3. Map of Colombia and Ecuador showing locality records for *Eleutherodactylus cadenai* (triangle), *E. cornutus* (circles), and *E. ingeri* (squares). Areas above 3000 m stippled; 1000 m contour is indicated by dotted line.

***Eleutherodactylus cerastes* Lynch**

Eleutherodactylus cerastes Lynch, 1975:25 [Holotype. USNM 195785, an immature female, Palma Real, Pichincha Province, Ecuador].

Eleutherodactylus sernai Rivero, 1984:101 [Holotype. CSJ 301, immature female, "Pampas", a site at the edge of the Parque Nacional Natural "Las Orquídeas", corregimiento de Calles, Municipio de Urrao, Departamento de Antioquia, Colombia, ca 1500 m]. New synonymy.

Eleutherodactylus cerastes is a small species of the *sulcatus* group (5 males 27.4-33.4 ($\bar{x}$ = 29.8) mm SVL, 9 females 44.4-55.8 ($\bar{x}$ = 47.0 ± 1.2) mm SVL) having (1) small discs on the fingers and toes, (2) skin of venter smooth, (3) no tarsal fold, (4) one elongate eyelid tubercle, (5) no lateral fringes on the digits, and (6) broad vomerine odontophores. Males lack vocal slits and nuptial pads. Externally, *E. cadenai, E. cerastes*, and *E. laticorpus* are very similar because each has a long thin tubercle on the upper eyelid. The skin of the dorsum of *E. cadenai* is much less tuberculate than is that of the other two species and *E. cadenai* has narrow, rather than arched vomerine odontophores.

Rivero (1984) named *E. sernai* on the basis of a specimen from western Depto. Antioquia, Colombia, and contrasted it with *E. cerastes* on the basis of a sharply inclined snout, smaller digital discs, smaller eyelid tubercle, smoother skin of the dorsum, and a groove between the eye and snout. **Rivero** (1984) also suggested that the two species differ in the development of cranial crests (less distinct in *E. sernai*). Based on the photograph of the holotype in **Rivero** (1984), the organism appears substantially distinct from *E. cerastes*. However, when I examined the holotype in Medellín in 1985, I discovered that the peculiar head shape was the product of the collector's treatment of the animal (preserved with the mouth open by means of raising the cranium from the horizontal plane). The Colegio de San José has several other specimens collected by the late Marco Antonio Serna and these differ from the holotype in ways that suggest to me that the holotype either died before preservation or was subjected to desiccation soon after preservation. I interpret the smoother skin, the deep facial groove, small eyelid tubercle, and the small discs as post-preservational artifacts. In the absence of any feature that cannot be so interpreted, I here place *Eleutherodactylus sernai* Rivero in the synonymy of *E. cerastes*.

The cranium of *E. cerastes* (Fig. 4-5) closely resembles those of several other species of the *sulcatus* group. The maxilla is deep with pits and small protuberances. The

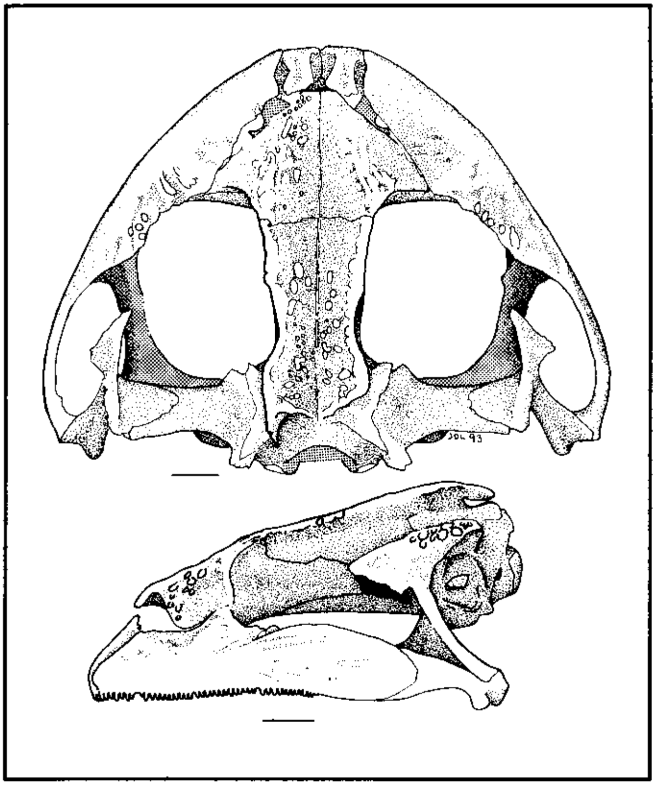

Figure 4. Dorsal and lateral views of cranium of *Eleutherodactylus cerastes* (UVC 8429). Scales equal 2 mm.

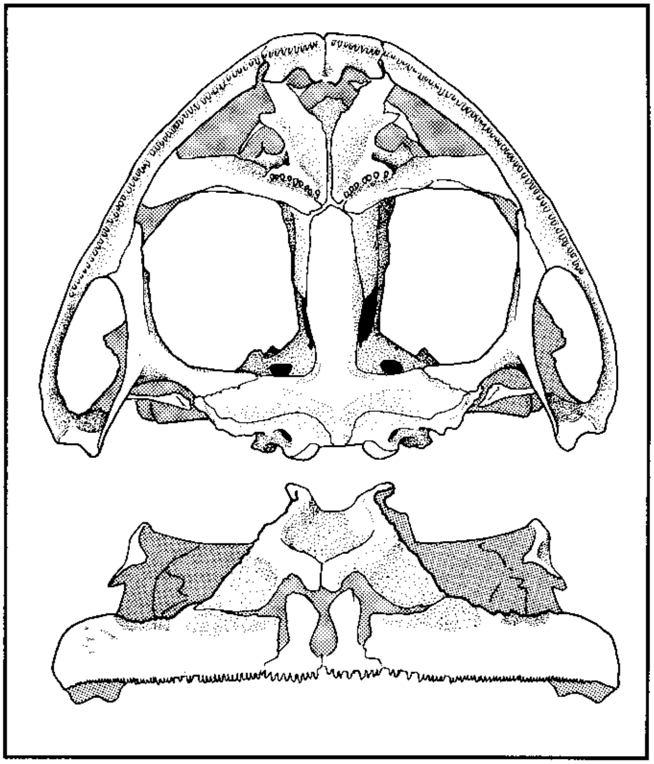

Figure 5. Ventral and frontal views of cranium of *Eleutherodactylus cerastes* (UVC 8429). Scale equals 2 mm.

quadratojugal is deepened anteriorly. The nasals and frontoparietals completely occlude the fontanelles and bear bony crests and low bony tubercles on the crests and in the furrow. The frontoparietals are not fused to the prootics. The squamosal bears an obvious otic shelf extending over the distal 40% of the *crista paroticae*. The otic crest (squamosal crest) is not elevated when viewed frontally (Fig. 5). The zygomatic ramus of the squamosal is deepened and flares laterally. The vomers are large and narrowly separated and bear massive odontophores that nearly meet medially and extend laterally to the middle or lateral border of the choanae.

Variation seen among the several skulls examined is partially ontogenetic. In the smallest specimens, the vomerine odontophores more closely approximate the condition usually described as "triangular". The smallest specimens examined also lack cranial crests. However, among most specimens, there is considerable variation, which I interpret as individual, in terms of the thickness or massiveness of the cranial crests and the presence of bony tubercles (Fig. 6). I interpret the presence of thin crests as an ontogenetic, rather than a phylogenetic, feature. The crests shown in Fig. 4 are of a large adult whereas those in Fig. 6 include several smaller and sexually immature specimens. In all specimens bearing cranial crests, there is an obvious constriction of the crests in the posterior part of the orbit followed by an increase in the separation of the crests internal to the epiotic eminences. In some specimens, a series of short bony spurs approximates the arrangement seen in *E. laticorpus* (**Myers & Lynch**, 1997). I am convinced that the similarity reflects ontogeny rather than relationship.

Distribution. *Eleutherodactylus cerastes* is distributed (Fig. 7) between 500 and 2300 m along the length of the Cordillera Occidental of Colombia and into northern Ecuador (**Lynch & Duellman**, 1997). All records of the species below ca 1200 m are from western Ecuador. Sympatry is anticipated between *E. cadenai* and *E. cerastes* in western Antioquia of Colombia and is known between *E. cerastes* and *E. helonotus* in Provincia de Pichincha of Ecuador. Additionally, *E. cerastes* is sympatric with *E. ruizi* in Depto. Valle del Cauca of Colombia with no apparent ecological distinction between the two species.

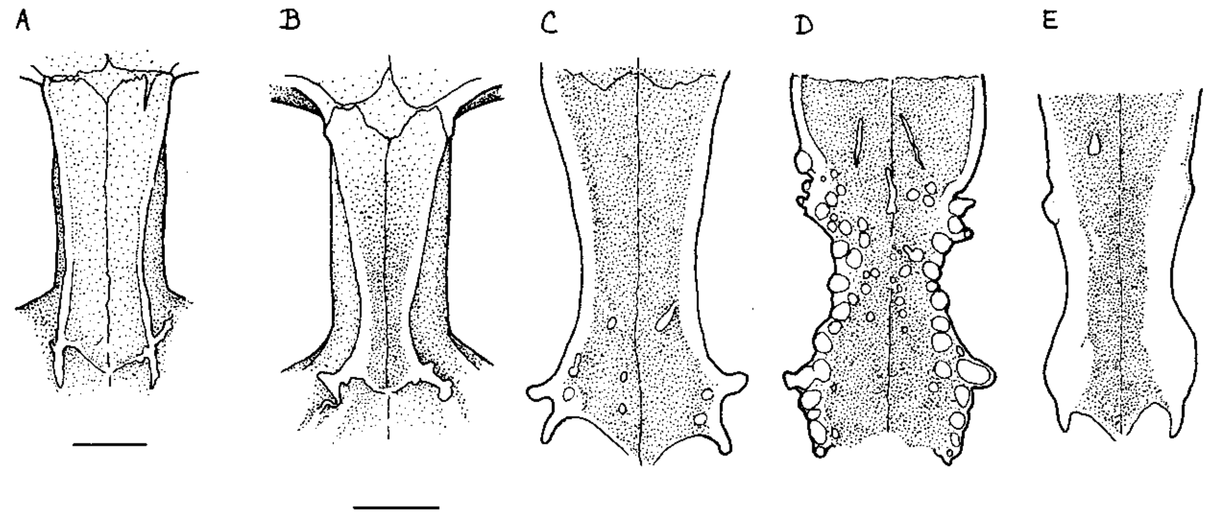

Figure 6. Variation in the expression of cranial crests in *Eleutherodactylus cerastes*. (A) ICNMHN 14096; (B) KU 144992; (C) ICNMHN 19205, juvenile female, 40.5 mm SVL; (D) ICNMHN 29064, juvenile female, 38.0 mm SVL; (E) ICNMHN 16601, adult female, 45.8 mm SVL. Scales equal 2 mm.

