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A SYNOPSIS OF THE FROGS  
OF THE GENUS *ELEUTHERODACTYLUS*  
FROM THE SIERRA NEVADA  
DE SANTA MARTA, COLOMBIA

BY JOHN D. LYNCH\* AND PEDRO M. RUÍZ-CARRANZA†

ABSTRACT.—Lynch, John D., and Pedro M. Ruíz-Carranza. 1985. A synopsis of the frogs of the genus *Eleutherodactylus* from the Sierra Nevada de Santa Marta, Colombia. *Occ. Pap. Mus. Zool. Univ. Michigan*, 711:1–59, figs. 1–21. The frogs of the genus *Eleutherodactylus* found in the Sierra Nevada de Santa Marta of Colombia include eight endemic species. Limited material is also available for two non-endemic species (*E. ruizi* and *E. w-nigrum*). The endemic species include those named by Ruthven (*E. carmelitae*, *E. delicatus*, *E. insignitus*, *E. megalops*, and *E. sanctaemartae*) as well as three species named here (*E. cristinae*, *E. ruthveni*, and *E. tayrona*). Diagnoses, descriptions, and illustrations are provided for all endemic taxa. All species of the genus found in the Sierra Nevada occur in cloud forests (1100–2500 m). All species are apparently active at night. Four are terrestrial (*E. carmelitae*, *E. megalops*, *E. insignitus*, and *E. ruthveni*), one is exclusively found in and on bromeliads (*E. tayrona*), and three are essentially leaf litter denizens by day but found on vegetation at night (*E. cristinae*, *E. delicatus*, and *E. sanctaemartae*). The non-endemic taxa are terrestrial. Jaw musculature and cranial osteology are described and skulls are illustrated for nine species (endemic species and *E. w-nigrum*).

On the basis of cranial morphology and external features, hypotheses of relationships with taxa in the Antilles and the Coastal Range of Venezuela are rejected. The affinities of species from the Santa Marta mountains are either with species found in the northern Andes of Colombia or with other Santa Martan species, but the lack of comparable data sets outside of the Sierra

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Nevada prevents definitive arguments. The Santa Martán fauna offers some support for the suggestion of Savage and DeWeese (1979, 1981) that Lynch's (1976) species-group arrangement is artificial.

Key words: *Eleutherodactylus*, *Colombia*, *frogs*.

RESUMEN.—Las ranas del género *Eleutherodactylus* que se encuentran en la Sierra Nevada de Santa Marta (Colombia) incluyen ocho especies endémicas. También hay muestras limitadas para dos especies que no son endémicas (*E. ruizi* y *E. w-nigrum*). Las especies endémicas incluyen aquellas descritas por Ruthven (*E. carmelitae*, *E. delicatus*, *E. insignitus*, *E. megalops*, y *E. sanctaemartae*) así como también tres especies nuevas descritas aquí (*E. cristinae*, *E. ruthveni*, y *E. tayrona*). Se presentan diagnósis, descripciones, e ilustraciones para todas las especies endémicas. Todas las especies que se encuentran en la Sierra Nevada ocurren en bosques nublados (1100–2500 m.s.m.) y evidentemente todas son de actividad nocturna. Cuatro especies son terrestres (*E. carmelitae*, *E. megalops*, *E. insignitus*, y *E. ruthveni*), una se encuentra únicamente dentro y sobre bromelias (*E. tayrona*), y tres ocurren en hojarasca durante el día pero se encuentran encima de la vegetación en la noche (*E. cristinae*, *E. delicatus*, y *E. sanctaemartae*). Las especies que no son endémicas son terrestres. Se describen la musculatura mandibular y la osteología craneal (y se ilustran los cráneos de nueve especies) (las endémicas y *E. w-nigrum*). Basados en la morfología craneal y en los caracteres externos, no compartimos las hipótesis de relaciones con especies de las Antillas y de la Cordillera de La Costa de Venezuela. Las especies de *Eleutherodactylus* de la Sierra Nevada pueden tener afinidades con especies de las Andes al norte de Colombia ó con especies de la Sierra Nevada de Santa Marta, ó con ambas, pero la carencia de datos comparables de las especies de Los Andes nos impide presentar argumentos definitivos en su favor. La fauna de Santa Marta ofrece algunas pruebas para las sugerencias de Savage y DeWeese (1979, 1981) en el sentido de que el arreglo de grupos de especies propuesto por Lynch (1976) es artificial.

Palabras clave: *Eleutherodactylus*, *Colombia*, *rana*.

## INTRODUCTION

The Sierra Nevada de Santa Marta (Fig. 1) rises abruptly from a roughly triangular base out of the Caribbean lowlands of northern Colombia to an altitude of 5800 m. Its herpetofauna was described by Alexander Ruthven (1922) whose work remains the most useful reference concerning the Santa Martán amphibians and reptiles even today. Duellman (1979) characterized the amphibian fauna of the Sierra Nevada as Andean and largely endemic. The forests of the Caribbean lowlands are dry forests (Espinal, 1977) with an amphibian fauna typical of seasonal climates (*Bufo*, *Ceratophrys*, *Hyla*, *Leptodactylus*, and *Physalaemus*) contrasting sharply with the wet cloud forests of at least the northern and western flanks of the Sierra Nevada. At elevations above 1000 m, the only amphibian genera are those typical

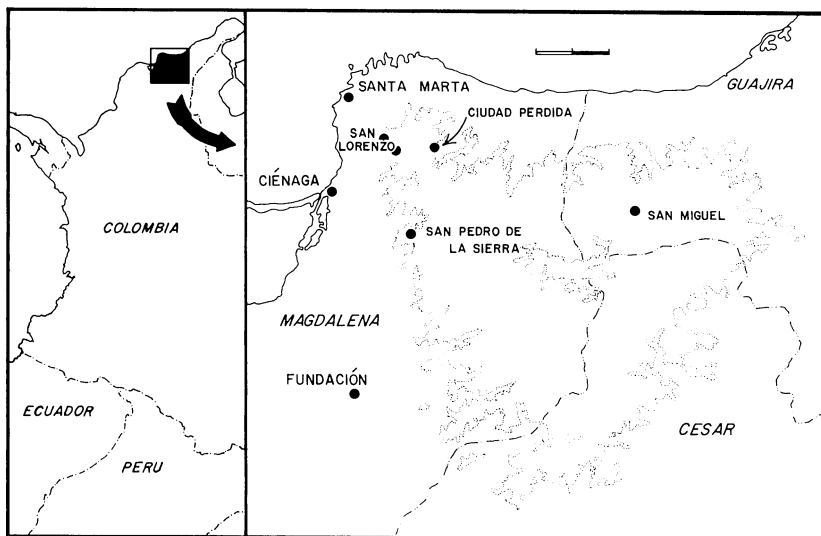


FIG. 1. Map of Sierra Nevada de Santa Marta showing localities and place names mentioned in text. Contour lines of 1000 and 4500 meters are shown. Scale equals 20 km.

of the northern Andes—*Atelopus*, *Bolitoglossa*, *Centrolenella*, *Colostethus*, *Cryptobatrachus*, and *Eleutherodactylus*, as well as *Geobatrachus*, an endemic eleutherodactyline genus (Ardila, 1979).

The Sierra Nevada is isolated both ecologically and physically from the other highland areas of northwestern South America. In spite of its isolating lure, relatively little herpetological exploration has been accomplished since the investigations in the early part of the century. An even more severe shortage of investigation has been directed at the geographically proximate Serranía de Perijá and northern Cordillera Oriental. Presently, the region is rendered even more isolated by the activities of illicit agriculture.

Of the seven amphibian genera known from the Sierra Nevada de Santa Marta, only *Eleutherodactylus* is represented by appreciable diversity. *Atelopus* is represented by two endemic species. *Bolitoglossa* is represented by *B. savagei*, which was also reported from the Mérida Andes of Venezuela (Brame and Wake, 1963). *Colostethus* is represented by two endemic species, one at low elevations (500–700 m) and one in higher cloud forests (Duellman, 1979; Ruthven, 1922; personal observations). The genera *Centrolenella*, *Cryptobatrachus*, and *Geobatrachus* are represented by one endemic species each. At least

nine species of *Eleutherodactylus* are known from the Sierra Nevada (we question the record of a tenth, *E. ruizi*).

Alexander Ruthven (1915) reported a frog which he called *Hylodes cruentus* Peters from the Sierra Nevada and described its reproductive biology. He later (Ruthven, 1917a, 1917b, 1917c, 1922) named five species of *Eleutherodactylus* (*E. carmelitae*, *E. delicatus*, *E. insignitus*, *E. megalops*, and *E. sanctaemartae*) from cloud forest sites on the northern slopes of the massif. Thus, in 1922, the eleutherodactyline frog fauna of the Sierra Nevada consisted of five endemic species named by Ruthven and *E. cruentus* (reported from the Sierra as well as Lower Central America).

Cochran and Goin (1970) reported five other species of *Eleutherodactylus* from the Sierra (*E. affinis*, *E. calcaratus*, *E. cornutus cornutus*, *E. vertebralis*, and *E. w-nigrum*) and further reduced the once-apparent endemicity with reports of *E. megalops* from Departamento Cundinamarca (Cordillera Oriental) and of *E. sanctaemartae* from Departamento Tolima (Cordillera Central). Lynch (1975) considered the juvenile specimen reported as *E. cornutus* by Cochran and Goin (1970) to be *Amblyphrynus ingeri* (also reported by him from the Cordilleras Central and Oriental) but later (Lynch, 1981a) corrected a previous error by recognizing *E. ruizi* as distinct from *E. ingeri*. He reported the Santa Martan specimen as *E. ruizi*. We are doubtful of that record and believe that *E. ruizi* occurs only in cloud forests in the Cordilleras Central and Occidental of Colombia. Lynch (1978) reported *E. prolixodiscus* from the northern Cordillera Oriental of Colombia and from the Sierra Nevada. In the same paper, he pointed out that the frogs reported as *E. cruentus* by Ruthven (1915, 1922) represent a composite (*E. prolixodiscus* and an undescribed taxon, "Ruthven's *cruentus*") [but see the account for *E. tayrona*, named below] and that Cochran and Goin's Santa Martan records of *E. affinis*, *E. calcaratus*, and *E. vertebralis* were based on misidentifications.

The record of *E. megalops* (MCZ 19223, 19952–55) from Chamega (possibly equals Chamizal?), Depto. Cundinamarca, is based on a misidentification, although we are not prepared to identify those specimens at this time. Cochran and Goin's (1970) record of *E. sanctaemartae* from Departamento Tolima is based on an adult female (UMMZ 56435) of *E. sanctaemartae*. We are inclined to believe that the locality data stem from a confusion of data. Cochran and Goin's (1970) record of *E. w-nigrum* from the Sierra Nevada is based on one of Ruthven's paratypes of *E. insignitus* (MCZ 4074); we agree with the identification but find it difficult to understand why Ruthven would

fail to note so different a frog in his series of types. Lynch (1978:21) regarded the record as questionable.

At present, six species are considered Santa Martan endemics (*E. carmelitae*, *E. delicatus*, *E. insignitus*, *E. megalops*, *E. sanctaemartae*, and "Ruthven's *cruentus*"), one species is non-endemic (*E. prolixodiscus*), and two other non-endemic species (*E. ruizi* and *E. w-nigrum*) are questionable.

Although Duellman (1979) and Lynch (1978) pronounced the Santa Martan fauna Andean, their conclusions are based on the use of shared elements, a methodology now known to yield erroneous results (Nelson and Platnick, 1981:398–409; Savage, 1982:498–500). Other authors have suggested affinities with the fauna of the Coastal Range of Venezuela (Rivero, 1961; Walker and Test, 1955) or the West Indies (Lynch, 1976:17).

Our interest in the *Eleutherodactylus* of the Sierra Nevada is prompted by a desire to understand the evolution of the genus in northwestern South America. Because the massif shows some Andean influence and because it is so trenchantly isolated (ecologically and geographically) from the Andes, we anticipated that a study of the relationships of the *Eleutherodactylus* there might (1) allow some resolution of the debate about the relationships among frogs of the genus in general (Lynch, 1976; Savage and DeWeese, 1979, 1981) and (2) allow some resolution of the various biogeographic suggestions (Andean, Antillean, and Coastal Range).

The junior author carried out herpetological investigations in the Sierra Nevada in May 1976 collecting on the Serranía San Lorenzo (around and possibly above Ruthven's major collecting area) on the northwestern flank and in the cloud forests above San Pedro de la Sierra on the western flank. We collected together on the Serranía San Lorenzo in late June 1983 in order to obtain information on the natural histories of the frogs as well as to take photographs and color notes of living frogs. Early in the study of the preserved materials we realized that additional undescribed species occurred on the Sierra Nevada and that Lynch (1978) erred in identifying Santa Martan frogs as *E. prolixodiscus*. The collections we have gathered (housed in the Instituto de Ciencias Naturales) include specimens of nine species of *Eleutherodactylus* (*E. carmelitae*, *E. delicatus*, *E. insignitus*, *E. megalops*, *E. sanctaemartae*, *E. w-nigrum*, and three new species which are described herein). Although we are confident that the eleutherodactyline fauna of the Serranía San Lorenzo is now known, we suspect that additional species will be found as other areas of the Sierra Nevada are subjected to intensive collecting.

## MATERIALS AND METHODS

We have examined 1053 specimens of the nine species discussed in this paper including the holotypes of all names except *Hylodes w-nigrum* (photos seen). Skeletons were prepared as Alizarin-red preparations. All measurements were taken with dial calipers to the nearest 0.1 mm. Terminology follows that of Lynch and Duellman (1980) except for jaw musculature (which follows Starrett, 1968). Throughout the text, specimens are identified by their catalogue numbers and an acronym for the museum collection. Those acronyms are:

BMNH	British Museum (Natural History), London
ICN	Instituto de Ciencias Naturales, Bogotá
INDERENA	Instituto Nacional de Recursos Naturales y del Ambiente, colección batracológica, Venado de Oro, Bogotá
KU	Museum of Natural History, University of Kansas, Lawrence
LACM	Natural History Museum, Los Angeles County, Los Angeles
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
SCNLS	Sociedad de Ciencias Naturales La Salle, Caracas
SMF	Senckenbergen Naturforschenden Forschungsinstitut, Frankfurt-am-Main
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C.

KEY TO SANTA MARTAN  
*ELEUTHERODACTYLUS*

The species of the Sierra Nevada are easily distinguished if adults are available because they differ in body size and expression of cranial crests. Adult males of three species (*E. insignitus*, *E. ruthveni*, and *E. sanctaemartae*) lack nuptial pads on the thumbs. The sizes (expressed as SVL:snout-vent lengths) of adults (examined by us) of the nine Santa Martan species are listed below with indications of which have cranial crests (name, size range of males in mm, size range of females in mm, and cranial crests if any):

<i>E. carmelitae</i>	29.9–39.2	36.4–48.8	no crests
<i>E. cristinae</i>	37.8–42.7	58.2–62.7	crests in ♀♀
<i>E. delicatus</i>	22.1	27.9–31.3	crests in ♀♀
<i>E. insignitus</i>	41.2–41.8	48.4–55.8	no crests
<i>E. megalops</i>	18.9–27.1	27.7–34.4	no crests
<i>E. ruthveni</i>	24.5–32.3	31.1–45.5	crests in ♀♀
<i>E. sanctaemartae</i>	24.9–40.6	39.2–45.7	no crests
<i>E. tayrona</i>	15.1–25.1	22.6–30.2	no crests
<i>E. w-nigrum</i>	31.8–42.0	57.5–67.0	no crests

1. Skin of venter smooth .....	2
Skin of venter arcolate .....	4

2. Tympanum recessed in cavity ..... *E. carmelitae*  
 Tympanum superficial ..... 3
3. Groin and concealed surfaces of thighs dark, with pale spots; no vocal  
 slits in males; narrow pads on digits (Fig. 2) ..... *E. insignitus*  
 Groin and concealed surfaces of thighs cream, spotted with black;  
 vocal slits in males; broader pads on digits ..... *E. w-nigrum*
4. Posterior surfaces of thighs bearing brown network ..... *E. megalops*  
 Posterior surfaces of thighs various but never finely reticulated with  
 brown, either uniformly colored or bearing pale spots or blotches ..... 5
5. Posterior surfaces of thighs uniform brown; no enlarged heel  
 tubercles ..... 6  
 Posterior surfaces of thighs spotted or barred with brown or bearing  
 large pale spots; elongate tubercle on heel or not ..... 7
6. Digits bear large pads (Fig. 2) ..... *E. tayrona*  
 Digits bear narrow pads (Fig. 3) ..... *E. ruthveni*
7. Upper eyelids bearing conical tubercles; heel and outer edge of  
 tarsus bearing pungent tubercles ..... 8  
 Upper eyelids, heel, and outer edge of tarsus bearing only small,  
 non-conical tubercles; posterior surfaces of thighs bearing large  
 pale (yellow or orange) spots; digital pads large (Fig. 3) ..... *E. sanctaemartae*
8. White stripe on posterior throat and chest; underside of shank barred  
 brown and cream; adult males at least 37.8 mm SVL, adult females  
 at least 58.2 mm SVL ..... *E. cristinae*  
 Throat and venter cream with brown spots (no chest stripe);  
 underside of shank spotted cream, brown, and black;  
 adults less than 35 mm SVL ..... *E. delicatus*

### ACCOUNTS OF SPECIES

The following accounts provide diagnoses (and, if necessary, descriptions), data on measurements and proportions, colors in life, and natural history notes for each of the nine species of *Eleutherodactylus* we recognize in the Sierra Nevada. We consider the published descriptions of *E. carmelitae*, *E. insignitus*, and *E. megalops* adequate and do not redescribe these species. We provide a description of *E. sanctaemartae* [even though that of Cochran and Goin (1970) is adequate] because we have a more complete survey of its variation. The published descriptions of *E. delicatus* by Ruthven (1917c) and by Cochran and Goin (1970) are inadequate because they are based on a juvenile of indeterminate sex and a juvenile (not an adult) female, respectively. These accounts are intended to facilitate comparisons with other species and to update the information base on each species. In some cases, taxonomic issues are discussed (under Remarks). Aside from including relevant data in the diagnoses, osteological and myological data are not reported in the accounts of species (see Cranial Morphology). The species groups mentioned in the text are those of Lynch (1976).

*Eleutherodactylus carmelitae* Ruthven

Figs. 2, 4–5, 17

*Eleutherodactylus carmelitae* Ruthven, 1922:51–52 (Holotype, UMMZ 54528, a juvenile female, obtained at Quebrada Viernes Santo, Cerro San Lorenzo, Depto. Magdalena, Colombia, 5000 ft. [1524 m], on 16 July 1920 by A. G. Ruthven); Cochran and Goin, 1970:421–23.

DIAGNOSIS.—1) skin of dorsum smooth with low, flat warts, that of venter smooth; indistinct dorsolateral folds; 2) tympanum obscure, resting in a depression on side of head; 3) snout ovoid in dorsal view, rounded in lateral profile; snout short; canthus rostralis rounded; 4) IOD as wide as upper eyelid; no cranial crests but interorbital region furrowed because muscles extend anteriorly on skull; no tubercles on upper eyelid; 5) vomerine odontophores large, oval in outline, separated medially by a distance equal to  $\frac{1}{3}$  an odontophore width; 6) males lack vocal sac and slits; glandular, gray nuptial pads on thumbs of males; 7) first finger shorter than second (when equally adpressed); digital pads of moderate size, pads of III–IV wider than length of inner metatarsal tubercle; discs broader than long; 8) no lateral fringes on fingers; 9) no ulnar tubercles; 10) no tubercles or folds on heel or tarsus; 11) two metatarsal tubercles, inner elongate, 3 times size of outer; no supernumerary plantar tubercles; 12) toes lack lateral fringes or keels and webbing; toe pads all wider than length of inner metatarsal tubercle; 13) brown above with darker blotches; markings on limbs and flanks edged with cream; venter dusky cream with cream spots; posterior surfaces of thighs brown with cream spots; 14) males 29.9–39.2 mm SVL, females 36.4–48.8 mm SVL.