Eleutherodactylus cornutus (Jiménez de la Espada)

Limnophys cornutus Jiménez de la Espada, 1870:60 [Type-locality: Río Suno, San José de Motí, Provincia Napo, Ecuador; holotype apparently lost].

Limnophys napaeus Jiménez de la Espada, 1870:60 [Type-locality: Río Suno, San José de Motí, Provincia Napo, Ecuador; holotype apparently lost]. Synonymy by Lynch, 1975:28.

Strabomantis cornutus: Jiménez de la Espada, 1872:85.

Hylodes cornutus (part): Boulenger, 1882:220.

Ctenocranius cornutus: Melin, 1941:49.

Eleutherodactylus cornutus cornutus (part): Rivero, 1961:55.

Eleutherodactylus cornutus: Gorham, 1966:66.

Eleutherodactylus cornutus remains a rare species but was confused with several species (**Lynch**, 1975). The salient features of the species are: (1) fingers and toes bearing small discs, (2) skin of venter smooth, (3) fold along inner edge of tarsus, (4) elongate eyelid tubercle, (5) toes bearing lateral fringes, and (6) broad vomerine odontophores. The skin of the dorsum is prominently tuberculate.

Perhaps the most significant contribution of **Lynch** (1975) was to distinguish *E. cornutus* and *E. sulcatus*, two species that had been confused completely by **Rivero** (1961) and **Cochran & Goin** (1970). The former species has a smooth venter and an elongate eyelid tubercle whereas the latter has areolate skin on the venter and only small eyelid tubercles. The two species are also distinguished easily because the posterior surfaces of the thighs are brown in *E. cornutus* and bear large cream spots in *E. sulcatus*. Lastly, *E. cornutus* is a cloud forest species whereas *E. sulcatus* is a lowland species, and osteological features place *E. cornutus* with the Andean species, not with those of the lowlands.

The cranium (Fig. 8) is slightly wider than long. The individual available for skeletal preparation is not an adult female, but rather an immature (nearly adult) one. Accordingly, some of the features evident in the cranium may reflect ontogenetic rather than systematic features (e.g., the separation of the vomers and lack of ornamentation of the roofing bones). The most important osteological features are (1) that the cranial crests diverge anteriorly-posteriorly, (2) the bicapitate head of the quadratojugal, (3) elevated squamosal crest of the otic ramus, (4) relatively short [compared to *E. ingeri* and *E. sulcatus*] otic shelf of the squamosal, and, possibly, (5) the evident crests over the nasal bones. This last character is only hinted at by the available cranium (Fig. 8) but one must recall that this is a juvenile, not an adult, specimen.

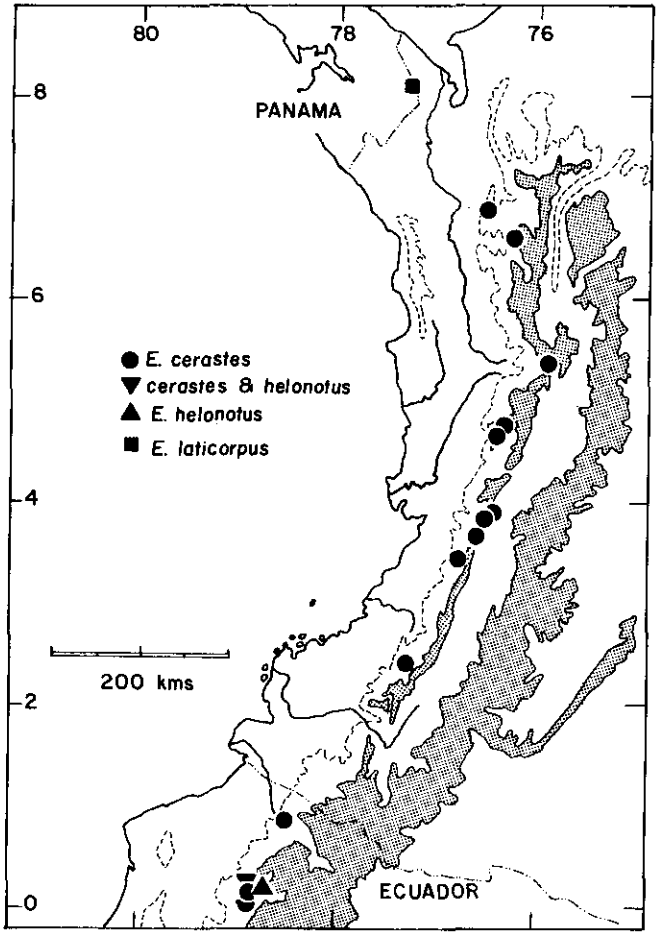

Figure 7. Map of western Colombia and Ecuador showing locality records for *Eleutherodactylus cerastes, E. helonotus,* and *E. laticorpus*. Area above 2000 meters is stippled. Dashed line is 500 m contour.

Distribution. Lynch (1975) reported this species from the cloud forests of eastern Ecuador only. In 1990, the author and Pedro Ruiz found *E. cornutus* in extreme western Depto. Caquetá of Colombia. I suspect that the species is distributed farther north along the eastern flank of the Cordillera Oriental but collecting is impossible because of political instability (Fig. 3).

Eleutherodactylus helonotus **(Lynch)**

Amblyphrynus helonotus Lynch, 1975:19 [Holotype. BMNH 1970.178, an adult female, Río Pitzara, Provincia Pichincha, Ecuador].

Eleutherodactylus helonotus: Lynch, 1981:318.

Lynch (1975) described this species on the basis of two females and no additional specimens have come to light in spite of considerable additional collecting on the western slopes of the Andes of Ecuador. The holotype is an adult female 69.6 mm SVL whereas the paratype (60.6 mm SVL) is a subadult female. The salient features of the species are: (1) fingers lacking discs [but toes thought to have narrow discs], (2) skin of venter areolate, (3) no tarsal folds, (4) upper eyelid bearing low tubercles, none elongate, (5) toes bearing lateral fringes, and (6) broad vomerine odontophores. Additionally, the species is distinctive because the dorsum bears large, flattened warts.

Because it is known from only two specimens, housed in different museums, osteological information on *E. helonotus* is very limited. Before I described it, I carried out limited dissections of each specimen (such being the one of the advantages of discovery). On the basis of osteological features evident by reflecting the skin of the head and augmented by stereoradiographs, limited osteological information is available (Fig. 9). The capitate end of the quadratojugal is bifurcate as in all other Andean species of the *sulcatus* group but all other osteological features appear to be plesiomorphic within the *sulcatus* group.

Distribution. Known only from two localities in western Ecuador (Fig. 7); the species is probably distributed at elevations between 1000 and 2000 meters in cloud forests.

Eleutherodactylus ingeri **(Cochran & Goin)**

Hylodes cornutus (part): Boulenger, 1882:220-221.

Eleutherodactylus cornutus (part): Dunn, 1944:26.

Amblyphrynus ingeri Cochran and Goin, 1961:543. [Holotype. FMNH 81915, an adult female, San Isidro, 8 km S Gachalá, Municipio de Gachalá, Departamento de Cundinamarca, Colombia,2350 m].

Eleutherodactylus ingeri:: Lynch, 1981:318.

This very distinctive frog remains quite rare. Two adult males are 33.1-38.0 mm SVL and two gravid females are 49.2-52.5 mm SVL. Salient features are : (1) fingers lacking discs but small discs on toes, (2) skin of venter areolate, (3) inner tarsal fold, (4) upper eyelid bearing one conical tubercle, (5) toes bearing lateral fringes, and (6) vomerine odontophores broad. Contrary to **Lynch**'s (1981) report, males have vocal slits. **Lynch** (1981) provided a detailed description of the skull of a near-adult female. The availability of a juvenile (Fig. 10) confirms some of Lynch's expectations concerning transformation of characters, most importantly as concerns the closure of the cheek in the adult. Additionally, juveniles lack cranial crests and have narrow vomerine odontophores.

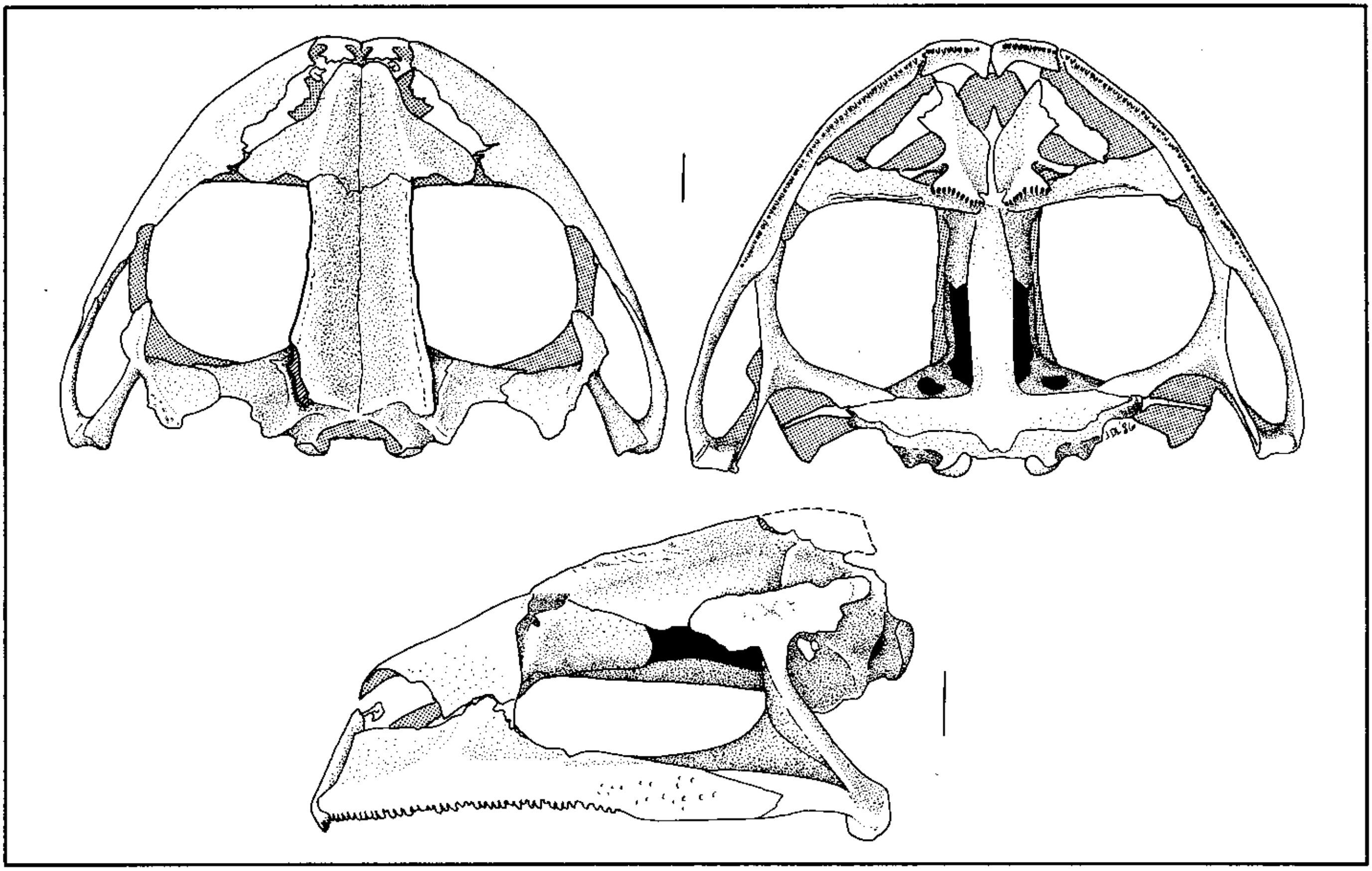

Figure 8. Cranium of *Eleutherodactylus cornutus* (KU 123448). Scales equal 2 mm.

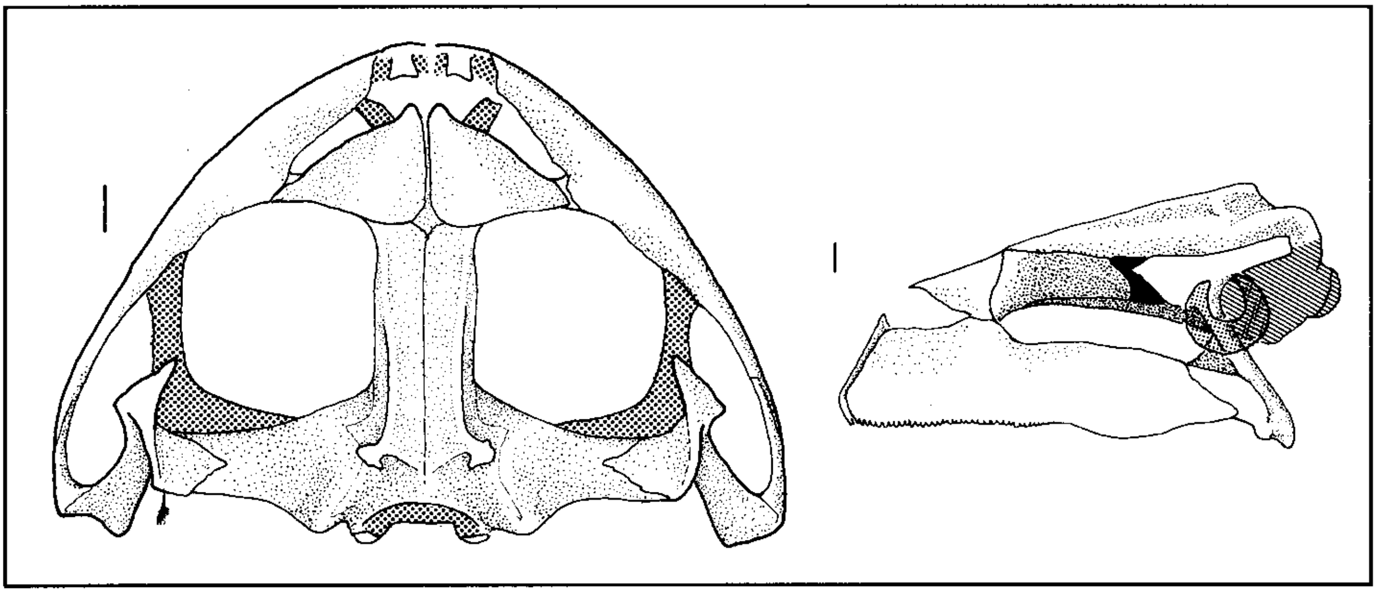

Figure 9. Dorsal and lateral views of crania of *Eleutherodactylus helonotus*. Based on radiographs and limited dissections of the holotype and paratype. Dorsal view based primarily upon USNM 195784; lateral view based primarily upon BMNH 1970.178. However, each drawing is a composite. Stippling in lateral view represents cartilage. Scales equal 2 mm.

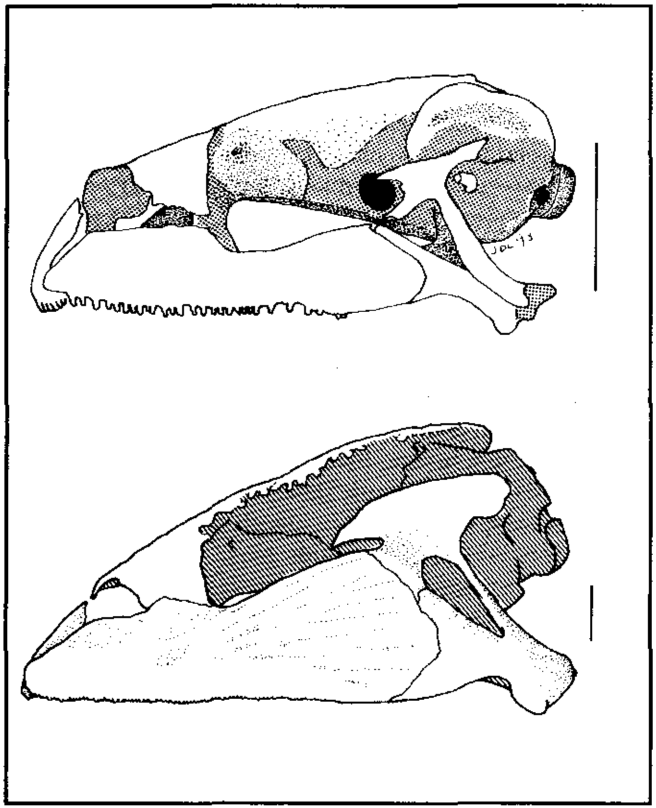

Figure 10. Lateral views of crania of *Eleutherodactylus ingeri* [top: ICNMHN 6173, juvenile female, 17.2 mm SVL (cartilage is stippled). bottom: ICNMHN 2507, adult female]. Scales equal 2 mm.

Distribution. *Eleutherodactylus ingeri* is known from elevations between 1700 and 2300 m on both the eastern and western slopes of the Cordillera Oriental in departamentos Cundinamarca and Santander (Fig. 3). The absence of records from Depto. Boyacá probably represents only failure to collect.

Eleutherodactylus laticorpus Myers & Lynch

Eleutherodactylus laticorpus Myers & Lynch, 1997:4. Holotype. AMNH 100000, an adult female, southwest sector of the Cerro Tacarcuna massif, Darién Province, Panamá, 1590 m.

No additional information is available for this recently-described species except as concerns its relationships (see below). The salient features of this toad are: (1) small discs on fingers and toes, (2) skin of venter smooth, (3) no tarsal fold, (4) upper eyelid bearing one long conical tubercle, (5) toes lacking lateral fringes, and (6) vomerine odontophores broad.

Distribution. Known from two mountains on the frontier between Colombia and Panamá, 1410-1630 m (Fig. 7).

Eleutherodactylus necopinus sp. nov.

Hylodes cornutus (part): Peracca, 1914:107.

Eleutherodactylus cornutus cornutus (part): Cochran and Goin, 1970:444.

Amblyphrynus ingeri (part): Lynch, 1975:15-19.

Eleutherodactylus ruizi (part): Lynch, 1981:319-321

Holotype. ICNMHN 24604, an adult female collected 9 November 1990 by A. Cadena and H. López.

Paratypes. Males: ICNMHN 13969, 32280, 37573, 37575, 37577, 37590, 37604, 37607. Females: ICNMHN 28614, 32284, 37578-81, 37584, 37587, 37592-93, 37596, 37599-603, 37612, IND-AN 5397 (see Appendix 1 for localities).

Type-locality. COLOMBIA, Departamento de Quindío, Municipio Filandia, vereda El Roble, Reserva Forestal Bremen (Buena Quebrada), Quebrada las Cruces, 2050 m.s.n.m.

Etymology. Latin, meaning unexpected; in reference to my surprise at discovering that the frogs from the Cordillera Central could be distinguished from those of the Cordillera Occidental by details of the crania (when externally, they are nearly identical).

Diagnosis. (1) skin of dorsum coarsely tuberculate in small specimens, smoother with sharp ridges and scattered tubercles in larger specimens, that of venter areolate; head width 51-59% SVL; (2) tympanum prominent, round; (3) snout round in dorsal view, sloping in lateral profile; canthus rostralis prominent, concave; lips weakly flared; (4) upper eyelid with 2-4 conical tubercles; (5) prevomerine odontophores median and posterior to choanae, triangular in outline; (6) males with vocal slits but no nuptial pads; (7) first finger longer than second; fingers lacking discs; (8) fingers bearing thick lateral keels; (9) ulnar tubercles subconical; (10) no tubercles on heel or outer edge of tarsus; inner tarsal fold present; (11) two metatarsal tubercles, inner oval, four times size of round outer; numerous supernumerary plantar tubercles; (12) toes bearing lateral fringes, no webbing, narrow toe discs; toe III longer than toe V; (13) gray to brown above with brown or black markings; throat brown with cream flecks, venter cream with modest to dense reticulation of brown; (14) adults large, males 32.0-39.8 ($\bar{x}$ = 37.1 ± 1.2, n = 7) mm SVL, females 52.8-67.7 ($\bar{x}$ = 58.8 ± 0.8, n = 20) mm SVL.

Eleutherodactylus necopinus is most closely related to *E. ruizi* and is most similar to that species as well (I cannot consistently distinguish the two species externally). At least for specimens 25 mm SVL and larger, the two can be distinguished easily by probing (with a needle) the supratemporal region for the presence of a median otic plate (*E. ruizi*) or its absence (*E. necopinus*).

Description. Head not as wide as body, wider than long; snout round in dorsal view, sloping in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis massive (due to underlying bony ridges), slightly convex; loreal region concave, sloping to lip; lips not greatly flared, even in adult females; eyes small, upper eyelid bearing 2-4 elongate tubercles as well as several shorter ones; large lateral cranial crests produce deep furrow on center of head; crests extending anteriorly to a point just posterior to nostrils, posterior ends of crests end in bosses; skin between crests bearing transverse fleshy folds and small tubercles; supratympanic fold extending behind tympanum, its outline obscured by underlying crest of otic ramus of squamosal; tympanum visible externally, annulus raised at edges, except dorsally; tympanum separated from eye by tympanum length; postrictal tubercles moderate in size; skin of sides of head and areas lateral to cranial crests bearing many small tubercles; choanae oblique (long axis 45° from midline), not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, each size of a choana or slightly larger, broader than long, bearing a row of 7-8 teeth, separated by a distance equal 1/4 width of an odontophore; tongue broadly oval, slightly wider than long, posterior edge not adherent to floor of mouth, bearing slight indication of posterior notch; vocal slits present in adult males.