*Eleutherodactylus carmelitae* is assigned to the *fitzingeri* group (*sensu* Lynch, 1976) because it has smooth skin on the venter. However, it is unique among South American taxa of that group in having the first finger shorter than the second (Fig. 2). It is unique in having depressed tympana (Fig. 4)—all other species have superficial tympana.

DESCRIPTION.—See Cochran and Goin (1970:421–423). In life, *E. carmelitae* is green with dark brown to black markings (Fig. 5) edged with pale green (the limbs may be more yellowish-green than dorsum) dorsally; throat dark gray with cream flecks, venter and undersides of legs pale dirty olive-cream; posterior surfaces of thighs brown; tops of digit tips bearing white spots; iris blood red.

*Proportions*: Most specimens examined by us are juveniles. Adult males ( $n = 3$ ): shank/SVL 55.9–59.4 ( $\bar{x} = 57.5$ )%; HW/SVL 38.6–



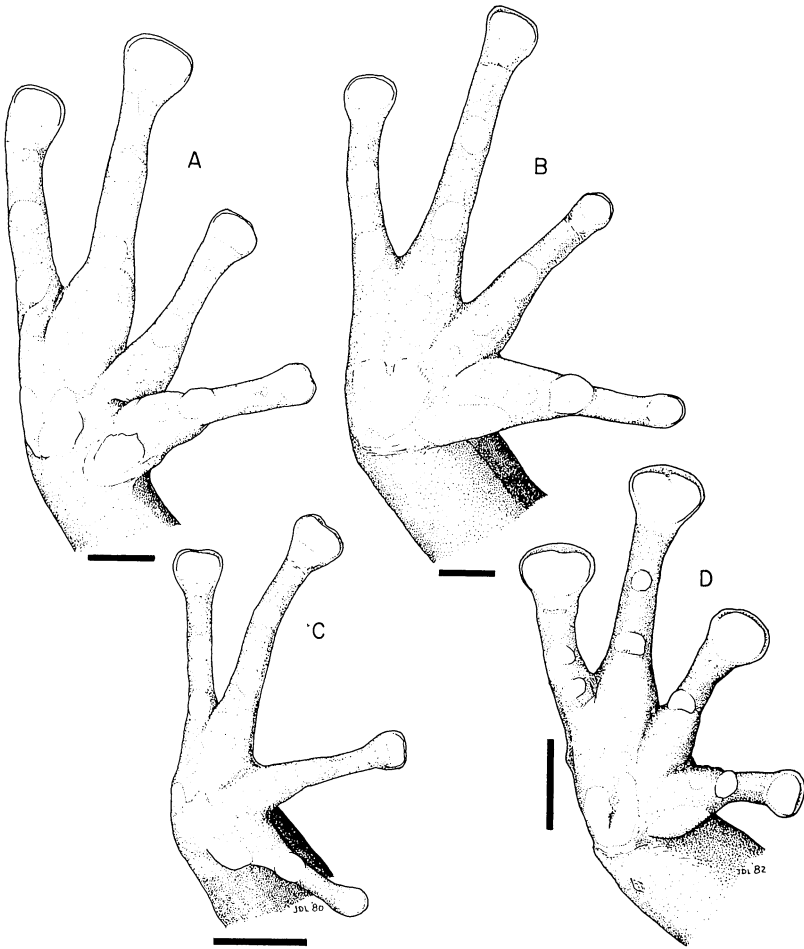


FIG. 2. Hands of Santa Martan *Eleutherodactylus*: (A) *E. carmelitae*, ICN 1654; (B) *E. insignitus*, ICN 701; (C) *E. megalops*, LACM 114501; (D) *E. tayrona*, ICN 3009. Scales equal 2 mm.

40.6 ( $\bar{x}$  = 39.6)%; upper eyelid/IOD 125.0–144.4 ( $\bar{x}$  = 132.1)%; tympanum/eye 19.6–21.2 ( $\bar{x}$  = 20.1)%; E-N/eye 55.4–67.9 ( $\bar{x}$  = 60.9)%. Adult females ( $n$  = 2): shank/SVL 54.2–55.6%; HW/SVL 40.9–41.6%; upper eyelid/IOD 100.0–108.1%; tympanum/eye 21.0–26.2%; E-N/eye 67.2–68.4%.

NATURAL HISTORY.—*E. carmelitae* is a terrestrial, nocturnal frog. During the day, individuals occur beneath rocks or in leaf litter,

especially along streams. At night, specimens are found on the ground or low (less than 20 cm high) vegetation or twigs. During a heavy rain on 29 June 1983, no calling was heard. Unlike other *Eleutherodactylus* found at this site, *E. carmelitae* rapidly hopped away from collectors.

REMARKS.—The lack of congruence of venter texture and finger lengths in this species lends credence to Savage and DeWeese's (1979, 1981) criticism of Lynch's (1976) species groups arrangements for the genus. We place *E. carmelitae* in the *fitzingeri* group with hesitation.

DISTRIBUTION.—Known only from the Serranía San Lorenzo (1524–2200 m) on the northwestern corner of the Sierra Nevada de Santa Marta.

*Eleutherodactylus cristinae* sp. nov.

Figs. 3, 5–7, 19

*Eleutherodactylus vertebralis* (in part): Cochran and Goin, 1970:432.

*Eleutherodactylus delicatus*: Lynch, 1978:21.

HOLOTYPE.—KU 168558, a juvenile female, from W slope Cerro Kennedy, 10 km E El Campaño, Municipio Santa Marta, Depto. Magdalena, Colombia, 1850 m, obtained on 29 June 1974 by William E. Duellman.

PARATYPES.—KU 168561, 11 km E El Campaño, 2000 m; LACM 114499–500, San Lorenzo; ICN 702, 739, Serranía San Lorenzo, 1960–2200 m; ICN 8237, Serranía San Lorenzo, 1900 m; ICN 3950, between Minca and San Lorenzo, 1530–2100 m; UMMZ 176885, Cuchilla Yerbabuena, SE San Pedro de la Sierra, 2000 m.

REFERRED SPECIMENS (JUVENILES).—ICN 8238–39, Serranía San Lorenzo, 1900 m; ICN 2676, Serranía San Lorenzo, 2200–2600 m; ICN 3779, Cincinnati, corregimiento Minca, 1530 m.

DIAGNOSIS.—1) skin of dorsum shagreened (more coarse posteriorly), that of venter areolate; dorsolateral folds reaching level of sacrum; 2) tympanum prominent, round, superficial; 3) snout sub-acuminate in dorsal view, round in lateral profile; snout moderate-length; canthus rostralis sharp; 4) IOD broader than upper eyelid; cranial crests evident in adult females; one tubercle on each eyelid; 5) vomerine odontophores large, oval in outline, separated medially by a distance equal to  $\frac{1}{4}$  an odontophore width; 6) males with internal vocal sac, vocal slits; non-spinous nuptial pads on thumbs of males; 7)

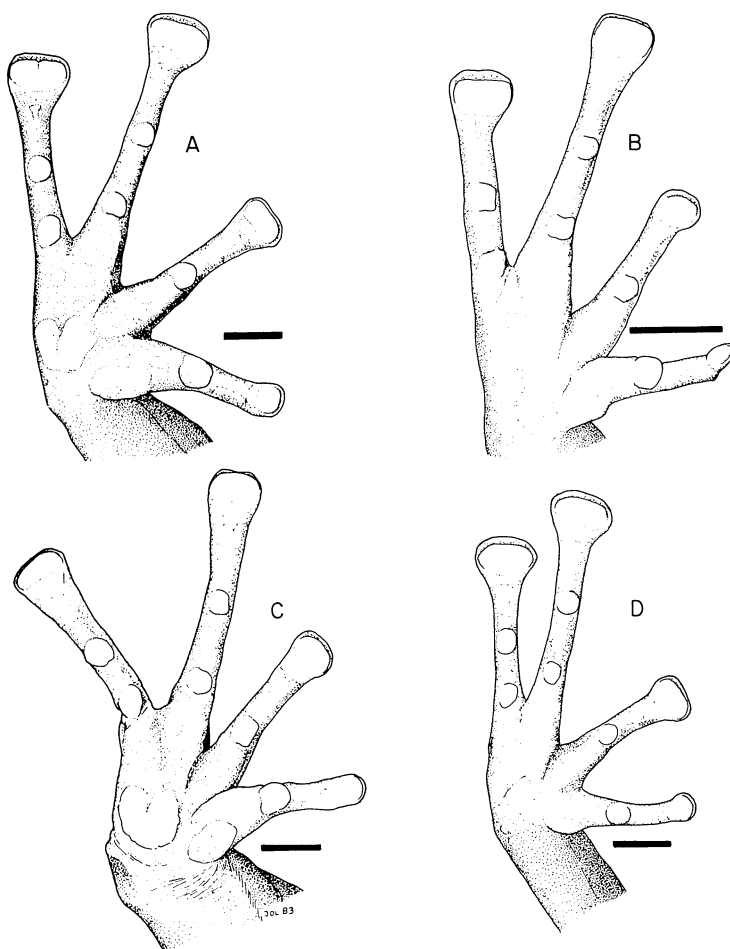


FIG. 3. Hands of Santa Marten *Eleutherodactylus*: (A) *E. cristinae*, LACM 114500; (B) *E. delicatus*, ICN 3029; (C) *E. ruthveni*, ICN 3014; (D) *E. sanctaemartae*, LACM 114508. Scales equal 2 mm.

first finger shorter than second; finger pads large (larger than ear), width of outer pads greater than length of inner metatarsal tubercle; discs broader than long; 8) fingers bear lateral keels; 9) row of subconical ulnar tubercles; 10) tubercles on heel and outer edge of tarsus; 11) two metatarsal tubercles, inner elongate, 4 times size of outer; small supernumerary tubercles at bases of toes II-IV; 12) toes bear lateral keels, no webbing; toe pads smaller than those of fingers;

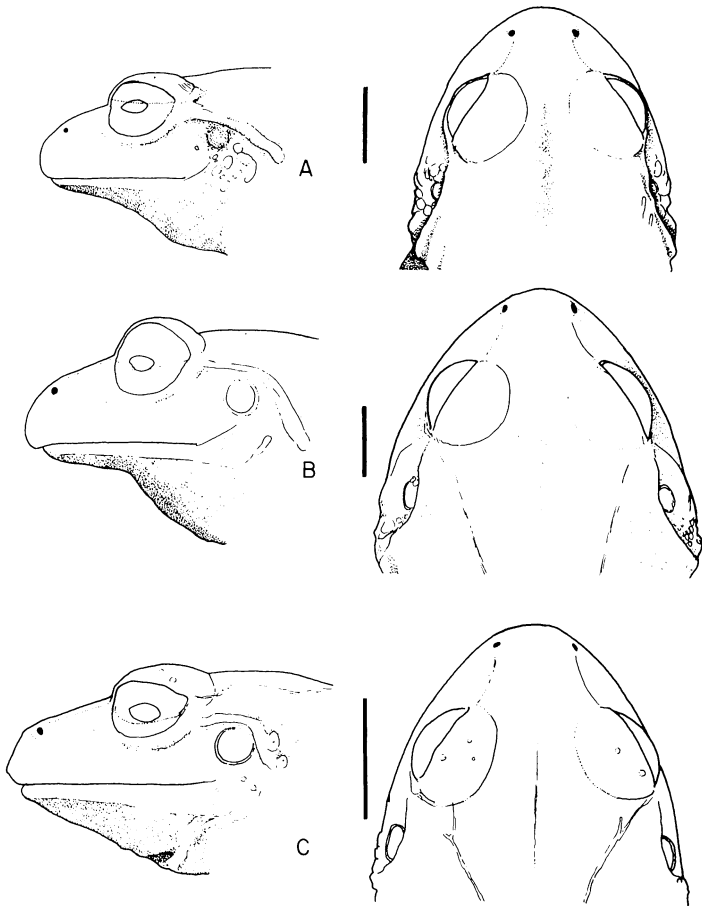


FIG. 4. Heads of Santa Martán *Eleutherodactylus*: (A) *E. carmelitae*, ICN 1654; (B) *E. insignitus*, ICN 701; (C) *E. megalops*, ICN 3013. Scales equal 5 mm.

13) brown above (darkest laterally); row of white warts edged with dark brown on center of throat; throat and chest speckled with brown, otherwise venter cream; posterior surfaces of thighs brown with darker brown blotches; underside of shank barred brown and cream; 14) adults large, 3 males 37.8–42.7 mm SVL, two females 58.2–62.7 mm SVL.

*Eleutherodactylus cristinae* is assigned to the *unistrigatus* group. Among the numerous species of that group *E. cristinae* is distinctive in

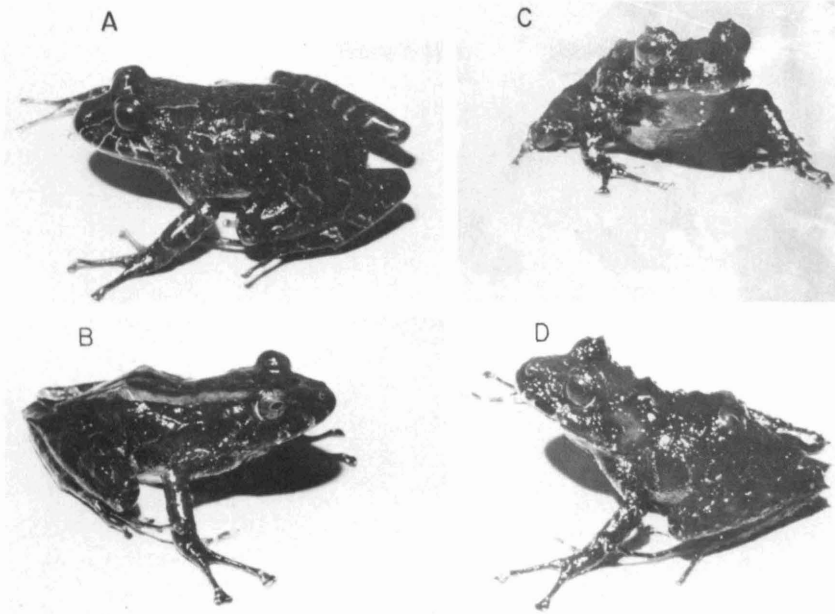


FIG. 5. Santa Martán *Eleutherodactylus*: (A) *E. carmelitae*, ICN 13975, 44.0 mm SVL; (B) *E. cristinae*, ICN 13979, 42.7 mm SVL; (C–D) *E. cristinae*, ICN 13978, 26.1 mm SVL.

the color pattern evident on the concealed surfaces of the limbs (Fig. 6). It is also large for a member of this group (see Lynch and Duellman, 1980:8–9, tables 1–3). Among species in the Sierra Nevada de Santa Marta, only *E. sanctaemartae* has large digital pads (Fig. 3) and similar proportions. However, *E. cristinae* and *E. sanctaemartae* are distinguished readily by size (*E. sanctaemartae* is much smaller), by the presence of cranial crests in adult females of *E. cristinae*, by the more distinct tubercles on the eyelids, forearms, heel, and tarsus of *E. cristinae*, and their color patterns.

**DESCRIPTION.**—Head wider than body, wider than long; snout subacuminate or subovoid in dorsal view, round in lateral profile; snout long; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis distinct (but not sharp), weakly sinuous; loreal region concave, sloping gradually to lips; lips weakly flared (most evident in adult females); prominent non-conical tubercle on upper eyelid (Fig. 7); no cranial crests palpable in males; edges of frontoparietals slightly upturned in females; interorbital space slightly wider than upper eyelid width; supratympanic fold distinct, angular (not



FIG. 6. Undersides of shanks of Santa Martán *Eleutherodactylus*: (A) *E. cristinae*, ICN 3950; (B) *E. delicatus*, ICN 3030; (C) *E. ruthveni*, ICN 3027; (D) *E. sanctaemartae*, LACM 114517. Scale equals 5 mm.

forming gentle curve posterodorsal to tympanum), concealing upper edge of tympanum; tympanum superficial, round, separated from eye by a distance equal to its diameter; postrictal tubercles conical; subconical tubercles anterior to and ventral to tympanum; choanae large, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, separated medially by a distance equal to  $\frac{1}{4}$  width of an odontophore, oval in outline, situated transversely on palate (width  $2\frac{1}{2}$  times length), bearing a transverse row of 8–10 teeth; each odontophore about 3 times size of a choana; tongue longer than wide (almost twice as long as wide), its posterior border shallowly notched, posterior  $\frac{1}{5}$  to  $\frac{1}{3}$  not adherent to floor of mouth; in males, long vocal slits posterolateral to tongue; vocal sac internal.

Skin of dorsum finely shagreened, becoming more coarse on lower back; folds forming “W” on occiput; dorsolateral fold extending from above tympanum to about level of sacrum where fold becomes indistinguishable; limbs shagreened and bearing scattered non-conical warts; flanks coarsely shagreened to warty with scattered larger warts;

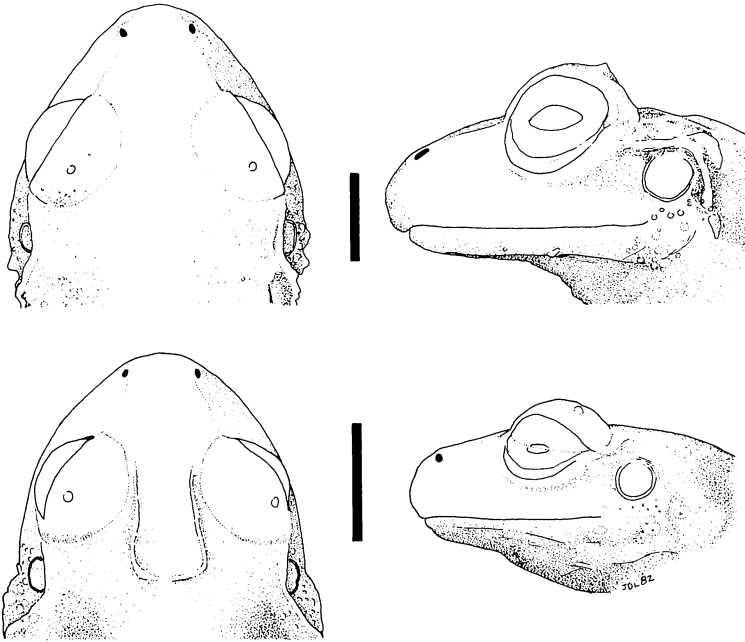


FIG. 7. Heads of *Eleutherodactylus cristinae* (top, LACM 114499) and *E. delicatus* (bottom, ICN 2670). Scale equals 5 mm.

venter areolate as are posterior one-half of ventral surfaces of thighs and area around vent; a pair of subanal warts; discoidal folds ill-defined; no anal sheath; forearm bears a row of subconical ulnar tubercles; palmar tubercle bifid, inner lobe largest; thenar tubercle oval, larger than palmar tubercle; numerous pungent supernumerary palmar tubercles; subarticular tubercles slightly larger than supernumerary palmars, non-conical, round (except for basal on third finger, longer than wide); fingers long and slender (Fig. 3), bearing lateral keels; pads large, apically rounded but almost truncate (no indentations), bearing broader than long discs on their ventral surfaces; pad of I narrower than tympanum, of II as wide as tympanum, of III and IV larger than tympanum; pad of III as wide as length of inner metatarsal tubercle; when equally adpressed, tip of I does not reach base of disc of II; white glandular nuptial pad on thumb of males.