Dorsum covered with small low warts with scattered larger warts and ridges, more prominent in juveniles (illustrated in photograph, identified as *Amblyphrynus ingeri*, by **Lynch**, 1975); warts larger on flanks, grading into granular venter; upper surfaces of limbs same as dorsum except with larger subconical warts and short ridges; some enlarged warts along lower edge of lower jaw; discoidal folds prominent, anterior to groin; no anal sheath; ulnar tubercles subconical, flattened anteroposteriorly, more prominent in juveniles than in adults; palmar tubercle bifid, larger than oval thenar tubercle; low supernumerary palmar tubercles; subarticular tubercles round, elevated, distal tubercles only half size of basal tubercles (fingers III-IV); thick lateral keels on fingers; fingers ending in simple tips (no expansion, no grooves); first finger longer than second ; no nuptial pads in males.

No enlarged tubercles on heel or notable tubercles along outer edge of tarsus (skin of tarsus bearing subconical tubercles); inner tarsal fold along distal 2/3 - 3/4 of tarsus; inner metatarsal tubercle twice as long as wide, 4 times size of round outer metatarsal tubercle; numerous supernumerary plantar tubercles; subarticular tubercles subconical, slightly longer than wide; toes bearing lateral fringes; tips of toes weakly expanded, bearing circumferential grooves; toe III longer than toe V.

Gray to grayish-brown with black markings along edges of ridges; ridges paler than ground color; cream interorbital bar inside dark brown interorbital blotch; black postnasal blotch and black labial bars separated by cream lines; tympanum brown; black supratympanic blotch and black patch on anteriormost flank; limbs with incomplete thin black bars; inner digits cream; throat brown with tiny cream spots, venter cream with dense to modest reticulum of brown or gray; pale blotches larger on undersides of shank and thighs.

Color in life. Head and anterior trunk pale brown, posterior trunk and limbs lavender-gray ; interorbital bar, folds on body and limbs cream with black flecks or spots ; fingers and toes cream ; groin, axilla, concealed surfaces of limbs spotted with brown (underside of shank barred cream and brown) ; ventral surfaces reddish-brown with dense flecking of lavender-brown ; canthus rostralis and lips marked with black, separated by cream ; tympanum black, annulus cream ; anterior limbs bear small red spots ; iris bronze with brown radii ; tongue pale orange, rest of mucosa of mouth cream. (Field notes of P. M. Ruiz, 9 Nov. 1990).

Measurements of holotype in *mm*. SVL 67.7, shank 32.0, HW 34.8, upper eyelid width 5.8, IOD 8.4, tympanum length 5.6, eye length 7.0, E-N 6.5.

Proportions (10 males, 20 females).— Males: tibia/SVL 51.8-61.3 (55.2 ± 1.0)%; HW/SVL 54.0-59.0 (55.8 ± 0.5)%; eyelid/IOD 75.0-115.2 (95.7 ± 3.6)%; tympanum/eye 78.0-96.3 (87.3 ± 2.1)%; E-N/eye 76.4-100.0 (88.8 ± 2.6)%. Females: tibia/SVL 45.6-53.4 (49.5 ± 0.05)%; HW/SVL 50.8-57.4 (53.4 ± 0.04)%; eyelid/IOD 65.5-98.6 (82.6 ± 2.3)%; tympanum/eye 50.0-84.0 (61.7 ± 2.1)%; E-N/eye 77.6-118.6 (95.7 ± 2.6)%.

Cranial morphology. The mandibular ramus of the trigeminal nerve passes lateral to the *m. levator posterior mandibulae subexternus* (*m. adductor mandibulae externus* of some authors) and the *m. depressor mandibulae* consists of a single muscle with about 60% of the fibers originating from the skull and tympanic annulus and 40% originating from the dorsal fascia (no "flap" is present). The cranium is notably broader than long (Fig. 11). The alary processes of the premaxillae are directed posterodorsally and relatively broad. The septomaxillae are large and lie just posterolateral to the tips of the alary processes. The *pars facialis* of the maxilla is deep and narrowly separated from the nasal bones. In profile, the maxillae are deep, even posterior to the orbit and broadly contact the quadratojugals. The quadratojugals are expanded anteriorly and on the lingual surfaces of the maxillae demonstrate the two heads, one lying along the dorsal border and one along the ventral border of the maxillae.

The nasals are in median contact except near their posterior edges and a roughly triangular in outline. The nasals bear prominent crests with some pitting and ornamentation (these are continuations of the cranial crests) ending just posterior to the anterior tips of the nasals. The frontoparietals contact the nasals and there is a small rhomboidal surface exposed of the sphenethmoid. The crests of the frontoparietals are markedly elevated above the roof of the braincase and slightly flared laterally. The crests diverge slightly as one moves posteriorly. The frontoparietals are not fused to the prootics. The occipital condyles are ventrolateral and are not stalked. The dorsal border of the foramen magnum is not extended.

The epiotic eminences are prominent posteriorly but not apparent anteriorly. The *cristae paroticae* are short and broad. The otic shelf of the squamosal extends medially about half the distance between the otic plate and the epiotic eminences. The squamosal crest (of the otic ramus) is elevated (Fig. 11-12, contrast with Fig. 5) and ornamented by pitting and extends slightly toward the braincase (in contrast to the condition seen in *E. ruizi*, the sister-species of *E. necopinus*). The otic ramus of the squamosal is deep as is the zygomatic ramus (Fig. 11) which flares laterally over the belly of the *m. levator posterior mandibulae*.

The palatal shelf of the premaxilla is broad but not dissected. The palatal shelf of the maxilla is relatively narrow and no pterygoid process is developed. The prevomers are large, in contact posteriorly, and bear triangular vomerine

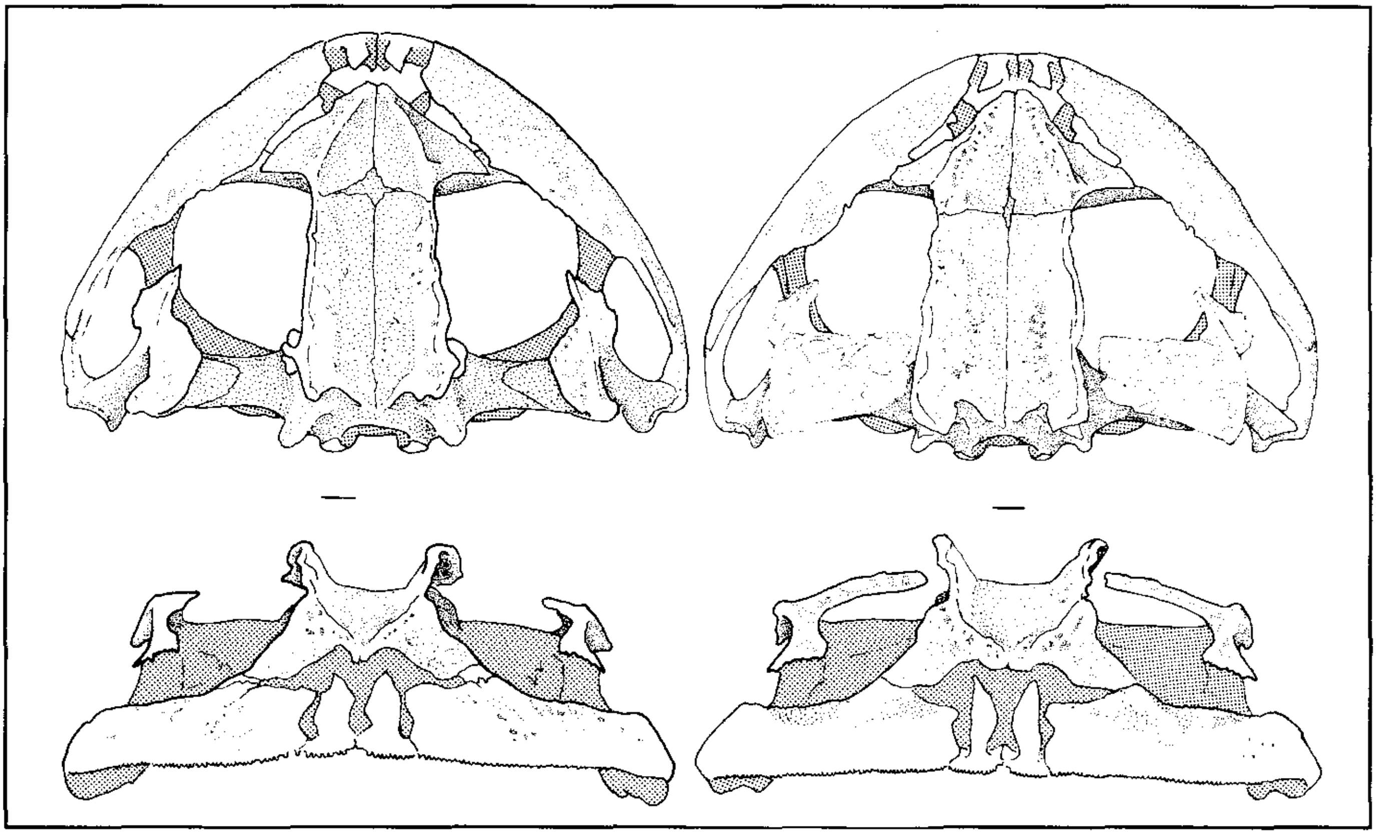

Figure 11. Dorsal and frontal views of skulls of *Eleutherodactylus necopinus* sp. nov. (left, ICNMHN 28614) and *E. ruizi*. (right, UVC 10008). Scales equal 2 mm.

odontophores which touch the neopalatines. The neopalatines are very broad (nearly touching medially) and bear slight ridges along their posteroventral edges. The cultriform process of the parasphenoid extends between the median tips of the neopalatines. The alary processes of the parasphenoid are perpendicular to the axis of the cultriform process and are broadly overlapped by the median rami of the pterygoids (Fig. 12).

The similarities between the crania of *E. necopinus* and *E. ruizi* are obvious (Fig. 11-12) in most details of the skulls. However, the most obvious difference is in the median extent of the squamosal crest which nearly reaches the frontoparietals in *E. ruizi* (Fig. 11). Each species is peculiar in having a posterolateral extension of the otic shelf (Fig. 11), prominent crests on the nasal bones, and frontoparietal crests that diverge slightly posteriorly (the latter characteristic shared as well with *E. cornutus*). The prevomers of *E. ruizi* are in median contact for the full extent of the prevomers whereas in *E. necopinus*, the anterior 3/4 of the bones are separated medially.

Distribution. Because the species is diagnosed on the basis of an osteological feature, identification of juveniles (less than 25 mm SVL) is problematic. However, the distribution appears to be the northern half of the Cordillera Central of Colombia at elevations of nearly 2000 m (Fig. 13).

Eleutherodactylus ruizi Lynch

Eleutherodactylus ruizi Lynch, 1981: 319 (Holotype. ICNMHN 5211, juvenile female from Reserva Forestal de Yotoco, Km. 18 carretera Buga a Loboguerrero, Departamento de Valle del Cauca, Colombia, 1590 m).

This species is nearly indistinguishable externally from *E. necopinus* but is readily distinguishable when crania are available (at SVL of 25 mm or greater). Six male *E. ruizi* are 29.8-45.1 ($\bar{x}$ = 37.8 ± 2.2) mm SVL and two gravid females are 59.7-70.0 mm SVL. The salient features of *E. ruizi* are identical to those of *E. necopinus* : (1) no discs on fingers, small discs on toes, (2) skin of venter areolate, (3) tarsal fold present, (4) conical tubercles on upper eyelid, (5) toes bearing lateral fringes,

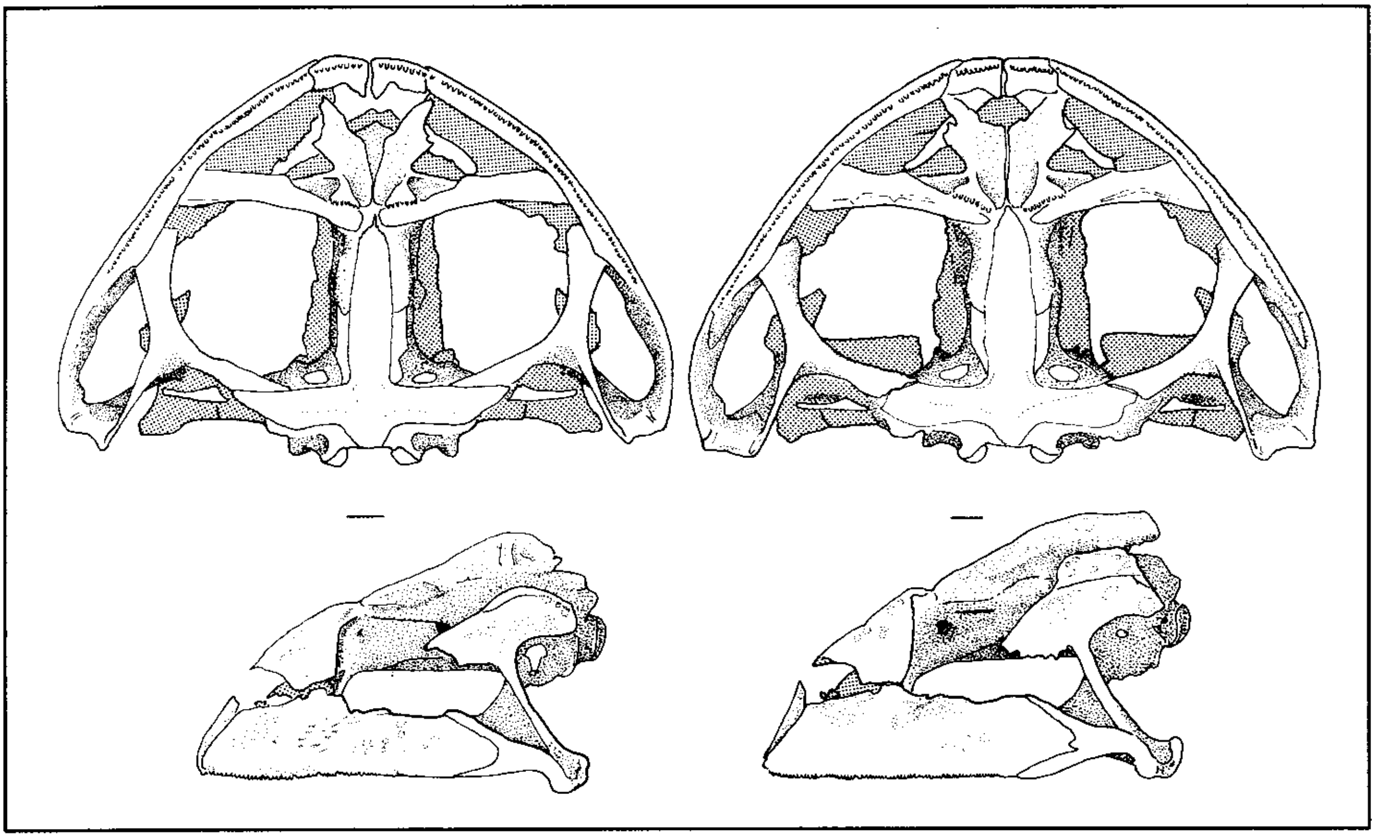

Figure 12. Ventral and lateral views of skulls of *Eleutherodactylus necopinus* sp. nov. (left, ICNMHN 28614) and *E. ruizi*. (right, UVC 10008). Scales equal 2 mm.

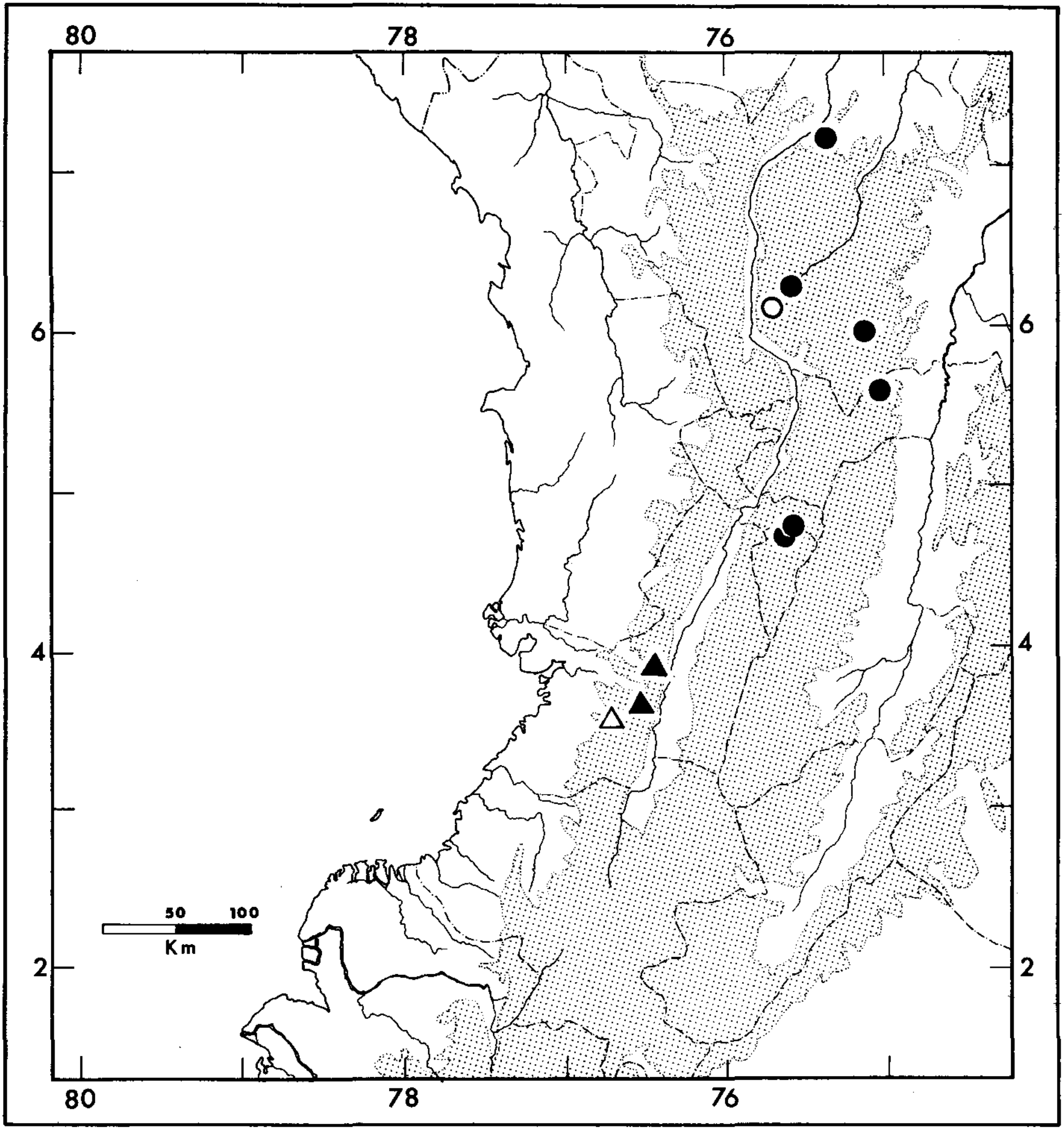

Figure 13. Map of western Colombia, showing locality records for *Eleutherodactylus necopinus* (circles) and *E. ruizi* (triangles). Areas above 1000 meters is stippled. Open symbols are for localities based on literature or photographs (no specimen vouchers).

and (6) vomerine odontophores triangular (not broad). Males have vocal slits but lack nuptial pads.

Distribution. Known only from four localities on the Cordillera Occidental in Depto. Valle del Cauca, Colombia, at elevations between 1500 and 2000 m (Fig. 11).

Eleutherodactylus sulcatus (Cope)

Hylodes sulcatus Cope, 1874:126 (Holotype. ANSP 11385, an adult female from Nauta, Depto. Loreto, Peru)

Hylodes macrocephalus Peracca, 1904:29 (Lectotype. larger of two specimens catalogued as MZS 2930, from Valle Santiago, Morono-Santiago Prov., Ecuador). Synonymy by Lynch, 1975:33.

Ctenocranius koki Melin, 1941:45. (Holotype. GNM 494, from Taracuá, Río Uaupés, Estado Amazonas, Brasil). Synonymy by Lynch, 1975:33.

Lithodytes cornutus (part): Andersson, 1945:45.

Eleutherodactylus macrocephalus: Peters, 1955:348.

Eleutherodactylus cornutus cornutus (part): Rivero, 1961:55.

[*Eleutherodactylus*] *koki*: Myers, 1962:198.

Eleutherodactylus sulcatus: Gorham, 1966:103; Lynch, 1975:33-35.

Lynch's (1975) account of this species remains current except as concerns distribution. Ontogenetic information confirms the expectations that cranial crests are derived and that narrow odontophores are primitive (Figs. 14-15). The salient features of this toad are : (1) fingers lacking discs, small discs on toes, (2) skin of venter areolate, (3) tarsal fold present, (4) small tubercles on upper eyelid, (5) toe fringes present, and (6) vomerine odontophores broad. Males lack vocal slits and lack nuptial pads. **Lynch's** (1981) assertion that *E. sulcatus* is the sister species of two Andean taxa (*E. ingeri* and *E. ruizi*) is rejected here (see below).

Distribution. *Eleutherodactylus sulcatus* is found in southern Colombia, western Brasil, and eastern Ecuador and Peru at elevations below 1100 m (Fig. 16).