Knee, heel, and outer edge of tarsus bearing subconical tubercles; no tubercles (or fold) on inner edge of tarsus; inner metatarsal

tubercle three times as long as wide, four times size of round, non-conical outer metatarsal tubercle; supernumerary plantar tubercles easily overlooked, small, at base of toes II-IV; subarticular tubercles subconical, longer than wide; toes bear narrow lateral keels but no webbing; toes long, slender; toe pads subtruncate (except on V, round), smaller than those of fingers; when flexed hind legs are held at right angles to sagittal plane, heels broadly overlap.

In preservative, dorsum brown, darkest laterally; edges of ridges and bases of warts dark brown or black; creamy-brown blotches evident on center of back; limbs dark brown; canthal stripe indistinct; supratympanic stripe and labial bars distinct, edged with cream; two labial bars radiating from eye; tympanum darker than adjacent skin; flanks bear ill-defined oblique bars edged with dusky cream, separated by pale areas extending up from venter; anal triangle not apparent; limb bars dark brown, rarely edged with cream; shank bars usually transverse, about as wide as interspaces; dorsal surfaces of inner two fingers and inner three toes cream with sparse brown flecking; venter cream; throat and, to lesser degree, chest speckled with brown; white stripe on chest (Fig. 5); flank color sharply set off from belly color; undersides of thighs cream with diffuse brown margins; undersides of shanks cream with partial brown bars (Fig. 6); anterior surfaces of thighs brown, invaded by thigh bars (edged with cream); posterior surfaces of thighs brown with darker brown extensions of thigh bars, sometimes invaded by cream from posteroventral surfaces of thighs, if so, posterior surfaces of thighs appear spotted with large black (or dark brown) spots on cream background.

In life, *E. cristinae* is green, maroon, or light and dark brown above with dark brown markings, flanks darker than dorsum; limbs barred brown or black on olive-brown background; throat light and dark brown with white streak edged with brown (Fig. 5); venter greenish-yellow, reticulated with brown; gray blotches on posterior surfaces of thighs; inner digits, axillae, much of venter, and undersides of hind limbs pale yellow; iris pale brown with gray horizontal streak and fine black reticulations. At night, the predominant color is gray.

*Measurements of holotype in mm:* SVL 41.8, shank 25.0, HW 17.0, head length 16.5, upper eyelid width 4.0, IOD 4.4, tympanum 1.9, eye 5.1, E-N 5.1.

*Proportions:* Adult males ( $n = 4$ ): shank/SVL 57.6–59.3 ( $\bar{x} = 58.4$ )%; HW/SVL 39.2–40.5 ( $\bar{x} = 39.9$ )%; upper eyelid/IOD 93.9–100.0 ( $\bar{x} = 97.2$ )%; tympanum/eye 35.1–46.3 ( $\bar{x} = 40.7$ )%; E-N/eye 83.9–100.0 ( $\bar{x} = 91.1$ )%. Juvenile and adult females, SVL 37.5–62.7 mm ( $n = 5$ ): shank/SVL 53.9–60.0 ( $\bar{x} = 57.7$ )%; HW/SVL 37.6–40.7 ( $\bar{x} = 39.2$ )%;



upper eyelid/IOD 77.0–100.0 ( $\bar{x}$  = 88.9)%; tympanum/eye 34.6–45.4 ( $\bar{x}$  = 38.6)%; E-N/eye 88.4–100.0 ( $\bar{x}$  = 96.4)%.

ETYMOLOGY.—Named for our friend and colleague Maria Cristina Ardila-R.

NATURAL HISTORY.—Individuals were found at night perched on twigs and forest-floor plants in the cloud forests beside a stream. Two individuals were found along the roadside in a recently cut area during a heavy rainstorm. Frogs were 0.5–1.0 m above the forest floor.

DISTRIBUTION.—Known from the Serranía San Lorenzo (1530–2200 m), the vicinity of Ciudad Perdida (2250 m), and above San Pedro de la Sierra (2000 m) on the northern and western flanks of the Sierra Nevada de Santa Marta.

*Eleutherodactylus delicatus* Ruthven

Figs. 3, 6–8, 19

*Eleutherodactylus delicatus* Ruthven, 1917c:1–3 (Holotype, UMMZ 50519, a juvenile, obtained at San Lorenzo, Depto. Magdalena, Colombia, 5000 ft. [1524 m], on 21 July 1913 by A. G. Ruthven); Ruthven, 1922:53; Cochran and Goin, 1970:401–403.

DIAGNOSIS.—1) skin of dorsum shagreened, bearing occipital ridges, that of venter areolate; dorsolateral folds on anterior one-half of body; 2) tympanum prominent, round, superficial, its length  $\frac{1}{3}$  eye length; 3) snout ovoid in dorsal view, round in profile; snout short; canthus rostralis sharp; 4) IOD as wide as upper eyelid; low cranial crests evident in females; one small pungent tubercle on each eyelid; 5) vomerine odontophores large, triangular in outline, separated medially by distance equal to  $\frac{1}{3}$  an odontophore width; 6) males with vocal slits and subgular vocal sac; males with nuptial pads on thumbs; 7) first finger shorter than second; digital pads moderate-sized, pads on fingers III-IV nearly as wide as inner metatarsal tubercle is long; discs broader than long; 8) fingers bear lateral keels; 9) small ulnar tubercles present; 10) conical tubercle on heel; three small tubercles on outer edge of tarsus, none on inner edge; 11) two metatarsal tubercles, inner elongate, 3 times size of subconical outer; no supernumerary plantar tubercles; 12) toes with lateral fringes, no webbing; pads of toes smaller than those of fingers; 13) brown above with little indication of markings; flanks and ventral surfaces cream, boldly

spotted with brown; posterior surfaces of thighs cream barred with brown or black; 14) one adult male 22.1 mm SVL, four adult females 27.9–31.3 mm SVL.

*Eleutherodactylus delicatus* is assigned to the *unistrigatus* group and is distinct in having knobbed cranial crests on the frontoparietals and squamosals (Fig. 19). The species has long been recognized by the conical tubercles on the heels. The combination of eyelid and limb tubercles seen in *E. delicatus* occurs widely in the *unistrigatus* group; in the Sierra Nevada de Santa Marta, the combination also occurs in *E. cristinae*, a much larger frog.

DESCRIPTION.—Head as wide as body (less so in gravid females), broader than long; snout subovoid in dorsal view (Fig. 7), round in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis distinct, straight; loreal region concave, sloping gradually to lips; lips weakly flared (most evident in large females); small, pungent tubercle on upper eyelid; cranial crests present (Figs. 7, 19); interorbital space as wide as upper eyelid; supratympanic fold distinct, angular, barely concealing upper edge of tympanum; tympanum distinct, superficial, round, separated from eye by slightly less than its length; postrictal tubercles conical; small, subconical tubercles anterior, ventral, and posterior to tympanum; choanae round (slightly longer than wide), not concealed by palatal shelf of maxillary arch; vomerine odontophores large, median and posterior to choanae, separated medially by a distance equal  $\frac{1}{3}$  to  $\frac{1}{2}$  width of an odontophore, subtriangular in outline, each about  $1\frac{1}{2}$  times size of a choana, bearing a slanted row of 5–7 teeth; tongue longer than wide, its posterior border notched, posterior  $\frac{2}{5}$  not adherent to floor of mouth; in males, long vocal slits posterolateral to tongue; vocal sac internal.

Skin of dorsum coarsely shagreened with narrow mid-dorsal ridge; ridges forming reverse parentheses in occipital region; low dorso-lateral folds extending to a point just posterior to sacrum; skin of limbs more finely shagreened, with small ridgelets; another fold extending ventral from just posterior to tympanum; flanks grading into areolations of venter; similar areolation on posterior thigh surfaces lateral to vent; skin of venter coarsely areolate, that on throat with finer areolation; discoidal folds well anterior to groin; no anal sheath or enlarged tubercles around vent; ulnar tubercles of forearm scarcely evident; palmar tubercle divided into smaller outer and larger inner (twice size of outer); thenar tubercle oval, about size of inner palmar tubercle; palmar supernumeraries numerous, round, pungent; subarticular tubercles round, basal tubercles subconical,

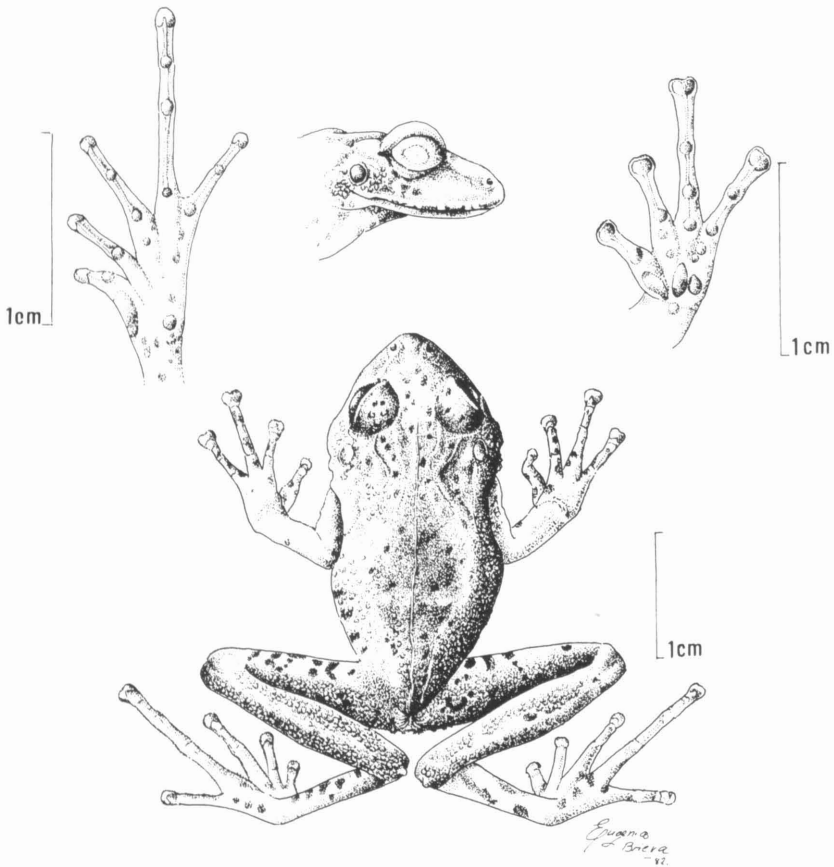


FIG. 8. *Eleutherodactylus delicatus*, ICN 3030, adult female.

more distal tubercles flatter; fingers long and slender, bearing narrow lateral fringes; pads moderate-sized (Fig. 3), feebly indented at tips (except II), bearing broader than long discs on their ventral surfaces; pads of I and II smaller than tympanum, of III and IV larger than tympanum; width of pad of III slightly less than length of inner metatarsal tubercle; first finger shorter than second; white, glandular, nuptial pad on thumb of male, thumb swollen.

Small conical tubercle on upper edge of heel; no tubercles or folds on inner edge of tarsus, a row of three small tubercles on outer edge of tarsus; inner metatarsal tubercle barely elongate (length  $2\frac{1}{2}$  times

width), 3 times size of round, subconical outer metatarsal tubercle; distinct supernumerary plantar tubercles at bases of toes II, III, and IV; subarticular tubercles subconical, longer than wide; toes long and slender, bearing lateral keels but no webbing; toe pads apically rounded, discs broad; toe pads smaller than those of fingers, pads I and V smallest; when flexed hind legs are held at right angles to sagittal plane, heels overlap.

In preservative, dorsum pale to dark brown with little evident pattern except scattered darker brown (or black) flecks (Fig. 8); canthal-supratympanic stripe and labial bars ill-defined; flanks cream with dark brown (nearly black) spots; ventral surfaces cream with dark brown spots (spots as large as pad of third finger); underside of shank spotted (Fig. 6); posteroventral surface of thigh not spotted (but anteroventral surface is spotted); anterior surfaces of thigh barred with narrow black bars; posterior surfaces of thigh barred or cream with black spots; anal triangle relatively distinct.

*Proportions:* Adult males ( $n = 2$ ): shank/SVL 54.5–65.6%; HW/SVL 39.7–40.8%; upper eyelid/IOD 91.7–107.7%; tympanum/eye 34.2–35.3%; E-N/eye 73.5–76.3%. Juvenile and adult females, SVL 24.4–34.4 mm ( $n = 7$ ): shank/SVL 56.3–59.8 ( $\bar{x} = 58.0$ )%; HW/SVL 36.6–41.3 ( $\bar{x} = 38.9$ )%; upper eyelid/IOD 83.8–113.3 ( $\bar{x} = 100.2$ )%; tympanum/eye 31.0–39.5 ( $\bar{x} = 35.2$ )%; E-N/eye 68.8–100.0 ( $\bar{x} = 80.6$ )%.

NATURAL HISTORY.—*E. delicatus* remains poorly known. Most of the specimens seen by us were collected at elevations higher than the San Lorenzo (Cerro Kennedy) area visited by most herpetologists sampling the Sierra Nevada de Santa Marta. Our failure to find this species in June 1983, while simultaneously encountering seven of the species of the genus known to us from the Sierra Nevada, suggests that the species is one of a higher altitudinal stratum than that we sampled (1700–2200 m).

DISTRIBUTION.—Known from only three general localities: above San Pedro de la Sierra (2450–2500 m) on the western flank of the Sierra Nevada de Santa Marta and from the Serranía San Lorenzo (1524 m and 2260–2600 m) on the northwestern flank of the Sierra Nevada.

*Eleutherodactylus insignitus* Ruthven

Figs. 2, 4, 9, 17

*Eleutherodactylus insignitus* Ruthven, 1917a:1–4 (Holotype, UMMZ 48393, an adult female, obtained in the heights east of San

Miguel, Depto. Guajira, Colombia, 6000–7000 ft. [1829–2134 m], on 24 April 1914 by M. A. Carriker); Cochran and Goin, 1970:424–425.

DIAGNOSIS.—1) skin of dorsum smooth with occipital folds, that of venter smooth; no dorsolateral folds; 2) tympanum superficial, small; 3) snout ovoid in dorsal view, rounded to almost truncate in lateral profile; canthus rostralis relatively sharp; 4) IOD wider than upper eyelid; lateral margins of frontoparietals weakly upturned; non-pungent tubercles on eyelids; 5) vomerine odontophores large, oval in outline, separated medially by a distance equal to  $\frac{1}{3}$  an odontophore width; 6) males lack vocal slits; thumb of male swollen but lacking nuptial pad; 7) first finger longer than second; digital pads narrow, slightly wider than digits but all narrower than length of inner metatarsal tubercle; discs broader than long; 8) feeble lateral keels on fingers; 9) no ulnar tubercles except low antebrachial; 10) small tubercle on heel (non-pungent); no tarsal folds or tubercles; 11) two metatarsal tubercles, inner elongate, 3 times size of outer; no

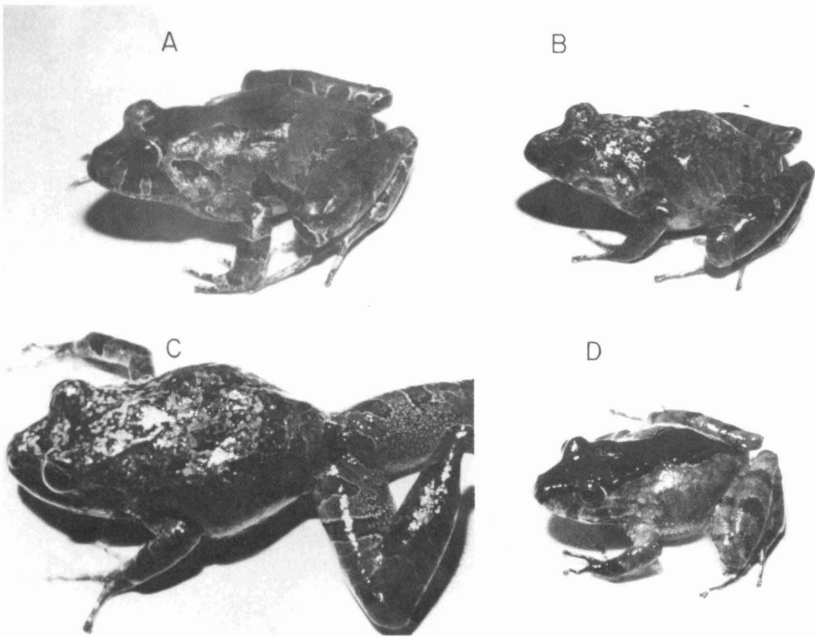


FIG. 9. Santa Martán *Eleutherodactylus*: (A) *E. insignitus*, ICN 13983, 36.2 mm; (B–C) *E. megalops*, ICN 13987, 31.3 mm SVL; (D) *E. megalops*, ICN 13990, 21.0 mm SVL.

supernumerary plantar tubercles; 12) toes with narrow lateral fringes, no webbing; toe pads larger than those of fingers; 13) brown above with dark occipital folds; little indication of markings on upper surfaces (Fig. 9); groin, anterior and posterior surfaces of thighs dark brown, spotted with cream; underside of shank dark brown with cream marbling; ventral surfaces cream speckled with brown in females, brown with cream spots in males; 14) adults large, two males 41.2–41.8 mm SVL, seven females 48.4–55.8 ( $\bar{x}$  = 50.6) mm SVL.

*Eleutherodactylus insignitus* is a member of the *fitzingeri* group most similar to *E. actites*, *E. lymani*, *E. viridicans*, and *E. w-nigrum* (montane species in Colombia, Ecuador, and northern Perú). Males of *E. insignitus* and *E. viridicans* lack vocal slits and non-spinous nuptial pads (present in the other three). Like *E. w-nigrum*, *E. insignitus* lacks any trace of an inner tarsal fold. The digital pads of *E. insignitus* (Fig. 2) are narrow, as in *E. viridicans* (see illustration in Lynch, 1977:5), compared with those of *E. w-nigrum* (see illustration in Lynch, 1979a:230). The dark areas of the posterior surfaces of the thigh and groin enclosing cream spots (see Ruthven, 1917a: plate 1) are shared with *E. viridicans* (see Lynch, 1977:5, fig. 2); the two are most readily distinguished in that the dorsal pattern of *E. viridicans* is of bold dark spots and bars whereas in *E. insignitus* a pattern is scarcely evident.

DESCRIPTION.—See Cochran and Goin (1970:424–425).

*Proportions*: Adult males ( $n$  = 2): shank/SVL 55.7–57.8%; HW/SVL 40.4–40.5%; upper eyelid/IOD 105.9–109.7%; tympanum/eye 32.2–32.8%; E-N/eye 71.2–72.4%. Adult females ( $n$  = 7): shank/SVL 52.5–57.0 ( $\bar{x}$  = 54.9%); HW/SVL 38.2–41.9 ( $\bar{x}$  = 39.5%); upper eyelid/IOD 100.0–120.0 ( $\bar{x}$  = 110.1%); tympanum/eye 33.3–39.0 ( $\bar{x}$  = 35.6%); E-N/eye 74.6–83.3 ( $\bar{x}$  = 80.0%).

In life, *E. insignitus* is gray-brown with a bronze cast on the head; facial and limb markings black, outlined with white; groin and concealed surfaces of thighs white with black markings; throat and undersides of forelimbs pale orange, venter off-white with black reticulations; tops of digit tips white; iris reddish-brown with dark flecks.

NATURAL HISTORY.—*E. insignitus* is a terrestrial frog. Juveniles were found beneath rocks and logs along the edge of the road by day in June 1983. Another individual was found at night sitting on a rock in the forest proper. We suspected that adult *E. insignitus* would be found along streams at night but failed to encounter adults in June 1983. Only a few adults have been found since the original description.

DISTRIBUTION.—Known from the northern and western flanks of

the Sierra Nevada de Santa Marta (the type-locality east of San Miguel, Depto. Guajira, 1829–2134 m; the Serranía San Lorenzo, Depto. Magdalena, 1530–2000 m; and above San Pedro de la Sierra, Depto. Magdalena, 2000 m).

*Eleutherodactylus megalops* Ruthven

Figs. 2, 4, 9–10, 18

*Eleutherodactylus megalops* Ruthven, 1917b:3 (Holotype, UMMZ 48444, a juvenile female, obtained at San Lorenzo, Depto. Magdalena, Colombia, 5000 ft. [1524 m], on 16 July 1913 by A. G. Ruthven); Ruthven, 1922:52–53; Cochran and Goin, 1970:435–437.

DIAGNOSIS.—1) skin of dorsum shagreened and bearing numerous slightly larger warts and short ridges (Figs. 9–10); that of venter areolate; no dorsolateral folds but most specimens have short folds along the upper flanks; 2) tympanum superficial, annulus distinct, higher than long; 3) snout ovoid in dorsal view, round in lateral profile; snout short; canthus rostralis relatively sharp; 4) IOD broader than upper eyelid; no cranial crests; non-pungent tubercles on upper eyelids; 5) vomerine odontophores moderate-sized, oval in outline, separated medially by a distance equal to an odontophore width; 6) males with vocal slits, internal vocal sac; glandular, white nuptial pad on thumb of reproductive males; 7) fingers long, first finger slightly shorter than second (when both equally adpressed); digital pads small (Fig. 2), all about as broad as length of inner metatarsal tubercle; discs broader than long; 8) lateral fringes evident only at bases of fingers; 9) no ulnar tubercles; 10) small and indistinct tubercles on heel and outer edge of tarsus; 11) two metatarsal tubercles, inner elongate, 3 times size of outer; indistinct supernumerary plantar tubercles; 12) toes bear narrow lateral fringes at their base, no webbing; toe pads as large as those of fingers; subconical subarticular tubercles; 13) brown above with darker markings; posterior surfaces of thighs finely reticulated with brown; groin and anterior surfaces of thighs have more coarse reticulation; throat brown, spotted with cream; venter cream with small brown spots (rarely reticulated with brown); 14) adults small, males 18.9–27.1 ( $\bar{x} = 23.9 \pm 0.5$ ,  $n = 51$ ) mm SVL, females 27.7–34.4 ( $\bar{x} = 31.0 \pm 0.5$ ,  $n = 42$ ) mm SVL.

*Eleutherodactylus megalops* is a member of the *unistrigatus* group but of otherwise uncertain affinities. The head appears large, but this characteristic does not suggest relationships with other species. The

fingers are long and slender with slight apical dilations (Fig. 2); these traits are uncommon among species of the *unistrigatus* group. The size of the digital pads, lengths of the digits, and chunky body form (Fig. 9) are presumed to be terrestrial adaptations masking the relationships of *E. megalops* (such a physiognomy is seen in some *fitzingeri* group species in Central America as well as in some species of *discoidalis* group in northern South America). The species is most readily distinguished from congeners by virtue of its throat pattern (brown with cream spots).

DESCRIPTION.—See Cochran and Goin (1970:435–436); however, the described individual is an adult female rather than a male as they stated.

*Proportions*: Adult males ( $n = 10$ ): shank/SVL 53.2–57.6 ( $\bar{x} = 54.6$ )%; HW/SVL 39.8–42.9 ( $\bar{x} = 40.7$ )%; upper eyelid/IOD 95.0–150.0 ( $\bar{x} = 119.8$ )%; tympanum/eye 26.3–37.1 ( $\bar{x} = 31.5$ )%; E-N/eye 65.8–82.9 ( $\bar{x} = 75.3$ )%. Adult females ( $n = 10$ ): shank/SVL 52.8–57.9 ( $\bar{x} = 54.7$ )%; HW/SVL 38.5–42.1 ( $\bar{x} = 40.5$ )%; upper eyelid/IOD 91.7–126.1 ( $\bar{x} = 109.4$ )%; tympanum/eye 28.9–41.5 ( $\bar{x} = 33.4$ )%; E-N/eye 71.1–89.2 ( $\bar{x} = 80.5$ )%.

In life, the most common coloration of *E. megalops* is as follows: dorsum brown to reddish-brown, with darker markings (sometimes flecked or accentuated with black); ventral surfaces off-white with brown reticulation; groin often washed with pale salmon, if so, posterior surface of thighs behind knee salmon; posterior surfaces of thighs bearing fine reticulation of brown; lower venter orangish in those individuals having salmon colors in groin; iris gray above with black reticulation and brown below. Occasional individuals have a dark green ground coloration. In the live samples we saw, some olive-brown individuals bridge the apparent gap in ground coloration but in a small sample the species might appear polychromatic.

NATURAL HISTORY.—*E. megalops* is by far the most common frog encountered by day in leaf litter and/or beneath rocks or logs. We believe these individuals are disturbed from diurnal resting places (which happen to be easily accessed by collectors). Although we did not carefully record data (because *E. megalops* is so common in collections and we did not actively seek them), we estimate that in diurnal collections *E. megalops* accounts for 75–95% of the frogs found outside of bromeliads. At night, *E. megalops* is apparently less common (because *E. sanctaemartae* becomes so apparent). However, *E. megalops* is active; individuals are found on rocks, the ground, or on very low vegetation either in the forest or alongside the edges of the roads. We consider our data adequate to characterize *E. megalops* as a

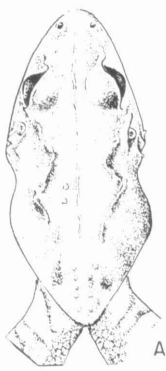


nocturnal terrestrial frog; the species appears to be less common along streams than away from them.

Ruthven (1917b:6) reported *E. megalops* from near sea level (Don Diego) to as high as 7500 feet (2286 m). We have not found *E. megalops* lower than 1300 m but have found it as high as 2450 m. The species is very abundant at cloud forest sites on the north and west faces of the Sierra Nevada.

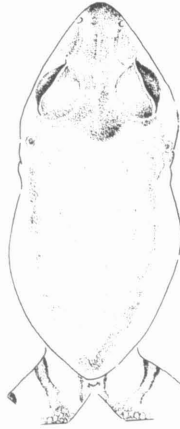
REMARKS.—In the original description, Ruthven (1917b:5–6) commented on the variability evident in his samples to the extent that “. . . it is possible that another species is represented. . . .” We concur with Ruthven that the variability in presence of dorsal ridges and enlarged tubercles when coupled with color pattern is extensive (Fig. 10) but that it is nowhere discontinuous. Even more complex polymorphisms have been described for other species of the genus (e.g., Savage and Emerson's, 1970, account of *E. bransfordii*). In general, frogs of the genus *Eleutherodactylus* exhibit pattern (and more rarely ridge and wart) polymorphisms.

The most common morph (Fig. 10A-C) consists of frogs with little (10A) or no (10B) evidence of markings on the dorsum, or more rarely having a rough “W” in the scapular region and a chevron on the sacrum (10C). These three specimens bridge nearly continuous variation. Of the 70 specimens (in a sample of 105) having the “common morph”, three have very thin pale vertebral stripes as well. In the “common morph”, skin ridges are not well developed and tend to be expressed whenever dark markings are present. We recognize as a separate morph those frogs having dark pigment anteriorly and light pigment posteriorly (Fig. 10D)—three of 105 specimens exhibit the morph with little evidence of ridges. The “mid-dorsal raphe morph” (Fig. 10E-F) accounts for 12 of 105 specimens. In these frogs, paravertebral ridges border the pale raphe (Fig. 10E) or there is a network of ridges in dark markings lateral to the raphe (Fig. 10F). Fifteen of the 105 frogs have sinuous paravertebral folds (Fig. 10H) or dorsolateral folds (Fig. 10G). Eight specimens have pale flanks with dark pigment between the sinuous paravertebral folds (Fig. 10H) but two present dark flanks with pale pigment between the folds. Four specimens are like that illustrated as Fig. 10H except the paravertebral folds are straighter and edged with pale pigment medially on the anterior one-half. A single specimen (ICN 743) has dorsolateral folds surrounding a pale dorsum with darker flanks (Fig. 10G). In this specimen, some paravertebral ridges are evident just lateral to the vertebral column. The remaining five specimens of the sample appear to represent the “common morph” except the pattern (if



1 cm

A



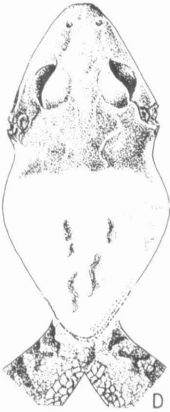
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B



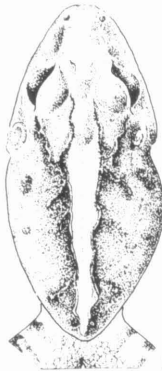
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C



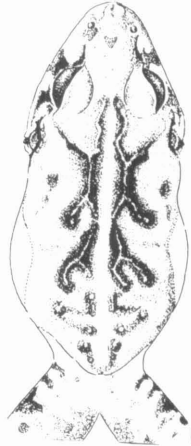
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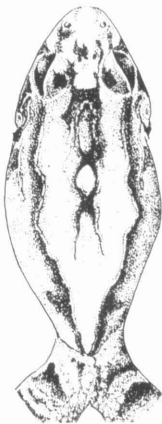
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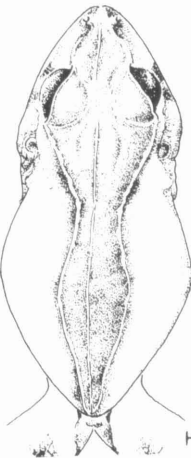
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F



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G



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H

*Oreophryne*  
*bovini*

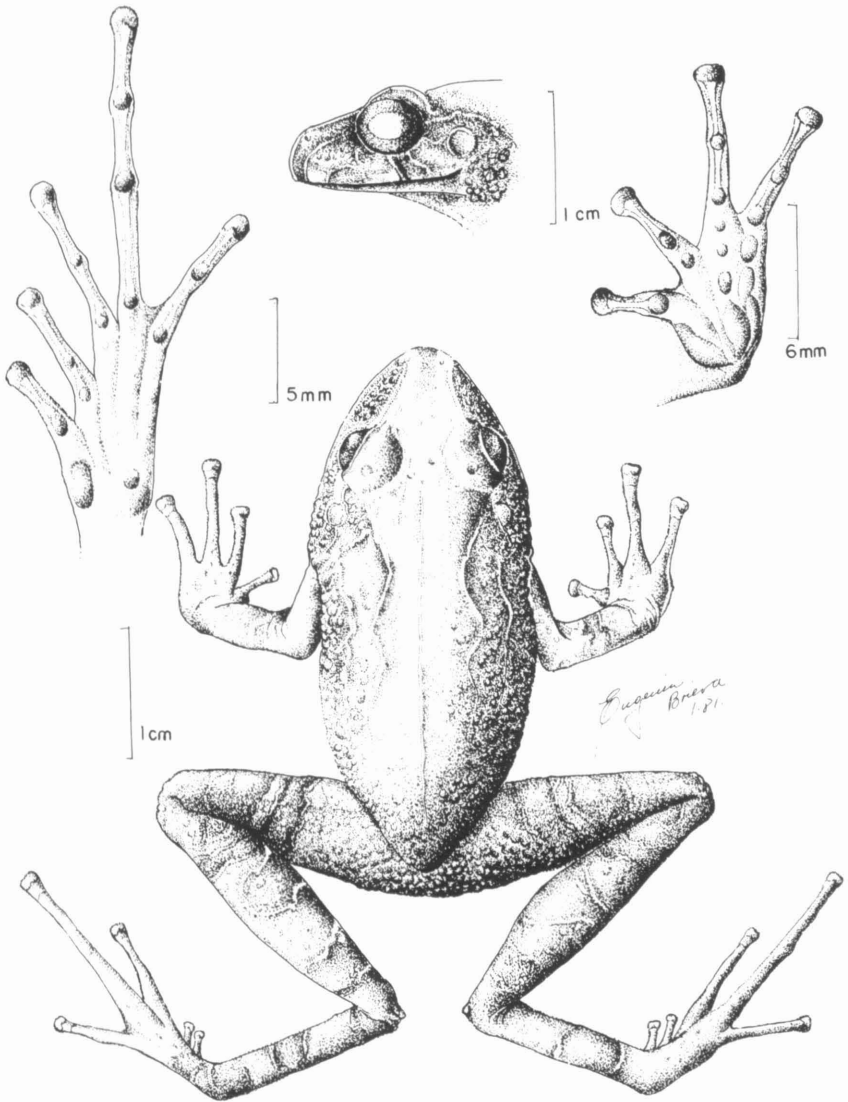


FIG. 11. *Eleutherodactylus ruthveni*, ICN 3016, paratype.

FIG. 10 (opposite). Pattern and skin ridge variants in *Eleutherodactylus megalops*. (A) ICN 748, (B) ICN 1649, (C) ICN 1668, (D) ICN 2685, (E) ICN 747, (F) ICN 705, (G) ICN 743, and (H) ICN 4733.

present) is overlain with white dots or spots edged with brown or black; these spots are especially common on the flanks and sides of the head.

*Eleutherodactylus ruthveni* sp. nov.

Figs. 3, 6, 11–13, 20

*Eleutherodactylus calcaratus*: Cochran and Goin, 1970:392–93.

*Eleutherodactylus vertebralis*: Cochran and Goin, 1970:432.

*Eleutherodactylus sanctaemartae*: Lynch, 1978:21.

HOLOTYPE.—ICN 3011, an adult female, from the Serranía Cebolleta, approximately 8 hours by foot E San Pedro de la Sierra, Municipio Ciénaga, Depto. Magdalena, Colombia, 2450 m, one of a series obtained by Pedro M. Ruíz et al. in May 1976.

PARATYPES.—ICN 3012, 3014–18, 3027–28, 3031, 3033–35, 3039, collected with the holotype; ICN 13178–79, UMMZ 176887–88, Cuchilla Yerbabuena, finca of Alfonso Vanegas, 2500 m.

DIAGNOSIS.—1) skin of dorsum smooth anteriorly, bearing low warts posteriorly, that of venter areolate; sinuous paravertebral folds (Fig. 11) from eyelid to just beyond sacrum; dorsolateral folds continuous to level of sacrum, then discontinuous as rows of warts; 2) tympanum prominent, superficial; 3) snout subacuminate in dorsal view, round in lateral profile; snout long; canthus rostralis sharp; 4) IOD broader than upper eyelid; cranial crests present; no tubercles on upper eyelid; 5) vomerine odontophores large, subtriangular in outline, separated medially by a distance equal to  $\frac{1}{3}$ – $\frac{1}{2}$  width of an odontophore; 6) males with internal vocal sac, vocal slits; no nuptial pads on thumbs of males; 7) first finger slightly shorter than second; pads of fingers moderate-sized, that of 3rd finger almost as wide as inner metatarsal tubercle is long; discs broader than long; 8) fingers bear feeble lateral keels; 9) ulnar tubercles indistinct; 10) small tubercle on heel, none on tarsus; 11) two metatarsal tubercles, inner elongate, 2–3 times size of outer; no supernumerary plantar tubercles (or faintly evident at bases of toes II–IV); 12) toes bear faint lateral keels, no webbing; toe pads smaller than those of fingers; 13) brown above with darker brown markings; venter cream, densely reticulated with brown, throat darker; groin, anterior and posterior surfaces of thighs, and ventral surfaces of shank brown; 14) adults moderate-sized, males 24.5–32.3 mm SVL, females 31.1–45.5 mm SVL, geographically variable.

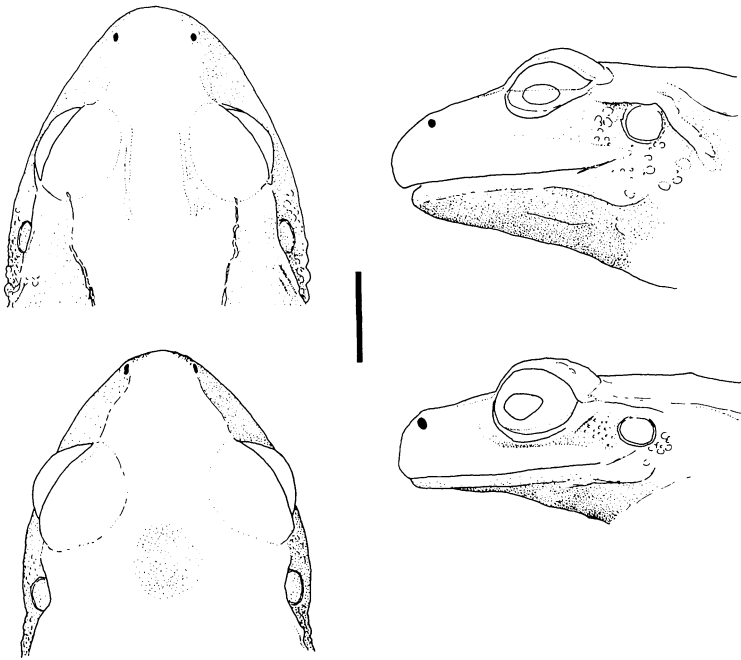


FIG. 12. Heads of *Eleutherodactylus ruthveni* (top, ICN 3014) and *E. sanctaemartae* (bottom, ICN 740). Scale equals 5 mm.

*Eleutherodactylus ruthveni* is assigned here to the *unistrigatus* group. Specimens were initially confused with *E. sanctaemartae* (under the assumption that they represented a pattern polymorphism). The two species differ in several respects. *Eleutherodactylus ruthveni* has narrow digital pads compared with *E. sanctaemartae* (Fig. 3), has a longer snout and prominent cranial crests (Figs. 12 and 20), and has brown concealed surfaces of the limbs (Fig. 6). We are aware of no close relatives of *E. ruthveni*.

DESCRIPTION.—Head slightly narrower than body, wider than long; snout subacuminate in dorsal view, round in lateral profile; snout long; nostrils not protuberant, directed dorsolaterally, not near tip of snout (Fig. 12, compare with *E. sanctaemartae*); canthus rostralis sharp, slightly concave; loreal region concave, sloping to lips; lips feebly flared; one low, non-pungent tubercle on upper eyelid; upper eyelid about as wide as interorbital distance; cranial crests present, evident as ridges between eyes (impressed on skin); supratympanic fold not clearly defined dorsally; tympanum superficial, annulus evident ex-

cept dorsally, round or slightly higher than long, separated from eye by a distance equal to  $1\frac{1}{4}$  tympanum length; numerous tubercles anterior, ventral, and posterior to tympanum, largest (postrictals) subconical; choanae oval (longer than wide), not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, each  $1\frac{1}{2}$  to 2 times size of a choana, separated medially by a distance equal to  $\frac{1}{3}$  –  $\frac{1}{2}$  width of an odontophore, subtriangular in outline, bearing 5–6 teeth in a transverse row along posterior border; tongue longer than wide, its posterior border bearing a shallow notch, posterior  $\frac{1}{3}$  not adherent to floor of mouth; in males, long vocal slits posterolateral to tongue; vocal sac internal.