Discussion

Relationships within the *sulcatus* group. Lynch (1975) attempted a cladogram of the species of the *sulcatus* group using externally visible characters but his efforts were flawed in part by viewing two species of *Amblyphrynus* as "more advanced" than the other species of the *sulcatus* group. With the discovery that he had confused two species under the name *Amblyphrynus ingeri*, **Lynch** (1981) began to employ osteological features to generate a cladogram. However, he persisted in thinking that areolate skin on the venter was a derived (and informative) feature. With the discovery of *E. cadenai*, **Lynch** (1986b) proposed that *E. cadenai, E. ingeri*, and *E. ruizi*

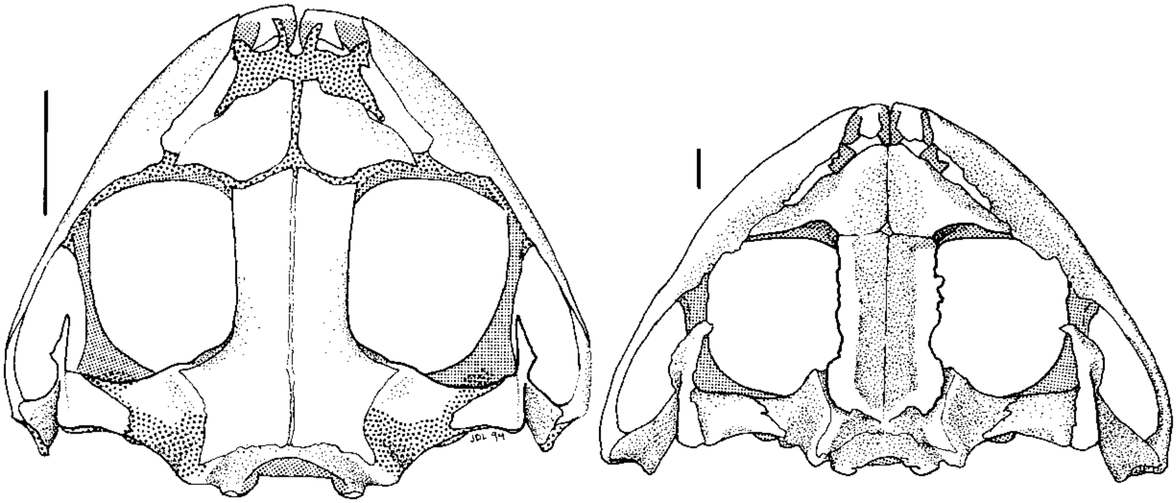

Figure 14. Dorsal views of crania of juvenile (KU 123584, 18.1 mm SVL) and adult (KU 100355) *Eleutherodactylus sulcatus*. Coarse stippling indicates cartilage. Scales equal 2 mm.

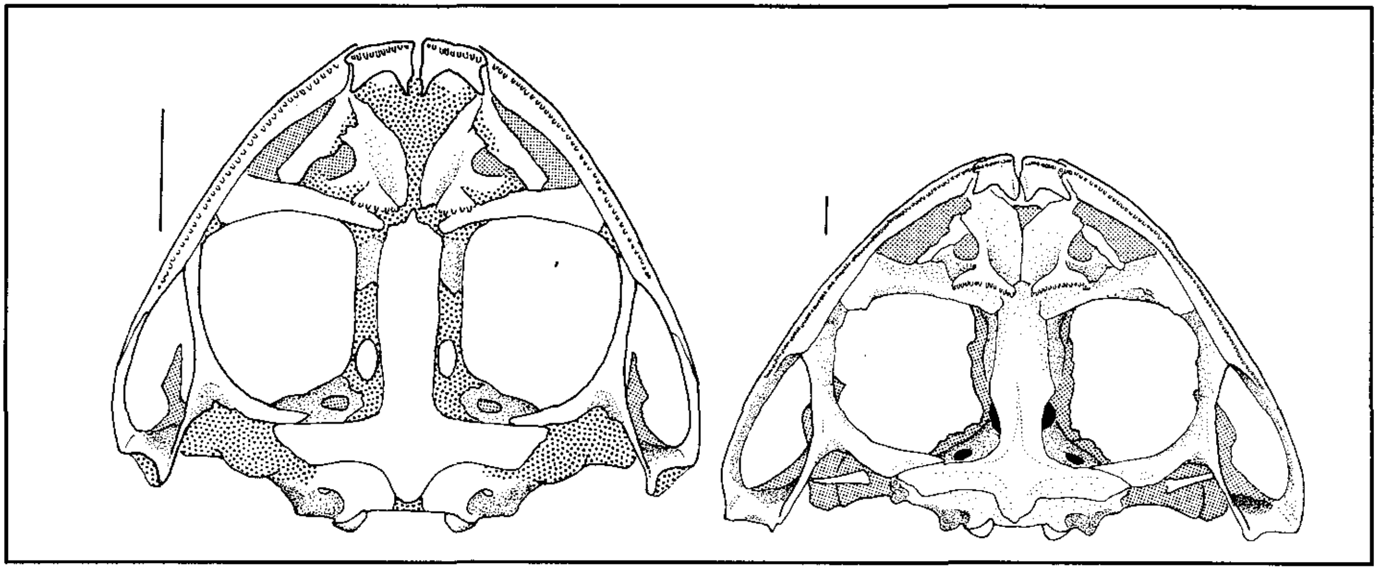

Figure 15. Ventral views of crania of juvenile (KU 123584, 18.1 mm SVL) and adult (KU 100355) *Eleutherodactylus sulcatus*. Coarse stippling indicates cartilage. Scales equal 2 mm.

formed a clade within the *sulcatus* group. This clade was defined on osteological characters. Even then, I wanted to obtain data on the crania of all the species of the group because I had become less enchanted by the match of external characters and character polarization schemes. The discovery that the broad-headed taxa were cleaved by a jaw muscle character (**Lynch**, 1986a) convinced me that a more careful approach would be necessary to obtain a cladogram of these taxa. One of the most surprising results of my study of the Colombian taxa (**Lynch**, 1986b) was the seemingly discordant biogeography and relationships of the species of the three Andean cordilleras — sister species (*E. cadenai* and *E. ingeri*) occurred on non-adjacent cordilleras with a less closely-related species (*E. ruizi*) separating them.

Part of my earlier discordant finding (**Lynch**, 1986b) was resolved with the discovery that the Cordillera Central populations referred previously to *E. ruizi* were a distinct species (*E. necopinus*). When *E. laticorpus* was described (**Myers & Lynch**, 1997), my survey of skeletons of this group was advanced sufficiently to identify a synapomorphy linking the Andean members of the *sulcatus* group. The osteological characters employed here (and in my previous papers) are summarized below:

(1) deepened posterior *pars facialis* of maxilla: This feature was indicated at the outset of this paper as a synapomorphy shared by all species of the *sulcatus* group and not evidenced elsewhere within the genus.

(2) bifurcate head of quadratojugal: **Myers & Lynch** (1997) introduced this feature and illustrated it. The plesiomorphic condition has only a dorsal extension of the quadratojugal along the lingual surface of the maxilla. This feature is evident in all species of the *sulcatus* group except *E. laticorpus* and *E. sulcatus*, the two species not distributed in cloud forests of the northern Andes.

(3) elevated squamosal crest: In those *Eleutherodactylus* having a squamosal crest, the crest is low and barely higher than the adjacent *cristae paroticae* (e.g., *E. cerastes*, Fig. 5). However, in *E. cadenai, E. cornutus, E. ingeri, E. necopinus* (Fig. 11), and *E. ruizi* (Fig. 11), the crest is elevated well above the level of the *cristae paroticae*.

(4) bony cheek: In *E. cadenai* (Fig. 2) and *E. ingeri* (Fig. 10), the zygomatic ramus of the squamosal makes articular contact with the posterodorsal portions of the *pars facialis* of the maxilla to enclose the adductors of the mandible behind a bony cheek. The ontogeny of this character is evident in *E. ingeri* (Fig. 10). This character was identified as an autapomorphy by **Lynch** (1981) and as a synapomorphy by **Lynch** (1986b).

(5) diverging crests of frontoparietals: most *Eleutherodactylus* having cranial crests have crests which are narrower posteriorly than anteriorly. These crests sometimes widen again posteriorly. *Eleutherodactylus cornutus, E. necopinus*, and *E. ruizi* are peculiar in that their crests diverge posteriorly and are narrowest near the anterior ends of the frontoparietals.

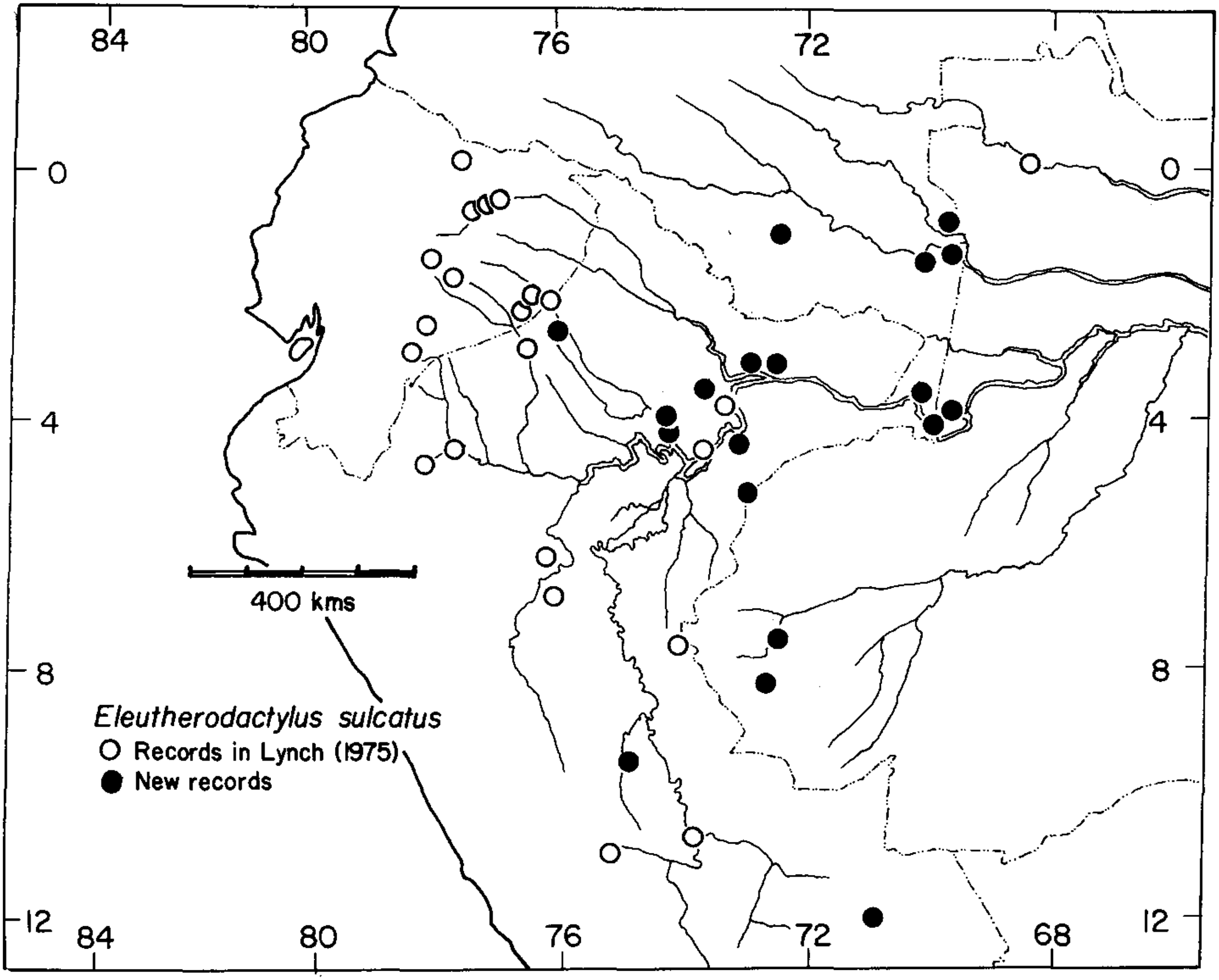

Figure 16. Map of western Amazonia, showing locality records for *Eleutherodactylus sulcatus*.