Skin of dorsum smooth anteriorly, feebly warty posteriorly; sinuous paravertebral folds from eyelids to level just posterior to sacrum; dorsolateral folds from eye to about level of sacrum, then continuing as rows of rounded warts; sagittal fold from just above vent to point above the second presacral vertebra; skin of limbs feebly warty; flanks areolate; skin about vent areolate, as in that on undersides of thighs, venter, throat; discoidal fold well anterior to groin; no anal sheath; no subanal tubercles; ulnar tubercles indistinct (present, but easily overlooked); palmar tubercle bifid, nearly divided, inner lobe largest; thenar tubercle oval, about size of inner lobe of palmar; supernumerary palmar tubercles numerous, pungent; subarticular tubercles round, non-conical; fingers bear feeble lateral keels; fingers long, slender (Fig. 3); digital pads poorly developed, truncate or very weakly indented (apically round on I); discs on ventral surfaces of pads, broader than long; pads of I and II not as wide as tympanum; pads of III and IV as broad as tympanum but do not cover it; pad of III almost as wide as length of inner metatarsal tubercle; when equally adpressed, I slightly shorter than II; thumb of male swollen, but not bearing nuptial pad.

No tubercles on knee or tarsus; one subconical tubercle on upper edge of heel; inner metatarsal tubercle  $2\frac{1}{2}$  times as long as wide, slightly more than twice size of round, non-conical outer metatarsal tubercle; plantar surface lacking supernumerary tubercles, or minute tubercles present at bases of toes II-IV; subarticular tubercles low, non-conical, slightly longer than wide; toes long and slender, bearing faint lateral keels, lacking webs; toe pads apically rounded, bearing broader than long discs on their ventral surfaces; toe pads smaller than those of outer fingers, smallest pads on I and V; when flexed hind legs are held at right angles to sagittal plane, heels broadly overlap.

In preservative, brown above with darker brown edging on parts of

paravertebral folds; pale line along upper edge of canthus from tip of snout across upper eyelid and along dorsal edge of supratympanic fold (edged laterally with dark brown); similar lines (intermittent) along dorsolateral folds; dark brown stripe from lip and snout (anterolateral to nostril) to eye, from eye to just anterodorsal to insertion of arm, edged below by cream line; labial bar from eye posteroventral to lip; three half-moon shaped marks on lip anterior to labial bar; labial markings edged with cream; less distinct oblique bar on anterior flank (from above arm) edged with cream; vague similar markings posteriorly on flank; anal triangle not apparent; markings on thighs, shanks, and arms darker brown than ground color, edged with dull cream; shank bars transverse, about as wide as interspaces; dorsal and ventral surfaces of digits gray-brown; venter cream heavily flecked (or finely reticulated) with brown, not forming pattern; throat more heavily stippled with brown than venter; undersides of thighs least heavily stippled with brown; dorsal pattern of shank encroaches underside of shank; anterior and posterior surfaces of thighs brown with some cream flecking or not.

*Measurements of holotype in mm:* SVL 40.7; shank 23.7; HW 15.0; head length 14.1; upper eyelid 3.5; IOD 3.7; tympanum length 1.8; eye length 4.8; E-N 4.2.

*Proportions:* Adult males ( $n = 14$ ): shank/SVL 55.8–61.0 ( $\bar{x} = 58.3\%$ ); HW/SVL 35.4–41.5 ( $\bar{x} = 38.4\%$ ); upper eyelid/IOD 78.6–115.4 ( $\bar{x} = 95.7\%$ ); tympanum/eye 26.5–43.2 ( $\bar{x} = 37.3\%$ ); E-N/eye 79.4–100.0 ( $\bar{x} = 87.8\%$ ). Juvenile and adult females ( $n = 14$ ), SVL 28.8–45.5 mm: shank/SVL 51.0–60.2 ( $\bar{x} = 57.9\%$ ); HW/SVL 36.0–39.9 ( $\bar{x} = 38.2\%$ ); upper eyelid/IOD 67.5–120.0 ( $\bar{x} = 94.7\%$ ); tympanum/eye 27.3–41.3 ( $\bar{x} = 34.4\%$ ); E-N/eye 79.5–94.6 ( $\bar{x} = 86.9\%$ ).

Individuals from the type locality are larger than those from the Serranía de San Lorenzo. Ten topotypic males are 28.0–32.3 ( $\bar{x} = 30.1 \pm 0.5$ ) mm SVL and six topotypic females are 39.2–45.5 ( $\bar{x} = 42.0$ ) mm SVL whereas for specimens from San Lorenzo, four males are 24.5–26.4 ( $\bar{x} = 25.4$ ) mm SVL and five females are 31.1–38.0 ( $\bar{x} = 34.1$ ) mm SVL. An opposite size difference is seen also in *E. tayrona* from the two localities.

We have color in life notes for only a few specimens, all from the Serranía San Lorenzo. Dorsum pinkish-tan, gray, or pale orange with darker markings; canthal-supratympanic stripe dark brown, not continuous with gray post-axillary blotch (Fig. 13); venter dirty white with gray spots; posterior surfaces of thighs gray with cream areas bordering thigh bands (which extend onto field of posterior thighs); iris

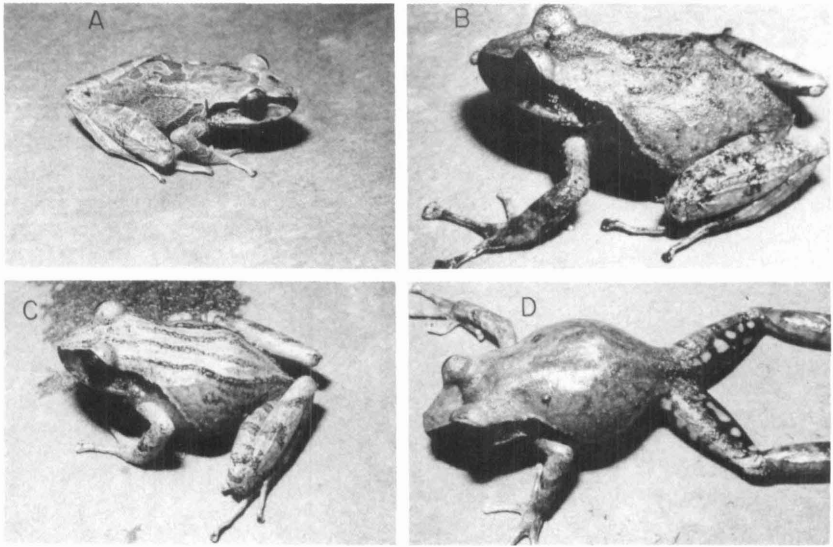


FIG. 13. Santa Martán *Eleutherodactylus*: (A) *E. ruthveni*, ICN 14048, 26.8 mm SVL; (B) *E. sanctaemartae*, ICN 14005, 43.2 mm SVL; (C) *E. sanctaemartae*, ICN 14003, 33.0 mm SVL; (D) *E. sanctaemartae*, ICN 14001, 34.5 mm SVL.

bright yellow-copper above, reddish-brown below, with a dark brown horizontal streak and black reticulation.

ETYMOLOGY.—This species is named for the late Alexander G. Ruthven, who initially discovered the diversity of eleutherodactyline frogs in the Sierra Nevada de Santa Marta and had the courage to name all he found.

NATURAL HISTORY.—In the late afternoon of 29 June 1983 we collected perhaps 150 *Eleutherodactylus* in leaf litter, in vegetation, and beneath rocks at a cloud forest site at 1720 m; those frogs, mostly released, consisted of *E. insignitus*, *E. megalops*, and *E. sanctaemartae*. Working the same and slightly higher sites (up to 1790) at night during a rain yielded several hundred *Eleutherodactylus* but no *E. ruthveni*. Collecting beneath rocks in subpáramo sites at 2150–2200 m (approximately 1 km above the Inderena cabaña San Lorenzo) by day yielded *E. carmelitae*, *E. megalops*, and *E. ruthveni*. Taken in conjunction with the absence of *E. ruthveni* in the UMMZ collections made between 1914 and 1922 and the relative abundance of this species in collections from above San Pedro de la Sierra (2450 m), we believe that *E. ruthveni* is most frequently encountered at elevations higher



than the mean elevation for *E. sanctaemartae*. Our data are inadequate at this point to decide if *E. ruthveni* is a terrestrial species although we suspect that it is more terrestrial than is *E. sanctaemartae*, a species with which we initially confused it.

DISTRIBUTION.—Known from the type-locality (2450–2500 m, west face Sierra Nevada) and the Serranía San Lorenzo (elevations associated with specimens given as 1800–2500 m, but probably all above 2100 m), on the northwestern corner of the Sierra Nevada.

*Eleutherodactylus sanctaemartae* Ruthven

Figs. 3, 6, 12–14, 20

*Eleutherodactylus sanctae-martae* Ruthven, 1917b:1 (Holotype, UMMZ 48605, an adult male, obtained at San Lorenzo, Depto. Magdalena, Colombia, 5000 ft. [1524 m], on 16 July 1913 by A. G. Ruthven); Ruthven, 1922:53; Cochran and Goin, 1970:411–413.

DIAGNOSIS.—1) skin of dorsum finely shagreened, that of venter areolate; low dorsolateral folds to about level of 7th vertebra; 2) tympanum prominent, superficial, round; 3) snout subacuminate to subovoid in dorsal view, round in lateral profile; snout short; canthus rostralis sharp; 4) IOD narrower than eyelid in males, about as wide as in females; no cranial crests; one tubercle on each upper eyelid; 5) vomerine odontophores large, triangular in outline, separated medially by a distance equal to  $\frac{1}{3}$  an odontophore width; 6) males with internal vocal sac and vocal slits; no nuptial pads on thumbs of males; 7) first finger shorter than second; large pads on outer fingers (width greater than length of inner metatarsal tubercle); discs broader than long; 8) lateral keels on fingers; 9) ulnar tubercles present, not conical; 10) non-conical tubercle on heel, indistinct tubercles on outer edge of tarsus; 11) two metatarsal tubercles, inner elongate, 3–4 times size of outer; supernumerary tubercles at bases of toes II–IV; 12) toes bear lateral fringes, no webbing; toe pads smaller than those of fingers; 13) cream to brown above with brown markings; face dark brown, edged above with cream line; limbs barred; groin, anterior and posterior surfaces of thighs, concealed surfaces of shanks brown with cream spots; 14) adults moderate-sized, males 24.9–40.6 ( $\bar{x}$  =  $33.8 \pm 0.8$ ,  $n$  = 19) mm SVL, females 39.2–45.7 ( $\bar{x}$  =  $42.2 \pm 0.7$ ,  $n$  = 8) mm SVL.

*Eleutherodactylus sanctaemartae* is a member of the *unistrigatus* group. The species is most easily distinguished from sympatric congeners by

virtue of its broad digital pads (Fig. 3) and large pale spots on the posterior surfaces of the thighs. The species exhibits pattern polymorphism (Fig. 14) as do many species of the genus. At present, *E. sanctaemartae* appears to be most closely related to an undescribed species (from the northern Cordillera Central of Colombia) confused with *E. latidiscus* by Cochran and Goin (1970).

DESCRIPTION.—Cochran and Goin's (1970) description is adequate but is based on an adult female, not a male as they stated. Head slightly wider than (males) to as wide as (females) body, head wider than long; snout subacuminate in dorsal view, round in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis sharp, sinuous; loreal region concave, sloping abruptly to lips; lips weakly flared in large females; small tubercles on upper eyelids; no cranial crests; depression on top of head (Fig. 12) result of large muscles adjacent to skull roof; interorbital space narrower than width of upper eyelid in males, as wide as upper eyelid in females; supratympanic fold not well-defined, concealing upper edge of tympanum; tympanum superficial, round, separated from eye by distance equal to 1 times length of tympanum; postrictal tubercles not distinct; numerous tubercles anterior, posteroventral, and posterior to tympanum, some larger than others, subconical; choanae oval, longer than wide, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, separated medially by a distance equal to  $\frac{1}{3}$  width of an odontophore, subtriangular in outline, each  $1\frac{1}{2}$  to 2 times size of a choana, bearing 8–10 teeth in a transverse row; tongue as long as wide, posterior border notched, posterior  $\frac{2}{3}$  not adherent to floor of mouth; long vocal slits lateral to tongue; vocal sac internal.

Skin of dorsum shagreened (Fig. 13), becoming coarser above pelvis; thin sagittal fold on lower back; some individuals have low occipital folds; dorsolateral folds extending posteriorly to level of second presacral; skin of limbs bearing fine ridgelets and small tubercles; flanks coarsely shagreened (grading into areolate venter) and bearing scattered larger tubercles; skin below vent, posterior one-half of ventral surface of thighs, venter, and to a lesser extent throat, areolate; discoidal folds well anterior to groin; no anal sheath; no enlarged anal tubercles; forearm bearing ulnar tubercles, antebrachial round, others elongate; palmar tubercle bifid, inner lobe largest; thenar tubercle oval, about size of inner lobe of palmar tubercle; supernumerary palmar tubercles pungent, smaller than subarticular tubercles; subarticular tubercles round, non-conical; fingers long and slender, bearing narrow lateral fringes; digital pads

well-developed, III and IV semi-truncate in outline, those of I and II round; discs broader than long; pad of I smaller than tympanum, of II equal to tympanum, of III and IV larger than tympanum; width of pad of III slightly greater than length of inner metatarsal tubercle; when inner two fingers are adpressed equally, tip of I reaches to base of disc of II; thumb of male not swollen, not bearing nuptial pad.

Knee, upper edge of heel, outer edge of tarsus bearing small tubercles (none on inner edge of tarsus); inner metatarsal tubercle barely elongate (length  $2\frac{1}{2}$  times width), 3 to 4 times size of round, non-conical outer metatarsal tubercle; small supernumerary plantar tubercles at bases of toes II–IV; subarticular tubercles subconical, longer than wide; toes long and slender, bearing lateral keels but not webbing; toe pads round, bearing broad discs, smaller than those of outer fingers, smallest on V; when flexed hind legs are held at right angles to sagittal plane, heels overlap.

Color pattern polymorphic, most common pattern is as follows: dorsum cream to brown, if brown, then no pattern is evident dorsally except shank bars; if paler, dark brown occipital reverse parentheses joining "X-shaped" mark above presacrals; vague spots above groin; pale line from tip of snout, along canthus, eyelid, above supratympanic fold onto anterior flank (following a ridge); below this line, frog is dark brown; this dark area is more or less continuous with dark pigment in groin and on anterior surfaces of thighs; tympanum paler than rest of side of head; limb markings brown, narrower than interspaces, shank bars oblique; limb bars subdivided by cream centers (in darker individuals limb bars edged with cream); venter stippled with brown (darkest on throat, undersides of limbs), breast and anterior chest bearing small brown spots; undersides of thighs blotched with pale brown; undersides of shanks pale brown, usually with pale spots (Fig. 6); groin and anterior surfaces of thighs bearing pale spots; in most specimens, posterior surfaces of thighs brown with pale spots; spots usually about size of pad of second finger; anal triangle evident in paler individuals.

In most (68%) individuals (Fig. 14A), the color pattern is simple. The boldly marked individuals are much less common (Fig. 14B–D), each morph accounting for 9–12% of the population.

In life, *E. sanctaemartae* is usually brown above with faint brown and black markings (other individuals have ground colors of olive-green, olive-tan, and reddish-brown); face dark brown; facial mark continues onto anterior flank, edged above with cream; flanks brown with a few cream spots; posterior surfaces of thighs olive to brown with yellow or orange spots; venter and throat variable, ranging from

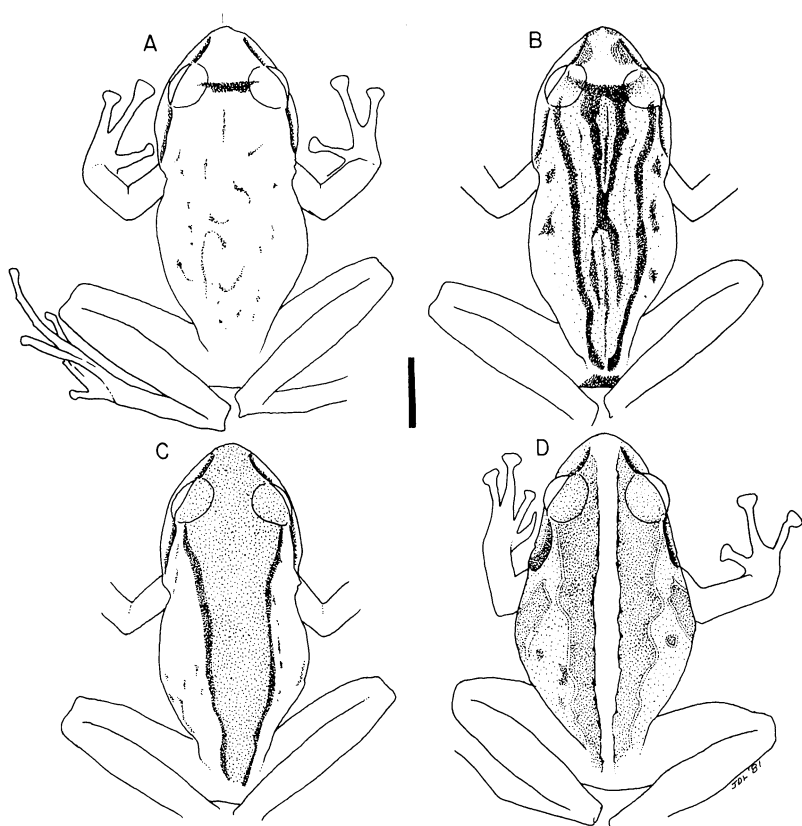


FIG. 14. Pattern polymorphism in *Eleutherodactylus sanctaemartae*: (A) ICN 710; (B) ICN 1655; (C) ICN 2669; (D) ICN 730. Scale equals 5 mm.

pale yellow with faint brown mottling to throat fleshy-gray or brown with heavy brown mottling on venter; iris bright copper with brown horizontal streak and black reticulation. The yellow spots on the posterior surfaces of the thighs are normal in adults; in juvenile frogs, the spots are most often orange or orange-yellow.

*Proportions:* Adult males ( $n = 19$ ): shank/SVL 49.7–61.4 ( $\bar{x} = 54.7$ )%; HW/SVL 34.8–39.7 ( $\bar{x} = 37.1$ )%; upper eyelid/IOD 87.5–128.1 ( $\bar{x} = 110.9$ )%; tympanum/eye 25.0–40.0 ( $\bar{x} = 32.1$ )%; E-N/eye 71.7–97.8 ( $\bar{x} = 84.2$ )%. Adult females ( $n = 7$ ): shank/SVL 45.8–54.8 ( $\bar{x} = 51.4$ )%; HW/SVL 36.4–39.9 ( $\bar{x} = 38.3$ )%; upper eyelid/IOD 86.0–118.4 ( $\bar{x} = 101.9$ )%; tympanum/eye 33.3–38.2 ( $\bar{x} = 35.8$ )%; E-N/eye 80.7–89.1 ( $\bar{x} = 86.1$ )%.

NATURAL HISTORY.—Collecting by day yielded few *E. sanctaemartae*; the individuals found were beneath stones or logs along the side of the road at 1720 m and were juveniles. During a rain between 1900 and 2230 hrs, hundreds of *E. sanctaemartae* were heard and seen calling. The chorus was continuous and frequently deafening between 1720 and 1790 m; above that elevation we detected some diminution of the volume but that reduction could as well have reflected the presence of openings in the forest (road cuts, pastures, etc.) that allowed considerable wind to penetrate near ground level and disturb the frogs.

At night in the forest, *E. sanctaemartae* was found on vegetation and branches 0.3–1.5 m above the ground; frogs were no more or less common along streams as in the forest away from streams. Most calling appeared to come from the forest edge beside the road where dense and clogged vegetation reached the ground. In freshly cut areas along the roadside, *E. sanctaemartae* was easily observed; individuals were seen perched on twigs of fallen trees (up to 2 m above ground) as well as on leaves of low vegetation. Calling males were most frequently found in somewhat concealed sites (calling from a clump of moss, in a smaller hollowed-out stump, sitting under leaves overhanging other leaves or twigs, etc.).

DISTRIBUTION.—On the northern and western flanks of the Sierra Nevada de Santa Marta, 1100–2450 m.

*Eleutherodactylus tayrona* sp. nov.

Figs. 2, 15–16, 21

*Hylodes cruentus*: Ruthven, 1915:1–6.

*Eleutherodactylus cruentus*: Ruthven, 1922:51; Cochran and Goin, 1970:428.

*Eleutherodactylus affinis* (part): Cochran and Goin, 1970:415.

*Eleutherodactylus prolixodiscus* (part): Lynch, 1978:20–21.

Ruthven's "*cruentus*": Lynch, 1978:20–21; Lynch, 1981b:182.

HOLOTYPE.—ICN 3060, an adult female, from the Serranía Cebolleta, approximately 8 hrs by foot E San Pedro de la Sierra, Municipio Ciénaga, Depto. Magdalena, Colombia, 2450 m, collected May 1976 by Pedro M. Ruiz and students.

PARATYPES.—ICN 3045, 3049, 3052–59, 3061–81, 3084, 3093–95, collected with holotype.

DIAGNOSIS.—1) skin of dorsum smooth to shagreened with many

short ridgelets, that of venter areolate; usually no dorsolateral folds, if present, low, extending to level of sacrum; 2) tympanum distinct, superficial, round; 3) snout subovoid in dorsal view, round in lateral profile; snout short; canthus rostralis moderately sharp; 4) IOD broader than upper eyelid; no cranial crests; low tubercles on upper eyelids; 5) vomerine odontophores low, small, triangular in outline, separated medially by a distance equal to an odontophore width; 6) males with external subgular vocal sac, vocal slits; white, non-spinous nuptial pads on thumbs of males; 7) first finger shorter than second; finger pads large, broader than length of inner metatarsal tubercle; discs broader than long; 8) fingers bear lateral keels; 9) antebrachial tubercle prominent; 10) small tubercle on heel, usually none on outer edge of tarsus; short inner tarsal fold; 11) two metatarsal tubercles, inner oval, 3–4 times size of outer; numerous supernumerary plantar tubercles; 12) toes bear lateral fringes, no webbing; toe pads as large as those of fingers; 13) brown above with darker brown spots; groin, anterior and posterior surfaces of thighs, and ventral surfaces of shanks brown; venter and throat finely peppered with brown (darkest on throat); 14) adults small, males 15.3–25.1 mm SVL, females 22.6–30.2 mm SVL (see below, geographically variable).

*Eleutherodactylus tayrona* is a member of the *lacrimosus* assembly (see Remarks); it differs from *E. boulengeri*, *E. brevifrons*, *E. bromeliaceus*, *E. eremitus*, *E. mendax*, and *E. petersi* in having feeble rather than obvious tubercles on the upper eyelids and heels (no tubercles in *E. lacrimosus*, *E. phoxocephalus*, and *E. prolixodiscus*). In some individuals, the lips are flared, almost as in *E. prolixodiscus* (compare Fig. 15 with Lynch's [1978:19] illustration), in contrast to the non-flared lips seen in the other eight species of the *lacrimosus* assembly. *Eleutherodactylus prolixodiscus* and *E. tayrona* are confused by Lynch (1978)—they are easily separated in life (*E. prolixodiscus* is green and the heart is visible through the skin of the chest whereas *E. tayrona* is reddish-brown and the heart is concealed). The two also differ in that *E. prolixodiscus* lacks an inner tarsal tubercle.

DESCRIPTION.—Head narrower than to as wide as body, wider than long; tip of snout pointed, otherwise snout subovoid in dorsal view, weakly protruding in lateral profile; nostrils weakly protuberant, directed dorsolaterally, near tip of snout; canthus rostralis angularly rounded, straight to weakly concave; loreal region weakly concave, sloping to lips; lips moderately flared (most obvious in adult females, less obvious in males and juveniles) in some individuals, not in others (Fig. 15); normally no tubercles on head, some individuals have small tubercles on upper eyelids; interorbital space flat, slightly broader

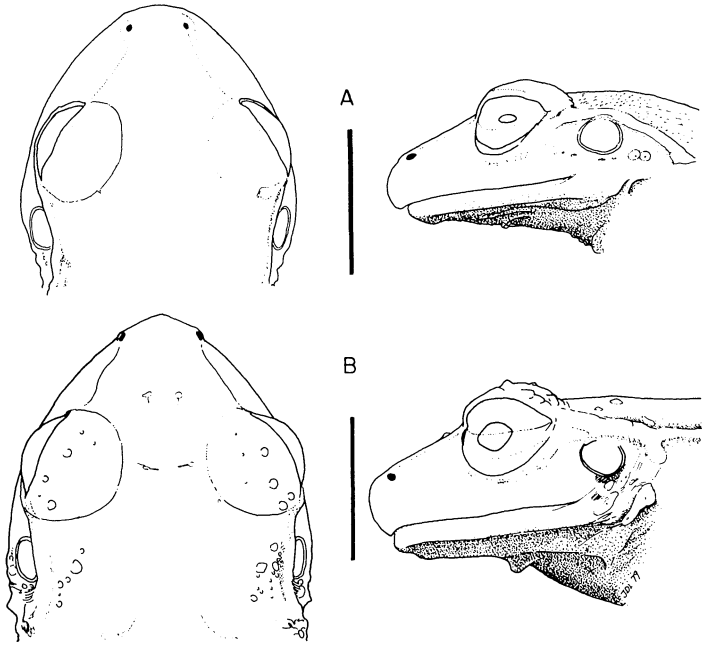


FIG. 15. Heads of *Eleutherodactylus tayrona*: (A) ICN 3918, individual with flared lips; (B) ICN 3060, individual having unflared lips. Scale equals 5 mm.

than upper eyelid, no cranial crests; tympanum prominent, directed laterally with slight dorsal and posterior orientation; supratympanic fold thick, obscuring upper edge of tympanum; tympanum round, superficial, separated from eye by a distance equal to its diameter; postrictal tubercles low; choanae relatively small, not concealed by palatal shelf of maxillary arch, slightly longer than wide; vomerine odontophores median and posterior to choanae, triangular in outline, separated medially by a distance equal to  $\frac{1}{2}$  width of an odontophore, each bearing a row of teeth along posterior edge; tongue rounded, its posterior edge feebly indented, posterior  $\frac{1}{3}$  to  $\frac{1}{6}$  not adherent to floor of mouth; males have subgular, external vocal sac.

Skin of dorsum finely shagreened (Fig. 16) without prominent folds or enlarged tubercles (indistinct vertebral fold evident in some individuals); in some individuals, low dorsolateral folds from eye to about level of sacrum); flanks areolate, as is venter; upper surfaces of limbs shagreened; anal opening slightly extended by short sheath; pair of large flat tubercles below vent; discoidal fold evident; skin

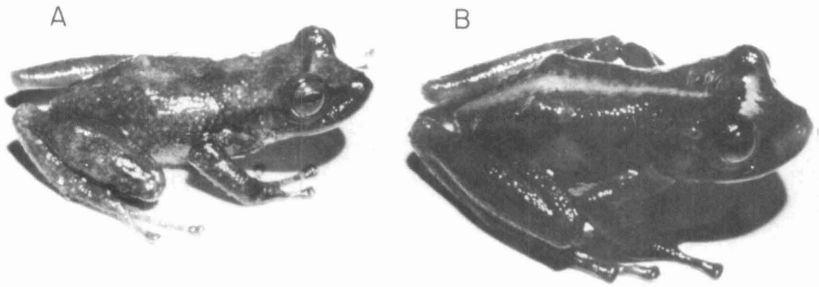


FIG. 16. *Eleutherodactylus tayrona*: (A) ICN 13999, 24.9 mm SVL; (B) ICN 14000, 28.0 mm SVL.

below vent and on underside of thighs areolate; forearm lacking ulnar tubercles except antebrachial; two palmar tubercles, each slightly smaller than oval thenar tubercle; numerous, round, pungent supernumerary palmar tubercles; subarticular tubercles round, subconical; fingers bearing fleshy lateral keels, most obvious at bases; all fingers bearing expanded pads at tips of digits, ventral surfaces of pads bearing broader than long discs; pads apically round, largest on fingers III and IV (larger than tympanum), that on II as large as tympanum, that on thumb smaller than tympanum; first finger shorter than second; thumbs of males swollen, bearing white, non-spinous nuptial pad.

Tiny, round tubercle on heel, usually none on outer edge of tarsus; single low tubercle on inner edge of tarsus about half-way between inner metatarsal tubercle and ankle, borne on indistinct fold; inner metatarsal tubercle twice as long as wide, 3–4 times size of round outer; numerous supernumerary plantar tubercles; toes bear narrow lateral fringes, no webbing; subarticular tubercles rounded, subconical; pad on toe I small, pads on other toes larger, those of toe IV as large as those of outer fingers; when flexed hind legs are held at right angles to sagittal plane, heels overlap; heel of adpressed hind leg reaches to just in front of eye.

*Coloration in preservative:* Uniform brown above with or without darker brown flecking and small spots, flanks darker than back; the brown ground color may be invaded by cream to produce an even more pale dorsum; in some individuals, pale blotches outlined with dark brown are evident along the center of the back and in others (ca. 10%) there is a pale raphe, edged with brown, from the occiput to the vent (Fig. 16). A dark interorbital bar is present and may be bordered



anteriorly by a pale bar. In about 10% of the specimens seen, there is a cream hairline stripe from the tip of the snout to the vent; the stripe divides what dorsal markings lie in its path. The ventral surfaces are finely stippled with brown. The concealed surfaces of the hind limbs are dark brown. Dark brown canthal-supratympanic stripes are the only consistent facial markings; labial marks consist of diffuse mottling on the upper lips. The limbs are barred in a few individuals (bars less than half width of interspaces). In most, the limbs are spotted with dark brown or lack any trace of pattern.

In life, *E. tayrona* is reddish-brown above with slightly darker flanks; face dark brown; vocal sac dirty yellow; venter pale yellow bronze washed with gray; posterior surfaces of thighs pale olive to reddish-brown; iris reddish-brown above, gray below. If the vertebral stripe is present, it is dull cream to dull orange.

*Measurements of holotype in mm:* SVL 25.9; shank 13.1; HW 9.8; head length 9.4; upper eyelid width 2.9; IOD 2.7; tympanum length 1.6; eye length 3.5; E-N 3.2.

*Proportions (based on topotypes):* Adult males ( $n = 14$ ): shank/SVL 46.4–52.8 ( $\bar{x} = 50.7\%$ ); HW/SVL 35.1–36.9 ( $\bar{x} = 36.0\%$ ); upper eyelid/IOD 76.6–105.0 ( $\bar{x} = 92.8\%$ ); tympanum/eye 37.0–51.7 ( $\bar{x} = 44.3\%$ ); E-N/eye 82.8–90.0 ( $\bar{x} = 85.7\%$ ). Juvenile and adult females ( $n = 15$ , SVL 18.7–28.5 mm): shank/SVL 47.8–52.5 ( $\bar{x} = 50.2\%$ ); HW/SVL 34.7–37.8 ( $\bar{x} = 36.0\%$ ); upper eyelid/IOD 86.7–107.4 ( $\bar{x} = 94.6\%$ ); tympanum/eye 34.4–46.7 ( $\bar{x} = 42.0\%$ ); E-N/eye 85.7–96.6 ( $\bar{x} = 91.2\%$ ).

Body size varies geographically (and possibly altitudinally). In topotypic material (2450 m), males are 15.3–19.7 ( $\bar{x} = 17.8 \pm 0.4$ ,  $n = 20$ ) mm SVL and females are 22.6–28.5 ( $\bar{x} = 25.0 \pm 0.5$ ,  $n = 11$ ) mm SVL, whereas in material from the Serrania de San Lorenzo (1500–2000 m), males are 20.6–25.1 ( $\bar{x} = 23.2 \pm 0.3$ ,  $n = 18$ ) mm SVL and females are 25.3–30.2 ( $\bar{x} = 27.7 \pm 0.5$ ,  $n = 10$ ) mm SVL. In a smaller sample from Ciudad Perdida (1300–2200 m) on the north face of the Sierra, males are 19.0–24.8 ( $\bar{x} = 21.5 \pm 0.5$ ,  $n = 13$ ) mm SVL and females are 25.5–28.4 ( $\bar{x} = 26.7$ ,  $n = 8$ ) mm SVL. This size difference is opposite to that seen in *E. ruthveni* (larger above San Pedro de la Sierra).

**ETYMOLOGY.**—The trivial name is used as a noun in apposition. It is derived from the term usually given to the preColumbian indian culture (*tayrona*) associated with the Sierra Nevada. It is purely conjectural that this small frog may have served as a model for the most common of the gold frogs recovered from the archeological sites in the Sierra.

NATURAL HISTORY.—Ruthven (1915) described much of the reproductive biology of this small frog. We have found it most often, as did Ruthven, in bromeliads growing on the ground or in trees. We traced no calls to this abundant frog in June 1983 (while collecting 7 of the 9 species known from the Sierra), probably because of the cacophony of *E. sanctaemartae* at the site. Most individuals were found by day in bromeliads (with *Bolitoglossa savagei* but no other amphibians). The few individuals seen at night were perched on bromeliad leaves; however, our primary activities were devoted to other species and we may have overlooked *E. tayrona*.

Embryos are found in bromeliads; egg masses are attached to the bromeliad leaves in a single layer. Eggs have been found in May, June, and November at the San Lorenzo site, suggesting that reproduction is aseasonal.

REMARKS.—There is a suite of diminutive bromeliad-dwelling *Eleutherodactylus* found in northwestern South America. In addition to their preference for microhabitat and their small body size ( $\sigma$   $\sigma$  14.0–29.9 mm,  $\text{♀}$   $\text{♀}$  16.5–38.4 mm SVL) these frogs are superficially similar at least in preservatives. These species include the species grouped as the *lacrimosus* assembly by Lynch and Duellman (1980) and Lynch (1980) (*E. bromeliaceus*, *E. eremitus*, *E. lacrimosus*, *E. mendax*, and *E. petersi*), those grouped as the *celator* assembly by Lynch and Duellman (1980) (*E. celator*, *E. colodactylus*, and *E. proserpens*) and a series of small Colombian species (*E. Boulengeri*, *E. brevifrons*, *E. proluxodiscus*, and *E. tayrona*), and the Ecuadorian *E. phoxocephalus*.

The impression of similarity is in large measure derived from these animals' broad, flat heads. That similar impressions occur to students of bromeliad-dwelling *Hyla* (Duellman, 1970:318–326, 409–416, 429–436) provides adequate warning that the similarities ought not be sufficient to form taxonomic groups. The *celator* assembly probably constitutes a separate monophyletic group whose synapomorphies are shortened digits and round canthus rostralis. We are not able to suggest synapomorphies for the other assembly but recognize it as a matter of convenience. The *lacrimosus* assembly thus contains the ten species cited above.

This species has been the most awkward with which to work. Lynch (1978) confused some specimens of *E. tayrona* with *E. proluxodiscus* because he emphasized snout shape, had long-preserved specimens from San Lorenzo, and detected apparent differences in ovum size. The extremes in snout shape (Fig. 15) seen in specimens from the Sierra Nevada are distinctive but no other character conforms with that apparent difference and in the large samples in the ICN collec-

tion the snout shape difference appears to be bridged. Our restudy of the samples previously considered to be *E. prolixodiscus*, other material from the Sierra Nevada, and a sample of *E. prolixodiscus* from Cerro Tamá, Depto. Norte de Santander, Colombia, results in the following conclusions: Lynch erred in characterizing *E. prolixodiscus* as having dorsolateral folds (apparently preservation artifacts), in terming the tongue fully adherent to the floor of the mouth, and in terming the digital pads truncate (apparently preservation artifacts).

*Eleutherodactylus prolixodiscus*' distribution was highlighted by Lynch (1978) because it was discontinuous and upland. We are aware of only three locality records for *E. prolixodiscus* (KU 132724–33, 30 km ENE Bucaramanga, road to Cucata, Depto. Santander, Colombia, 2485 m; ICN 10102–19, vicinity of Inderena cabaña Orocué, Parque Nacional Natural Tamá, Municipio Herrán, Depto. Norte de Santander, Colombia, 2300–2400 m; and SCNLS 8383–84, Betania, Distrito Junín, Estado Táchira, Venezuela).

DISTRIBUTION.—Known from the northern and western flanks of the Sierra Nevada de Santa Marta at elevations between 1300 and 2700 m.

*Eleutherodactylus w-nigrum* (Boettger)

Fig. 18

*Hylodes w-nigrum* Boettger, 1892:28. Holotype, SMF 3804, Zuru-cuchu, approximately 15 km W Cuenca, Prov. Azuay, Ecuador, 3500 m, in 1890 by C. F. Lehmann (photos seen but holotype not examined).

*Hylodes buergeri* Werner, 1899:476. Sole-surviving syntype, BMNH 1900.2.7.4 (reregistered as 1947.2.15.71), Alto de Sibaté near Bogotá and Fusagasugá, Depto. Cundinamarca, Colombia, 30 Dec. 1897, by O. Bürger. Böhme and Bischoff (1984:167) erred in reporting the holotype of *Hylodes buergeri* as lost. Insofar as we have been able to discover, a single specimen survived the wars in Europe.

*Eleutherodactylus insignitus* (in part): Ruthven, 1917a:1–4 (one paratype, MCZ 4074, is *E. w-nigrum*).

*Eleutherodactylus w-nigrum*: Cochran and Goin, 1970: 397; Lynch, 1978: 21; Lynch, 1979a:228–229.

DIAGNOSIS.—1) skin of dorsum shagreened with granules and warts on upper flanks, that of venter smooth; no dorsolateral folds; 2) tympanum prominent, superficial, its length  $\frac{1}{3}$ – $\frac{1}{2}$  that of eye; 3) snout rounded or ovoid in dorsal view, rounded in lateral profile;

canthus rostralis sharp; 4) upper eyelid <IOD; no pungent tubercles on eyelid; no cranial crests; 5) vomerine odontophores prominent, triangular in adults; 6) males with vocal slits and subgular vocal sac, white non-spinous nuptial pads on thumbs; 7) first finger longer than second; digital pads moderate-sized, pads on fingers III-IV as wide as inner metatarsal tubercle is long; discs wider than long; 8) fingers bearing lateral fringes/keels; 9) ulnar tubercles indistinct or absent; 10) heel and tarsus lacking pungent tubercles; 11) two metatarsal tubercles, inner elongate, 6–8 times size of round outer; supernumerary plantar tubercles few or absent; 12) toes bearing lateral fringes, no webbing; pads of toes as large as those of outer fingers; 13) dorsum tan to brown with brown interorbital bar, occipital W, sacral chevrons; flanks bearing dark brown/black spots; canthal-supratympanic stripe and labial bars prominent; posterior surfaces of thighs cream with brown/black spots; groin spotted with black (rarely mottled); venter cream to yellow with gray/brown spots; 14) adults large, males 31.8–42.0 ( $\bar{x} = 36.4 \pm 0.8$ ,  $n = 18$ ) mm, females 57.5–67.0 ( $\bar{x} = 63.0$ ,  $n = 4$ ) mm (northern Colombia only—Cordillera Central, Depto. Antioquia).