(6) posterolateral process of otic ramus: In most *Eleutherodactylus*, the otic ramus of the squamosal is parallel to the sagittal plane or it angles toward the sagittal plane posteriorly. However, in *E. necopinus* and *E. ruizi*, the otic ramus flares laterally posteriorly.

(7) median border of choanae angular: In *E. necopinus* and *E. ruizi*, the postchoanal portion of the vomer is straight (not curved) and approximately perpendicular to lateral border of the prechoanal portion of the vomer. The plesiomorphic condition, seen in all other *Eleutherodactylus*, demonstrates a curved lateral border to the choana.

(8) elongate otic shelf: **Lynch** (1981) noted that *E. ingeri, E. ruizi* (then including *E. necopinus*), and *E. sulcatus* share an elongated otic shelf covering much of the *cristae paroticae* dorsally and argued that the feature was a synapomorphy. Ontogenetic data confirm the polarity (see Fig. 14). This feature is seen as well in *E. necopinus* (here separated from *E. ruizi*) but not in the remaining species of the *sulcatus* group (nor elsewhere among the other 293 species of *Eleutherodactylus* examined by me).

(9) narrow (triangular) vomerine odontophores: Although **Lynch** (1975) argued that triangular odontophores are plesiomorphic within *Eleutherodactylus*, **Lynch** (1981) suggested that such processes represented a reversal for *E. ruizi*. The narrow odontophores seen in *E. necopinus* and *E. ruizi* are here treated as a derived condition within the *sulcatus* group. Inspecting juveniles of *E. cerates, E.*

ingeri, and *E. sulcatus* confirms **Lynch's** (1975) earlier view but cannot serve to reject **Lynch's** (1981) hypothesis, which is an unfalsifiable one. As popular as such *ad hoc* hypotheses might be, because they are unfalsifiable, they cannot be used in serious proposals of phylogenetic relationships, and this trait is not employed here.

Of the eight characters identified above, two (6 and 7) contain exactly the same phylogenetic information content (that *E. necopinus* and *E. ruizi* are sister species). Because those two characters have the same information content, I am not able to argue that they represent independent estimates of relationships; accordingly, only character 6 is used here. Character 8 is incompatible with characters 2, 3, 4, and 5. It may be that character 8 provides us with useful information but the choice is between viewing character 8 as misinformative or viewing characters 2-5 as misinformative, when each of the five characters provides an independent estimate of relationships. Character 6 (and/or 7) is compatible with each set. Characters 1-6 are combinable to produce a partially resolved hypothesis (Fig. 17). The incompleteness of this diagram is

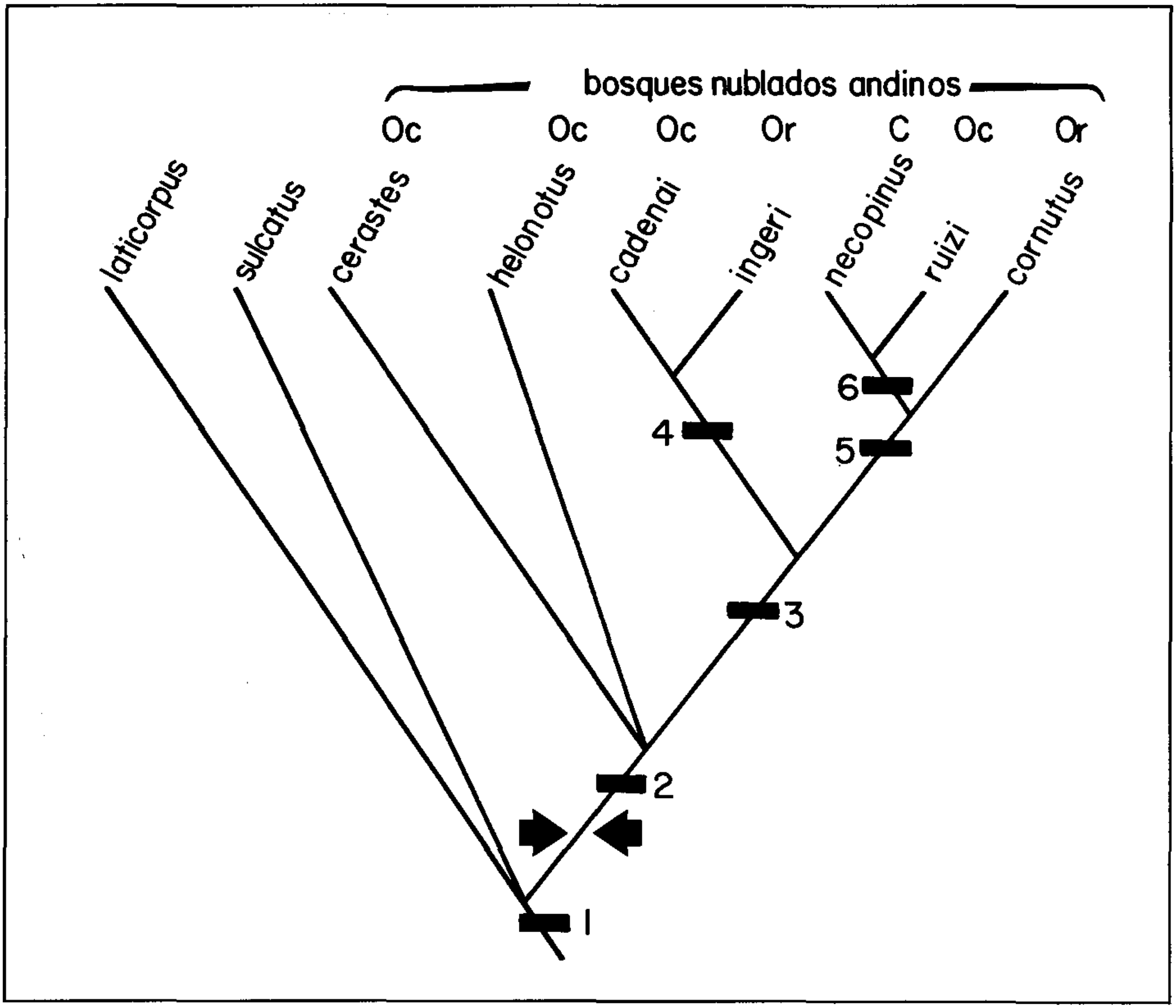

Figure 17. Cladogram of species of the *sulcatus* group. Numbers refer to characters identified in the text. Arrows indicate the optimized entry of this clade onto the Andes. For the andean clade, localities for species are indicated by Oc (Cordillera Occidental), Or (Cordillera Oriental), and C (Cordillera Central).

caused not by too much (conflicting) data, but rather by too little data. No data are available to resolve the trichotomy between *E. laticorpus, E. sulcatus*, and the Andean clade or to resolve the trichotomy between *E. cerastes, E. helonotus*, and the remaining Andean taxa. I suspect that these shortcomings derive from the dearth of knowledge concerning *E. helonotus* (skeleton known only from radiographs and limited dissection) and *E. laticorpus* (skeleton known only from a single immature female).

Although a fully resolved cladogram would be preferable to that presented in Figure 17, the data are not available and will not be available until those two rare frogs (*E. helonotus* and *E. laticorpus*) are better represented in collections. I have optimized (i.e., mapped) geography upon the cladogram and cloud forest habitats appear to be derived. Nonetheless, the most significant components of the cladogram are (1) that the Andean, or cloud forest, species form a clade within the *sulcatus* group and (2) that the general area cladogram for the Andes is [C. Oriental (C. Central + C. Occidental)], following the method of **Nelson & Platnick** (1981). If one views the *cadenai-ingeri* clade as a manifestation of the general component (represented by the *ruizi-necopinus-cornutus* clade), a paralogous[3] biogeographic relationship is identified. The absence of the first clade in the Cordillera Central can be explained by a postulated extinction (scarcely rejectable) or by inadequate collecting (the *ad hoc* hypothesis I prefer because it is possibly rejectable, i.e., a species not the nearest relative of *E. cadenai* might be found there).

With my prediction (here) of an undiscovered sister-species of *E. cadenai* in the Cordillera Central, we have a repeated set of components (paralogous) – C. Occidental + C. Central and C. Occidental + C. Central + C. Oriental as well as other elements in the cladogram representing the C. Occidental. This paralogy merely indicates that the diversification of the Andean clade of the *E. sulcatus* group antedates those Andean orogenies that produced the present geography.

Relationships of the sulcatus group to other Eleutherodactylus. **Lynch & Duellman** (1997) identified the *sulcatus* group as a Series within the subgenus *Eleutherodactylus*, in part anticipating this study. They provided a re-assessment of the general architecture of subgeneric classification of the genus and the convention of "Sections" was employed in anticipation that some additional subgenera would be recognized. The *sulcatus* group is one of several mainland groups exhibiting the plesiomorphic condition of toe lengths within the genus. Plesiomorphic features cannot be viewed as providing evidence of relationships but it was among other groups exhibiting the plesiomorphic condition of toe length that I was inclined to search for the sister group to the *sulcatus* group. The *nigrovittatus* group (**Lynch**, 1989) is here identified as the possible sister-group to the *sulcatus* group. Initially, such an identification appears remote but I would point out that each has arched vomerine odontophores (uncommon features among *Eleutherodactylus* in general) and that the maxilla of species of the *nigrovittatus* group appears deepened relative to most *Eleutherodactylus* (see illustrations in **Lynch**, 1989). At present, I suspect that most of the other similarities (at least to me) between frogs of the *nigrovittatus* and *sulcatus* groups represent plesiomorphies. However, such a relationship (sister groups) seems plausible to me at this juncture and deters me from proposing that the frogs of the *sulcatus* group should be recognized as a distinct subgenus of *Eleutherodactylus*. At present, no other species group (phenetic or cladistic) of *Eleutherodactylus* having the fifth toe shorter than the third appears to have any special similarity with frogs of the *sulcatus* group.

Acknowledgments. This study could not have been completed without the consent to prepare skulls and skeletons of a number of rare frogs. For those courtesies, I am grateful to **Fernando Castro** and, especially, **William E. Duellman** and **Pedro M. Ruiz-C. Barry Clarke** and **W. Ronald Heyer** graciously permitted extended loans of the type specimens of *Amblyphrynus helonotus* until I was able to obtain satisfactory radiographs. **Joseph Mendelson III** ("Sapo") prepared radiographs for me. Access to specimens and research space was provided by **F. Castro**, **W. E. Duellman**, **J. V. Rueda**, **P. M. Ruiz**, and the late **Marco Antonio Serna**. **William W. Lamar** graciously provided photographs and locality records for *E. sulcatus*, obtained during his explorations of Amazonian Peru. **Janalee Caldwell** and **Claude Gascon** loaned me material collected recently in western Brasil. **César Román-V.**, and especially, **J. Vicente Rueda-A.**, made efforts to increase the number of specimens available. Lastly, I am grateful for the companionship and help in fieldwork of **María Cristina Ardila**, **Fernando Castro**,

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[3] In recent years, authors have begun to apply phylogenetic terminology to biogeographic constructs. One such application uses the notion of paralogy (a form of serial homology identified to relate gene duplications) as an analogy in biogeography. Such paralogies have recently been considered a problem (**Nelson & Ladiges**, 1996) for authors using computer methods to generate area cladograms, on the grounds that paralogies do not represent independent estimates. The quest for "paralogy-free" trees seems to me an unnecessary precaution (as more inclusive groups are analyzed, the extent of paralogy increases to 100%, there being a single planet upon which life is known to occur).

Taran Grant, Jorge Restrepo, and **Pedro Ruiz,** on various occasions, during the past twenty years when I have searched for frogs of this species group.

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Appendix 1 (Specimens Examined)

Material reported previously with correct identifications (**Lynch**, 1975, 1986b; **Myers** and **Lynch**, 1997) is not listed here. For *E. sulcatus*, I also include records generously provided by Bill Lamar (those are documented by photographs and specimens deposited in Latin American collections). Institutional identifications follow **Leviton** et al. (1985). Cleared and stained skeletons for Alizarin only are identified as (A) whereas those stained for cartilage as well are identified as (AA).

Eleutherodactylus cadenai. (1). See **Lynch** (1986b).

Eleutherodactylus cerastes. (67). See **Lynch** (1975). COLOMBIA, Depto. Antioquia: Municipio Frontino, corregimiento de Murrí, carr. Nutibara a La Blanquita, Alto Cuevas, 1900 m (ICNMHN 14303 AA, 14304), km 16.5-17, carretera Nutibara a La Blanquita, 1900 m (ICNMHN 16601), 1700 m (ICNMHN, VR 3342-45, 3445-46), Municipio Urrao, "Pampas", Parque Nac. Natural Las Orquídeas (CSJ 301, holotype of *Eleutherodactylus sernai*, 328), Río Calles (CSJ 1033, 1049, 1060, 1099-1100, ICNMNH 14096, UVC 8274), vereda Calles, Quebrada de las Canoas, 1770-1870 m (ICNMNH 19205-07), Quebrada El Silencio, 1480-1540 m (ICNMHN 19208). Depto. Cauca: Municipio El Tambo, corregimiento 20 de julio, Fundación Proselva, Hda. El Tambito, 1470-1580 m (ICNMHN 33016, UVC, 1 not catalogued). Dept. Chocó: límite con Valle del Cauca, Municipio San José del Palmar, 26 km del cementerio El Cairo, 5.7 km por camino W Boquerón, 1900 m (ICNMHN 29065). Depto. Risaralda: Municipio Mistrató, vereda Mampay, quebrada Sutu, 1700-1940 m (ICNMHN 30513-14). Depto. Valle del Cauca: Municipio Dagua, corregimiento Queremal, finca San Pedro, 1750 m (UVC 11696-97, 11705-06,, 118847-49), Municipio El Cairo, vereda Las Amarillas, Boquerón, 2200-2250 m (ICNMHN 29064), Paso Galápagos, 2000 m (UVC 8029), Municipio La Cumbre, Bosque de San Antonio, ca 2000 m (UVC 5839, 8429), Municipio Yotoco, Bosque Reserva de Yotoco, ca 1600 m (UVC 5837).

Eleutherodactylus cornutus. (46). See **Lynch** (1975). COLOMBIA, Depto. Caquetá: Municipio Florencia, vereda La Portada, km 37.4 de Florencia hacia Garzón, 1350 m (ICNMHN 24240-41). Depto. Putumayo: 10.3 km W El Pepino, 1440 m (KU 168009). ECUADOR, Prov. Napo: 2 km SSW Río Reventador, 1490 m (KU 165222).

Eleutherodactylus helonotus. (2). See **Lynch** (1975), as *Amblyphrynus helonotus*.

Eleutherodactylus ingeri. (19). COLOMBIA, Depto. Cundinamarca: "Bogotá", (BMNH 69.7.25.11), Municipio Albán, Granja Padre Luna, ca 2000 m (ICNMHN 2507); Municipio Cabrera, vereda Nuñez, 16 km S Cabrera, 2400-2800 m (ICNMHN 13753); Municipio Gachal‡, San Isidro, 8 km S Gachal‡, 2350 m (FMNH 81915, holotype); Municipio Tena, [laguna] Pedro Palo, 2000 m (ICNMHN 10507, 10509-10, 13570). Depto. Santander, Municipio Charalá, corregimiento Virolín, vereda Cañaverales, carrretera El Olival a El Reloj, ca 1700 m (ICNMHN 4662, 6167-72, 6173 AA, 7380), Cuchilla de Fara, 3.5 km W Cañaverales, 1750 m (ICNMHN 32399, 33168).

Eleutherodactylus laticorpus. (5). See **Myers & Lynch** (1997).

Eleutherodactylus necopinus. (62). COLOMBIA, Depto. Antioquia: El Clara Creek (AMNH 39978-80), Medellín (AMNH 38639, 38649), Valdivia (FMNH 69742); Municipio Cocorná, autopista Medellín-Bogotá, Km. 65, Quebrada El Bihao, 1900-2000 m (ICNMHN 13967), vereda La Roca, Km. 62, 2000 m (ICNMHN 13968 AA, 13969). Depto. Caldas: Municipio Pensilvania, Km 24 vía Pensilvania a Arboleda, 2000-2150 m (ICNMHN 37573), Municipio Samaná, corregimiento Florencia, Rancho Quemado, 1950 m (ICNMHN 32280, 32284), El Estadero, 1800-2000 m (ICNMHN 37574-96, 37610-11 AA), 1850 m (ICNMHN 37597-608, 37609 AA. Depto. Quindío: Municipio Filandia, vereda El Roble, Reserva Forestal Buena Quebrada, 2050 m, (ICNMHN 24604). Depto. Risaralda: Municipio Pereira, vereda La Suiza, Hda. Suiza, 1950 m (ICNMHN 13724, 28614, 37612, 37613-14 AA, MOM 140-41, 186, IND-AN 5397). Depto. Tolima: Quindío mountains (MCZ 8237-38).

Eleutherodactylus ruizi. (19). COLOMBIA, Depto. Valle del Cauca: Municipio Dagua, Atuncelas, 1000-1400 m (UVC 6896, 10449), Municipio La Cumbre, vereda Chicoral, corregimiento Bitaco, 1800 m (UVC 10008, 21566), Hda. Himalaya, El Silencio, 1900 m (UVC 10906); Municipio Restrepo, Río Calima, Quebrada Las Ollas, 1180 m (ICNMHN, not catalogued, jhr 2573), Municipio Yotoco, Reserva Forestal Yotoco, 1590 m (KU 181992-93, ICNMHN 4933, 4961-62, 5211, 35086-87, UVC 5834-36, 5838, 5902).

Eleutherodactylus sulcatus (168) (See **Lynch**, 1975). No data (KU 100355, 124227 A). BRASIL, Edo. Acre : 5 uncatalogued specimens, Univ. Oklahoma Mus. Nat. Hist. Edo. Amazonas: Igarapé Belém, near Río Solimões (AMNH 97043-48), headwaters of Río Juruá (3 uncatalogued specimens, INPA, records courtesy of Claude Gascon). COLOMBIA, Depto. Amazonas: 50 km N La Chorrera (ICNMHN 3462), La Pedrera, 240 m (ICNMHN 36461-62), Puerto Nariño (MCZ 93642, 96856). Depto. Vaupés: Pamopetá, caño T' (W. Lamar, pers. comm.), Serranía Taraica, 240 m (ICNMHN 33662), Timbó (IND-AN 637). ECUADOR, Prov. Morona-Santiago: Cusuime, Río Cusuime, 320 m (AMNH 93657-67), Macuma (UIMNH 63075-76), Río Pastaza watershed (FMNH 36700), between Río Santiago and Río Pastaza, south of Macas, and the mouth of the Río Marañon (FMNH 42527). Prov. Napo: Avila, Río Napo (CAS-SU 5042), 30 km downriver (Río Napo) from Coca, 250 m (MCZ 95439), Lago Agrio, 330 m (KU 125937, 126172-76), Limon Cocha (UIMNH 90804), Puerto Libre, Río Aguarico, 570 m (KU 124128 AA), Santa Cecilia, 340 m (KU 123584AA, 126169-71AA, 146120, 148982, MCZ 58014). PERU, Depto. Huánuco: Río Llullapichis, 4-5 km upstream from Río Pachitea, finca Panguana (KU 171849-51), S slope Serranía Sira, "Pata Rojo", 1100 m (KU 154800). Depto. Loreto: Colonia (MNHN 1979.38-44), Caucho Caño, Río Momón (W. Lamar, pers. comm.), Explorama, vicinity of Yanamono (W. Lamar, pers. comm.), ExplorNapo, Río Sucusari (W. Lamar, pers. comm.), Monteverde, Río Tigre (W. Lamar, pers. comm.), Nuevo Horizonte, Río Tahuayo (W. Lamar, pers. comm.), Paujíl, Río Gálvez (W. Lamar, pers. comm.), 1.5 km N Teniente Lopez, 310-340 m (KU 222032), veintiocho, Río Nahaupa (W. Lamar, pers. comm.), Yagua village, headwaters of Río Loretoyacu (AMNH 96331-38), junction Río Yanamono and Río Amazonas (KU 220358, 220450). Depto. San Martín: 28 km NE Tarapato (KU 209478).