DESCRIPTION.—Cochran and Goin (1970:395–397). *Eleutherodactylus w-nigrum* varies geographically in size at maturity, patterns of markings on flanks and concealed surfaces of thighs, and color of groin and concealed limb surfaces (Lynch, 1979a:228–229; Lynch and Duellman, 1980). With only two specimens available from the Sierra Nevada (one a small juvenile) we are reluctant to characterize a population for which we have not seen living specimens. For body size, we utilized adults taken from the Cordillera Central, north of Medellín (see diagnosis). In these individuals, the pattern on the flanks and concealed thigh surfaces consists of black spots rarely coalescing. Living specimens are tan, gray, olive, or reddish-brown with rust-brown to brown markings above. The pale areas on the flanks, groin, and concealed limb surfaces are pale to bright yellow. The throat is white to pale yellow, sometimes lightly mottled with gray or brown. The venter is very pale yellow. The iris is bronze or copper (brightest above pupil) and bears a horizontal brown streak.

The species is poorly known in the Cordillera Oriental of Colombia. Specimens collected prior to 1945 are available from cloud forests near Bogotá but the only specimens secured recently from the Cordillera Oriental are from the vicinity of Virolín, Municipio Charalá, Depto. Santander. Too few specimens are available to characterize body size in the population. These frogs have spotted flanks and

concealed thighs and these concealed surfaces are white to pale yellow.

DISTRIBUTION.—Cloud forest between 800 and 3200 m, on eastern and western flanks of the Ecuadorian Andes and the Cordillera Central of Colombia. Also known from scattered localities in the Cordillera Occidental of Colombia, from the western flank of the Cordillera Oriental as far north as Virolín, and from two records on the northern face of the Sierra Nevada de Santa Marta. We believe the species' distribution is contiguous from the northern extremes of the Cordillera Occidental and Central south to the frontier between Ecuador and Perú. Too little collecting has been done in the Cordillera Oriental of Colombia between the vicinity of Bogotá and Florencia to address the distribution of *E. w-nigrum* in the southern Cordillera Oriental. We are impressed by the absence of *E. w-nigrum* from most localities we have sampled in the Cordillera Oriental.

#### ECOLOGICAL DESCRIPTIONS

All nine species known from the Sierra Nevada at Santa Marta occur in cloud forests. No *Eleutherodactylus* has been found in páramo habitats on the Sierra. Likewise, no *Eleutherodactylus* has been found in the xeric seasonal forests which occur at lower elevations on the northern and western flanks of the Sierra Nevada aside from Ruthven's (1917b) report of *E. megalops* from Don Diego (probably a *lapsus*; we could find no specimens from this locality; the record probably refers to the *finca* of the same name in cloud forests). *Eleutherodactylus w-nigrum* is the most poorly-known species from the Sierra Nevada (only two specimens have been found, both at higher elevations on the northern flank of the Sierra). Elsewhere the species is a terrestrial denizen of cloud-forest streams. *Eleutherodactylus delicatus* is likewise poorly known from the Sierra; insufficient data are available to be able to characterize its ecologic distribution. More data are available for the other seven species.

All are nocturnal frogs. Three (*E. carmelitae*, *E. insignitus*, and *E. megalops*) are clearly terrestrial. *Eleutherodactylus carmelitae* is a species strongly associated with streams but the other two are not; they are frequently found with *Geobatrachus walkeri*. *Eleutherodactylus ruthveni* is also apparently terrestrial but occurs only at the upper end of the elevations sampled to date (2200–2500 m), whereas the other three terrestrial species occur between 1300 and 2600 m. One species (*E. tayrona*) is restricted to bromeliads (arboreal or terrestrial). Two other

species (*E. cristinae* and *E. sanctaemartae*) are arboreal when active and only infrequently found on the forest floor.

There are only four general areas on the Sierra Nevada de Santa Marta from which collections are available. Two lie on the north face of the massif (San Miguel region in Depto. Guajira and Ciudad Perdida region in Depto. Magdalena; the former at elevations of ca. 1800–2150 m, the latter at ca. 1100–2200 m), one lies on the north-western corner (Serranía San Lorenzo, elevations ca. 1500–2500 m), and one lies on the western face (San Pedro de la Sierra region, elevations ca. 2000–2500 m). Specimens of all nine species known for the Sierra are available for the Serranía San Lorenzo, the most heavily collected area. Seven species are known from the San Pedro de la Sierra region, five from the San Miguel region, and only four from the Ciudad Perdida region. *Eleutherodactylus cristinae*, *E. megalops*, *E. sanctaemartae*, and *E. tayrona* are known from all four regions, but the other species are known from one (*E. carmelitae*), two (*E. delicatus*, *E. ruthveni*, and *E. w-nigrum*), or three (*E. insignitus*) areas. The numbers of species known from an area are roughly proportional to the numbers of specimens known (four or five species at Ciudad Perdida and San Miguel, respectively, with total samples of 57 and 67 specimens; San Pedro de la Sierra, 7 species, 127 specimens; San Lorenzo, 9 species, 649 specimens)—thus, we attach no significance to the lesser species densities at Ciudad Perdida and San Miguel. We do believe *E. carmelitae* to be lacking in the community above San Pedro de la Sierra.

## CRANIAL MORPHOLOGY

**JAW MUSCULATURE.**—Starrett (1968) and Savage and DeWeese (1981) emphasized attention to jaw musculature in seeking evidence of relationships between species of *Eleutherodactylus*. The senior author is preparing an extensive report on these traits but we here report the salient facts for the nine species found in the Sierra Nevada.

All nine species are identical in the aspects discussed by Starrett (1968) and Savage and DeWeese (1981). All lack the *m. adductor mandibulae externus superficialis* and have the *m. adductor mandibulae posterior subexternus*. The mandibular ramus of the trigeminal nerve passes lateral to the *m. adductor mandibulae posterior subexternus* (the "S" condition of Starrett, 1968, who reported this condition for one species we consider here, *E. w-nigrum*). This condition is apparently

plesiomorphic (Miyamoto and Tennant, 1984). All nine species agree in the morphology of the *m. depressor mandibulae* (approximately 60% of the fibers originate from fascia at the base of cavum tympanicum, medial edge of cartilage on ear [deep parts of tympanic annulus], a few fibers to the ventral edge of the crista parotica, and on the dorsal fascia overlying the *m. adductor mandibulae*; approximately 40% of the fibers originate from the dorsal fascia lying above the scapula. The division [60/40] is demarked by the emergence of the cutaneous ramus of nerve X through the *m. depressor mandibulae*. Superficially, the *m. depressor mandibulae* appears to consist of separate slips; however, digestion in 30% nitric acid fails to reveal more than a single slip having an internal tendon toward the insertion).

**CRANIAL OSTEOLOGY.**—In spite of the immense size of the genus *Eleutherodactylus* and the wide diversities in morphologies among the approximately 450 currently recognized species, little has been published to date concerning cranial osteology. Lynch (1971) proposed the division of the genus into alpha and beta sections based on some differences in skull morphology but deferred formal recognition because so few species had been examined osteologically. Published illustrations of skulls are available for five species of the *sulcatus* group (Lynch, 1971:145, 1975:13, 1981a:327–332), some illustrations are available for three species of the *biporcatus* group (Lynch, 1971:46, 49, 147, 1975:13), for three species of the *fitzingeri* group (Lynch, 1971:48, 51, 146), and for eleven species of the *unistrigatus* group (Lynch, 1968:297, 1971:44, 145, 147, 1979b:18, 27, 41, and Lynch and Trueb, 1980:394). Limited illustrations are available for one species of the *auriculatus* group (Lynch, 1971:49), two of the *inoptatus* group (Lynch, 1971:51, 147), and two of the *ricordi* group (Lynch, 1971:44, 146).

In light of the limited published material (illustrations and descriptions), we here provide illustrations (Figs. 17–21) for all nine species we recognize from the Sierra Nevada de Santa Marta. To avoid repetition, our descriptions are summarized here.

All skull bones normally encountered in frogs (premaxillae, septomaxillae, maxillae, nasals, sphenethmoid, frontoparietals, proötics, exoccipitals, squamosals, quadratojugals, plectra, vomers, palatines, pterygoids, and parasphenoid) are present in each of the nine species. Furthermore, none of the bones presents reduction (from modal size) or fusion.

The alary processes of the premaxillae are directed dorsally or slightly posterodorsally. In all species, the palatal shelf is only moderately broad and only moderately dissected (the extremes are be-

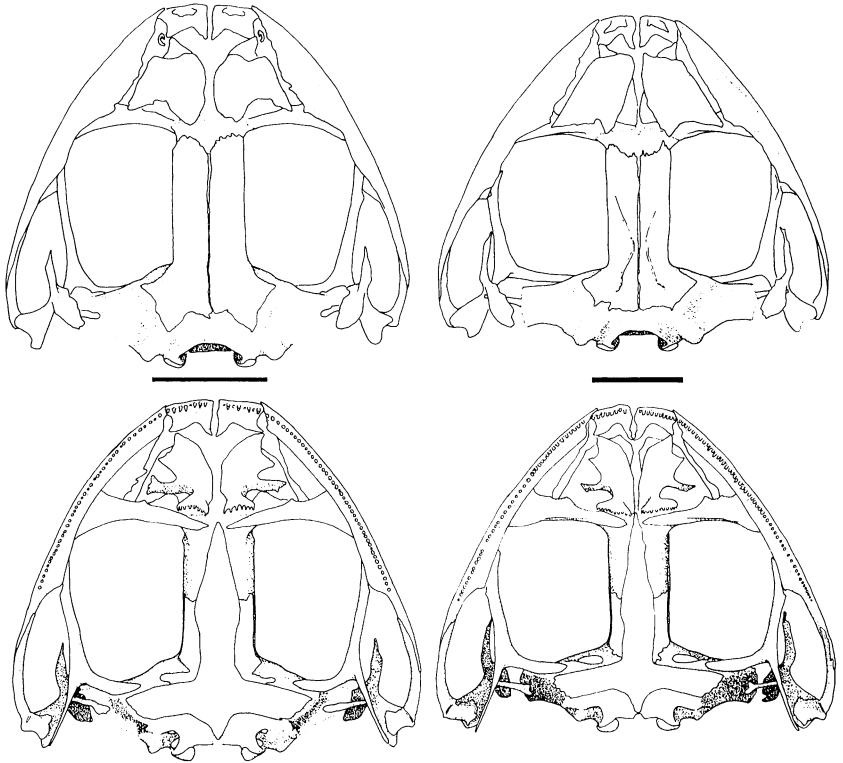


FIG. 17. Crania of *Eleutherodactylus carmelitae* (left, ICN 1654, juvenile female, 42.9 mm SVL.) and *E. insignitus* (right, ICN 701, juvenile female, 51.5 mm SVL). Scale equals 5 mm.

tween *E. megalops* and *E. sanctaemartae*). Little variation is evident in the remainder of the maxillary arch. The pars facialis of the maxilla is less deep in *E. w-nigrum* (Fig. 18) than in most species but, because so few specimens are available for most species, the difference may be insignificant. Considerable variation exists in the size and shape of the nasals (Figs. 17–21). They are narrowly separated in all but *E. w-nigrum*. The nasals of *E. carmelitae* are shaped rather differently than in any other species although those of *E. insignitus* are relatively similar (posteromedial extension). The variability in size and shape of the sphenethmoids in the illustrations partially (*E. carmelitae*, *E. cristinae*, and *E. insignitus*) reflects immaturity and partially (*E. tayrona*) reflects differences of shape. In each species, the nasals are widely



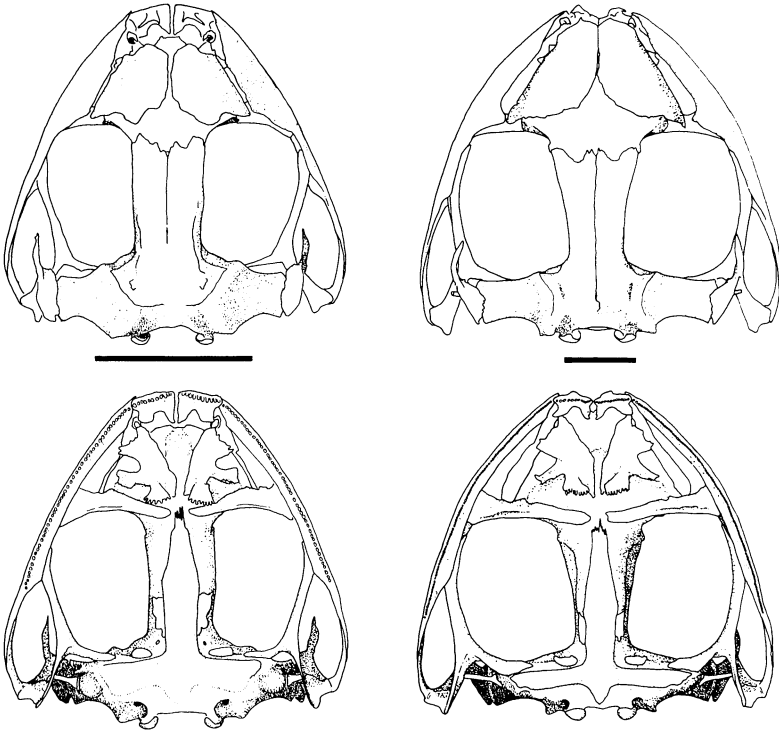


FIG. 18. Crania of *Eleutherodactylus megalops* (left, KU 170142, adult male, 24 mm SVL, scale equals 4 mm) and *E. w-nigrum* (right, KU 170094, adult female, 78 mm SVL, scale equals 5 mm).

separated from the frontoparietals. None of these species has an exposed frontoparietal fontanelle. Three shapes are apparent in the anterior edges of the frontoparietals: approximately transverse (*E. tayrona*); indented medially (*E. carmelitae*, *E. cristinae*, *E. insignitus*, *E. megalops*, *E. ruthveni*, *E. sanctaemartae*); extended medially and indented parasagittally (*E. w-nigrum*). The frontoparietals are equally broad throughout the length of the orbit in *E. carmelitae*, *E. insignitus*, *E. megalops*, and *E. tayrona* (Figs. 17, 18, 21). They are slightly narrower posteriorly than anteriorly in *E. ruthveni* and *E. sanctaemartae* (Fig. 20), and more markedly narrowed in *E. cristinae*, and *E. w-nigrum*. Because of the cranial crests, they broaden posteriorly in *E. delicatus* (Fig. 19). The frontoparietals are proportionately narrowest in *E. carmelitae* and *E. insignitus* (Fig. 17). *Eleutherodactylus megalops*

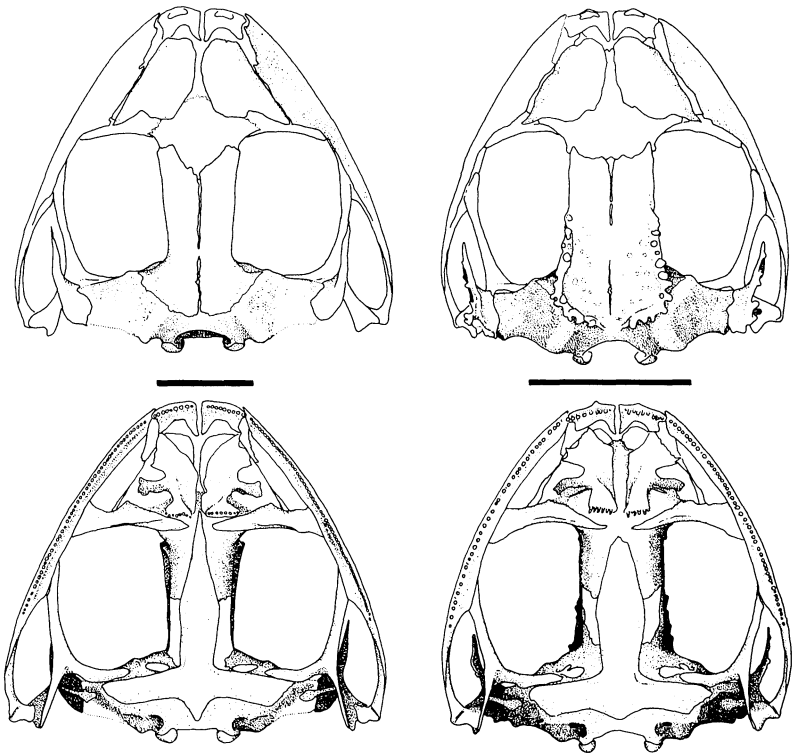


FIG. 19. Crania of *Eleutherodactylus cristinae* (left, ICN 739, young female, 50.2 mm SVL, scale equals 5 mm) and *E. delicatus* (right, ICN 3029, adult female, 29.2 mm, scale equals 4 mm).

exhibits slight keels on the edges of the frontoparietals and *E. insignitus* has thin keels nearer the midline (Fig. 17, 18). Pronounced frontoparietal crests are seen in *E. cristinae*, the very distinctive *E. delicatus* (Fig. 19), and in *E. ruthveni* (Fig. 20). In *E. w-nigrum* (Fig. 18), grooves are present on the posterolateral portion of the frontoparietals; the occipital artery lies in the groove. The epiotic eminences are obvious in each and the cristae paroticae vary from short and stout (*E. tayrona*) to rather long and slender (*E. insignitus* and *E. w-nigrum*). Each species has obvious otic plates on the squamosals; the otic plate is always short and only overlaps the crista parotica slightly. In *E. delicatus*, the squamosals are ornamented with bony knobs (Fig. 19).

The vomers of *E. tayrona* are narrower (Fig. 21) and less robust with longer (directed more posteriorly) dentigerous processes than in the

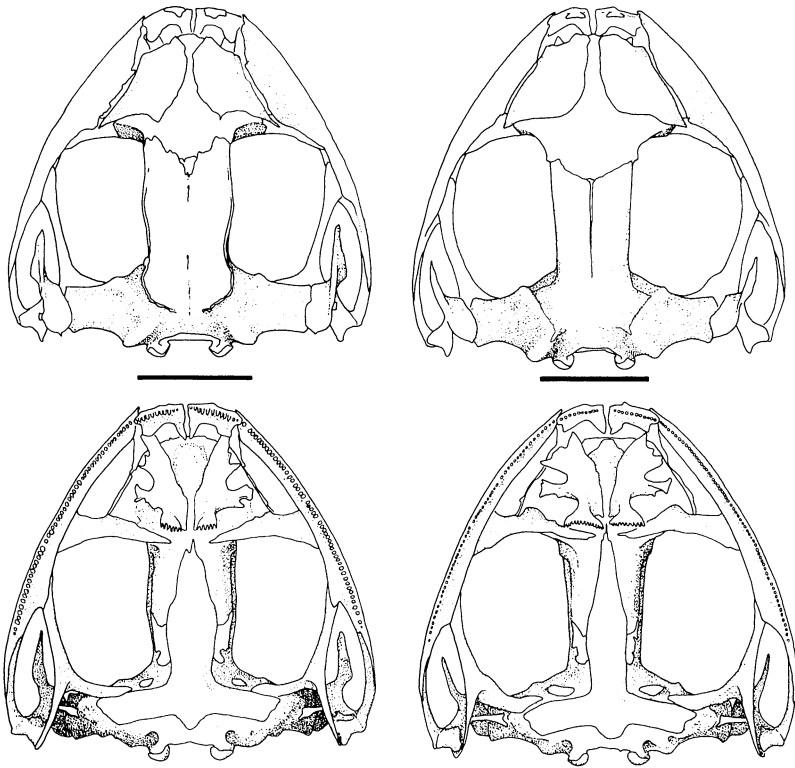


FIG. 20. Crania of *Eleutherodactylus ruthveni* (left, ICN 3014, adult female, 42.9 mm SVL) and *E. sanctaemartae* (right, ICN 740, adult female, 44.0 mm SVL); scale equals 5 mm.

other eight species. In *E. w-nigrum*, the dentigerous processes are further from the palatines than in the other eight species. The palatines are extended less medially in *E. tayrona* (Fig. 21) than in the other eight species. The cultriform process of the parasphenoid is blunter and/or shorter in *E. tayrona* (Fig. 21) than in the others although that of *E. delicatus* (Fig. 19) may be viewed as intermediate. The alary processes of the parasphenoid are deflected posteriorly in all but *E. w-nigrum* (Fig. 18); those of *E. tayrona* (Fig. 21) appear shorter than in the other eight species.

The anterior rami of the pterygoids are of moderate length (not reaching to palatines) in all but *E. w-nigrum* (reaching to palatines) but are shortest in *E. tayrona* (Fig. 21). The median rami of the pterygoids are long but do not closely approximate the parasphenoid alae in *E.*

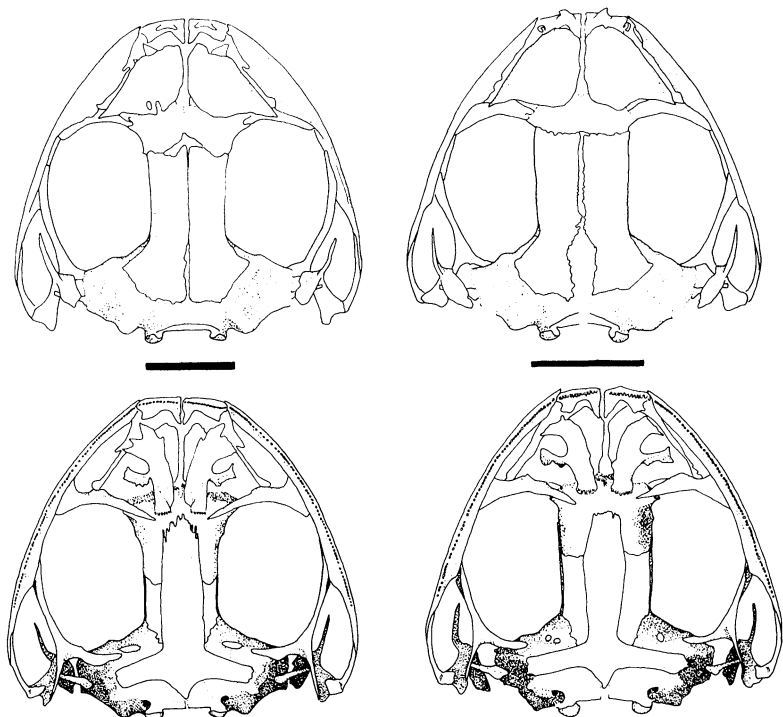


FIG. 21. Crania of *Eleutherodactylus tayrona* (left, ICN 3932, adult female, 30.2 mm SVL, flared lips, cf. Fig. 15A; right, ICN 3058, adult female, 24.6 mm SVL, unflared lips, cf. Fig. 15B). Scales equal 3 mm.

*tayrona* (Fig. 21). The occipital condyles are not stalked in any species and are widely separated in all.

In terms of skulls, *E. tayrona* forms one group, *E. w-nigrum* forms a second, and the remaining seven form a group in which *E. carmelitae* and *E. insignitus* form a subgroup.

#### RELATIONSHIPS OF SANTA MARTAN *ELEUTHERODACTYLUS*

If one views the four eleutherodactyline genera (*Dischidodactylus*, *Sminthillus*, *Syrrhophus*, and *Tomodactylus*) that are probably derivatives of *Eleutherodactylus* as coordinate with species groups, the genus contains some 27 species groups (12 Antillean, including *Sminthillus*; 5

from Mexico and Central America, including *Syrrhophus* and *Tomodactylus* but excluding three essentially South American groups having some Central American species; and 10 South American, including *Dischidodactylus*).

Cope (1862), Dunn (1926), Lynch (1976), and Schwartz (1958, 1964, 1965) used superficial traits to define species groups. These authors have employed primarily skin texture of the venter (smooth or areolate), lengths of the inner two fingers (thumb longest or thumb shortest), shape of the unguis flap (notched or entire), and length of vomerine odontophores (long, short, or absent). There are 24 possible combinations of these four characteristics but many are unknown. The nine Santa Martán *Eleutherodactylus* provide representatives for only three of the 24 combinations, as follows:

- Venter smooth, first finger shorter than second, unguis flap entire, vomerine odontophores short (*E. carmelitae*);
- Venter smooth, first finger longer than second, unguis flap entire, vomerine odontophores short (*E. insignitus*, *E. w-nigrum*);
- Venter areolate, first finger shorter than second, unguis flap entire, vomerine odontophores short (*E. cristinae*, *E. delicatus*, *E. megalops*, *E. ruthveni*, *E. sanctaemartae*, and *E. tayrona*).

The first combination is seen elsewhere, with the *alfredi* group (Mexico and Guatemala), the monotypic *karlschmidti* group (Puerto Rico), and the *symingtoni* group (Cuba). The second combination is seen elsewhere with the *biporcatus* group (in part, species in lower Central America and Chocóan South America), the *discoidalis* group (in part, species in northern Argentina, Bolivia, and southern Perú), the *fitzingeri* group (Mexico to Bolivia and eastern Brasil), and the *rhodopis* group (Mexico and Central America). The third combination is seen elsewhere with the *auriculatus* group (Antilles), the monotypic *melanostictus* group (Costa Rica and western Panamá), the *unistrigatus* group (Mexico to Bolivia and eastern Brasil), the *varleyi* group (Cuba and Hispaniola), and the monotypic *Dischidodactylus* (Cerro Duida, Venezuela).

Savage and DeWeese (1979, 1981) have argued that such combinations as those given above are merely based on "key characters" and that within the genus *Eleutherodactylus* such combinations have evolved time and time again. Those authors prefer to base species groups on characters of karyotypes, electromorphs, and jaw muscula-

ture. However, the geography of the alternatives in "key characters" is asymmetrical for unguis flaps (notched only in southeastern Brazilian forms), for shape of vomerine odontophores (long odontophores in the Greater Antilles, northern South America, and adjacent lower Central America), finger lengths (long thumbs only on Hispaniola for Antillean groups; both conditions are present in all mainland areas), and in texture of the venter (only smooth in Jamaican fauna, only areolate in Lesser Antilles; in all other areas, both smooth and areolate venters obtain). Another trait (head width), used by Lynch (1975, 1976), is likewise asymmetrical (broad heads are found only in species from lower Central America and northwestern South America whereas narrow [or normal] head widths occur throughout the range of the genus). Other traits are not so well-known but at least two are asymmetrical so far as is known ("E" condition of *m. adductor mandibulae* is known from Mexico, Central America, and Chococoan South America, "S" condition is seen throughout the range of the genus; the fusion of the frontoparietals and proötics is seen in some Mexican frogs and in many species from the Antilles but not elsewhere, whereas the absence of such fusion occurs throughout the mainland and in at least a few species from Hispaniola, Jamaica, and Puerto Rico). Such asymmetries belie Savage and DeWeese's (1979, 1981) suggestion of plasticity of "key characters."

The primary difficulty in assigning the Santa Martan species to species groups is that for most characters the apomorphic and plesiomorphic states are not now known or the states exhibited by the Santa Martan taxa are plesiomorphic (e.g., "S" condition of *m. adductor mandibulae*, non-fusion of frontoparietals and proötics). One trivial trait, which we take to be a synapomorphy (white digital pads) unites *E. carmelitae* and *E. insignitus*. This pair of species is further united by the pervasive similarities in skull bones (Fig. 17).

The suggestions by Walker and Test (1955), Rivero (1961), and Lynch (in Duellman, 1979) that some species of the Sierra Nevada de Santa Martan eleutherodactyline frog fauna have affinities with species from the Coastal Range of Venezuela cannot yet be sustained. It is of some interest, given the geographic proximity of the massif to the West Indies and its "island-like" form, that none of the species from the Santa Martas can be associated with the West Indian *Eleutherodactylus* placed in the Alpha series by Lynch (1971). In each of the nine species, the frontoparietals do not fuse to the proötics. In eight species, the median rami of the pterygoids extend further medially than the lateral extents of the parasphenoid alae (Figs. 17–20) and the bones are said to overlap. In *E. tayrona*, however, the

parasphenoid alae are shorter than those in the other taxa (although the median rami of the pterygoids are equally long in all nine and the two bones do not overlap (Fig. 21).

The Andean connection seems the most viable hypothesis to us at this time (when we are woefully ignorant of the osteology of most Andean eleutherodactyline frogs). We ignore, for purposes of biogeography, *E. ruizi* and *E. w-nigrum* for the reasons cited by Nelson and Platnick (1981). *Eleutherodactylus tayrona* appears to be a sister species of one of several species of the *lacrimosus* assembly in the Andes of northern Colombia. *Eleutherodactylus insignitus*, although apparently most closely allied to another Santa Marta form (*E. carmelitae*), seems clearly related to *E. viridicans* (Cordillera Occidental, Colombia). For the remainder, they appear most allied to one another but that in part derives from ignorance.

### SPECIMENS EXAMINED

*Eleutherodactylus carmelitae* (52). COLOMBIA: DEPARTAMENTO MAGDALENA: Municipio Santa Marta: Serranía San Lorenzo, ICN 1654, LACM 114497, 1524 m, UMMZ 51110-11; 1800-2000 m, ICN 8234-35; 1960-2200 m, ICN 741-42, 1662, 1682, 1701; 2200 m, ICN 8236; 6-7 km E El Campaño, 1720-1790 m, ICN 13005-07; 10 km E El Campaño, 1850 m, KU 167969-70; 11 km E El Campaño, 2000 m, KU 167971; 12 km E El Campaño, 2150-2200 m, ICN 13008; Finca La Granja, on road to San Lorenzo, USNM 150762-75, 150779, 150998, 151007; alto valle Rio Gaira, 1960 m, INDERENA 222-23, 237, 239, 243-44, 304-05, 306, 318; Quebrada Viernes Santo, 1524 m, UMMZ 54527-28, 54530, 54532-34.

*Eleutherodactylus cristinae* (28). COLOMBIA: DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena (Hierbabuena) SE San Pedro de la Sierra, 2000 m, UMMZ 176885. Municipio Santa Marta: heliport near Ciudad Perdida, 2250 m, ICN 12828-29; Serranía San Lorenzo, ICN 702, LACM 114499-500; 1900 m, ICN 8237-39; 1960-2200 m, ICN 739; 2200-2600 m, ICN 2676; 6-7 km E El Campaño, 1720-1790 m, ICN 13009-13; 10 km E El Campaño, 1850 m, KU 168558; 11 km E El Campaño, 2000 m, KU 168561; Cincinati, 1530 m, ICN 3779; Finca La Granja, on road to San Lorenzo, USNM 150863, 150873-75, 150877, 151005, 151013, 151019; between Minca and [Cerro] San Lorenzo, 1530-2100 m, ICN 3950.

*Eleutherodactylus delicatus* (16). COLOMBIA: DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, finca of Alfonso Vanegas, 2500 m, UMMZ 176886; Serranía Cebolleta, 8 hrs by foot E San Pedro de la Sierra, 2450 m, ICN 3026, 3029-30, 3037-38, 3048. Municipio Santa Marta: Serranía San Lorenzo, 1524 m, UMMZ 50159, 54573-74, 2200-2600 m, ICN 2665-68, 2670, 8240.

*Eleutherodactylus insignitus* (22). COLOMBIA: DEPARTAMENTO GUAJIRA: Municipio Riohacha: heights E San Miguel, 1829-2134 m, UMMZ 48393-94, 48397-99, 48402-03, 48404(2), 48407. DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, 2000 m, ICN 13164-66; Municipio Santa Marta: 6-7 km E El Campaño,

1720–1790 m, ICN 13014–17; between Minca and Estación San Lorenzo, 1530–2100 m, ICN 3949; Serranía San Lorenzo, 1700–2000 m, ICN 701, 8241–43.

*Eleutherodactylus megalops* (492). COLOMBIA: DEPARTAMENTO GUAJIRA: heights E San Miguel, 1829–2134 m, UMMZ 48395, 48405(8), 48484(4), 48485(5), 48486(5), 48487(4), 50161, 54525. DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, 2000 m, ICN 13167–77; 5.7 km E San Pedro de la Sierra, 2300 m, MCZ 88333–39; Serranía Cebolleta, 8 hrs by foot E San Pedro de la Sierra, 2450 m, ICN 3006, 3013, 3019–20, 3032, 3036. Municipio Santa Marta: 6–7 km E El Campaño, 1720–1790 m, ICN 13018–29; 8 km E El Campaño, 1850 m, KU 168384–90; 11 km E El Campaño, 2000 m, KU 168391–419, 170141–42 (cleared and stained skeletons); 12 km E El Campaño, 2080 m, KU 168420–30; Cincinati, 1530 m, ICN 3756, 3759–60, 3762, 3774–76, MCZ 4755–56, UMMZ 48444–48, 48450–51, 48453–55, 48457, 48459–65, 48469, 48471, 48474–76, 48479, 48481(2), 48482(7), 48483, 54526; heliport W Ciudad Perdida, 1300 m, ICN 12830; heliport SW Ciudad Perdida, 2250 m, ICN 12831–47; alto valle Río Gairo, 1960 m, INDERENA 215–21, 224–25, 228–29, 231, 234, 236, 238, 241–42, 284–85, 287–89, 293, 295–303, 306; Serranía de San Lorenzo, 1524–2530 m, ICN 703–09, 711–13, 715, 717–18, 720–23, 725, 728, 731, 733–34, 738, 743–50, 752–56, 1649–53, 1656–57, 1659–61, 1663–81, 1683–86, 1688–1701, 2671–75, 2677–87, 2689–98, 3948, 4733, LACM 144501–06, 114509–15, MCZ 8981–82, UMMZ 48467–68, 48470, 48472–73, 48477–78, 54474–79, 54491–97, 54502, 54508–13, 54515, 54517–21, 54522(7), 54523(3); Finca La Granja, on road to San Lorenzo, USNM 150776–78, 150796–99, 150802–62, 150864–72, 150879, 150999–151000, 151003–04, 151006, 151008–12, 151014–18, 151020–23; Quebrada Viernes Santo, 1524 m, UMMZ 54480–88, 54498–501, 54505, 54524(2); Tagua (near San Lorenzo), UMMZ 54489–90.

*Eleutherodactylus ruthveni* (69). COLOMBIA: DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, finca of Alfonso Vanegas, 2500 m, ICN 13178–79, UMMZ 176887–88; 9.5 km E San Pedro de la Sierra, 2600 m, MCZ 88352–53, 88355, 88555; Serranía Cebolleta, 8 hrs by foot E San Pedro de la Sierra, 2450 m, ICN 3011–12, 3014–18, 3027–28, 3031, 3033–35, 3039. Municipio Santa Marta: 12 km E El Campaño, 2150–2200 m, ICN 13072–76; Serranía San Lorenzo, 1800–2500 m, ICN 8254–72; Finca La Granja, on road to San Lorenzo, USNM 150780–95, 150876, 150883–85, 151024–25.

*Eleutherodactylus sanctaemartae* (150). COLOMBIA: DEPARTAMENTO GUAJIRA: heights E San Miguel, 1829–2134 m, UMMZ 54544; vicinity Taquina, 2424–2727 m, UMMZ 50139–40, 54543(2). DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, 2000 m, ICN 13180–81; Cuchilla Yerbabuena, finca of Alfonso Vanegas, 2500 m, ICN 13182; 5.7 km E San Pedro de la Sierra, MCZ 88340–49; 9.5 km E San Pedro de la Sierra, 2600 m, MCZ 88350–51, 88556; Serranía Cebolleta, 8 hrs by foot E San Pedro de la Sierra, 2460 m, ICN 3010, 3025, 3051, 8273. Municipio Santa Marta: 6–7 km E El Campaño, 1720–1790 m, ICN 13030–71; 8 km E El Campaño, 1850 m, KU 168557; 10 km E El Campaño, 1850 m, KU 168559–60; 11 km E El Campaño, 2000 m, KU 168562–64; Cincinati, 1524 m, ICN 3780, UMMZ 48605, 54542; Ciudad Perdida, 1100 m, ICN 12848–54; heliport SW Ciudad Perdida, 2250 m, ICN 12855–64; Quebrada Viernes Santo, 1524 m, UMMZ 54538; Serranía San Lorenzo, 1800–2200 m, ICN 710, 714, 716, 719, 724, 726–27, 729–30, 732, 735–37, 740, 751, 1655, 1687, 2669, 8244–53, 8274–75, LACM 114498, 114507–08, 114516–19, 114522–27, 114530, MCZ 8972–73, UMMZ 51130, 54535, 54537, 54539, 54541, 54545, 55677; Finca La Granja,



on road to San Lorenzo, USNM 150881-82. DEPARTAMENTO TOLIMA: no other data, probably in error, UMMZ 56435.

*Eleutherodactylus tayrona* (222). COLOMBIA: DEPARTAMENTO GUAJIRA: heights E San Miguel, UMMZ 47015(2), 47016(2), 47017(4), 47018(3), 47019(3), 47020(3), 47021-25, 47028-36 (embryos, egg masses). DEPARTAMENTO MAGDALENA: Municipio Ciénaga: Cuchilla Yerbabuena, 2000 m, ICN 13183-84(5); Serranía Cebolleta, 2450 m, ICN 3007, 3009, 3021-24, 3041-43, 3045-46, 3049, 3052-84, 3093-95; Municipio Santa Marta: Cincinati, 1530 m, ICN 3764; heliport SW Ciudad Perdida, 2250 m, ICN 12890-96; ridge W Ciudad Perdida, 1300 m, ICN 12875-89; 6 km E El Campaño, 1720 m, ICN 13077-78; 12 km E El Campaño, 2150-2200 m, ICN 13079-80; San Lorenzo, UMMZ 48265, 54546-50, 54551-60 (eggs & embryos), 54561-69; Serranía San Lorenzo, 1530-2100 m, ICN 3864-3942; Serranía San Lorenzo, La Cumbre, 2134 m, UMMZ 63777(24), USNM 118727-28; Serranía San Lorenzo, finca La Granja, 2300-2700 m, USNM 150878, 151026.

*Eleutherodactylus w-nigrum* (2). COLOMBIA: DEPARTAMENTO GUAJIRA: heights E San Miguel, 1829-2134 m, MCZ 4074. DEPARTAMENTO MAGDALENA: Municipio Santa Marta: Serranía San Lorenzo, 2200 m, ICN 8276.

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