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THE SPECIES GROUPS OF THE SOUTH AMERICAN FROGS OF THE GENUS *ELEUTHERODACTYLUS*

(LEPTODACTYLIDAE)

By

JOHN D. LYNCH¹

The large number of names applied to frogs of the genus *Eleutherodactylus* probably has contributed to a certain reluctance of herpetologists to become involved with the systematics of the genus. As presently defined (Lynch, 1971), the genus occurs throughout the West Indies, in Central America from northern México to the Darién of Panamá, and over the South American continent as far south as northern Argentina.

The West Indian species (131 according to Schwartz and Thomas, 1975; Schwartz, 1976) have been arranged into 4 to 6 species groups by Dunn (1925, 1926), Schwartz (1958), and Shreve and Williams (1963). Although the limits of some of the species groups are open to question (Shreve and Williams, 1963; Schwartz, 1966), the arrangements have improved the situation regarding the systematics of the West Indian species.

The Mexican and Middle American herpetofauna includes approximately 70 species not found in the West Indies or South America (Lynch, 1970; Savage, 1973, 1975; Smith and Taylor, 1948; Stuart, 1963). Smith and Taylor's (1948) species-group arrangement was modified by Firschein (1951) and Lynch (1965, 1968a, 1970); at present six species groups are recognized. Savage (1973) recognized 9 groups for the Costa Rican fauna (two of those groups also are represented in México).

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The South American herpetofauna includes 141 recognized species (see lists in the accounts of the species groups). In spite of the diversity of species, few authors have attempted to recognize species groups. Lynch (1968b) proposed a preliminary grouping of the southeastern Brazilian species. Cochran and Goin (1970) recognized four groups of the genus in Colombia. Lynch (1975b), in anticipation of this paper, proposed recognition of two species groups for the broad-headed *Eleutherodactylus* of Central and South America.

Many of the groups heretofore recognized in Middle and South America are *Artenkreisen* largely defined on the basis of content. The "groups" recognized in México and Costa Rica are assemblages of quite similar species, but the boundaries between groups have not been defined. My attempts to define those boundaries have forced me to adopt a generally more conservative stance toward species groups; thus I combine the 9 groups Savage (1973) recognized in Costa Rica into three groups. My current view of the Mexican *Eleutherodactylus* prompts me to combine most of the *mexicanus*, *pygmaeus*, and *rhodopis* groups as a single group, the *rhodopis* group. "Synonymies" for several of the species-groups arrangements for *Eleutherodactylus* are summarized in Table 1. The following account is restricted largely to the South American species.

Acknowledgments.—For loan of type-specimens or provision of working space at their respective institutions, I am grateful to J. Böhlke, A. Capart, the late D. M. Cochran, G. F. deWitte, W. E. Duellman, J. Eiselt, A. G. C. Grandison, J. Guibé, B. Hansson, A. Leviton, E. Malnate, C. W. Myers, V. Parenti, the late J. A. Peters, G. Vestegren, C. F. Walker, E. E. Williams, and R. G. Zweifel. Travel to museums was supported by a Graduate School Honors Fellowship from The University of Kansas, The University of Nebraska Research Council, and the Visiting Scientists program of the Smithsonian Institution. I have profited from discussions with Werner C. A. Bokermann, William E. Duellman, Hobart M. Smith, Edward H. Taylor, and Charles F. Walker. Jaime Péfaur provided the Spanish summary.

MATERIALS AND METHODS

For this paper, data were obtained for each nominate species by one or more of the following: examination of the type-specimen (holotype or syntypes), data derived only from the original description, study of referred specimens, or data extracted from redescriptions of the type or other specimens. Original descriptions were studied for every species. I depended on redescriptions of the type-specimens for only two names (*affinis* and *frater*); in each

case, the redescription was that provided by Cochran and Goin (1970). If the holotype or syntypes were examined, that name bears an asterisk in the lists of species given for each species group.

The holotypes or syntypes of 116 of the 169 names and paratypes of 9 other names have been examined personally. Of the remaining 44 names, I am aware of only 8 for which the types are lost (*cornutus*, *diadematus*, *galdi*, *henselii*, *lacrimosus*, *napaens*, *pulchrigulus*, and *rubicundus*). Two names not considered here (*Hylodes graevenhorsti* Fitzingeri, 1861, and *Eleutherodactylus conspicillatus guayanensis* Rivero, 1968) are *nomina nuda* based on South American material. One other name long misapplied to South American frogs is *Hyla grisea* Hallowell. The data provided by Hallowell (1860) and Cope (1862a, 1862b, 1863) clearly indicate that the frog is a member of an assortment of species in Lower Central America and Chocoan South America. Savage (1974) stabilized the name by designating a common neotype for *Hylodes fitzingeri* O. Schmidt and *Hyla grisea* Hallowell.

The 169 trivial names are listed in Gorham's (1966) checklist as *Eleutherodactylus* with the following exceptions (listed in other genera): in *Basanitia* (*bolbodactyla*, *gehrtii*, *lactea*, *nigroventris*), in *Leptodactylus* (*pumilio*), in *Phrynanodus* (*nanus*), in *Syrphophus* (*areolatus*, *chalceus*, *coeruleus*, *festae*) and in *Trachyphrynus* (*myersi*). The following are names either not included in Gorham's (1966) checklist or named since 1963: *Craugastor pulchrigulus* Cope, 1862, *Eleutherodactylus anderssoni* Lynch, 1968, *E. bilineatus* Bokermann, 1974, *E. bokermanni* Donoso-Barros, 1970 (here emended to *E. bokermanni*), *E. boconoensis* Rivero and Mayorga, 1973, *E. calcarulatus* Lynch, 1976, *E. celator* Lynch, 1976, *E. cerastes* Lynch, 1975, *E. chloronotus* Lynch, 1970, *E. crenunguis* Lynch, 1976, *E. crepitans* Bokermann, 1965, *E. croceoinguinis* Lynch, 1968, *E. elassodiscus* Lynch, 1973, *E. gualteri* Lutz, 1974, *E. lanthanites* Lynch, 1975, *E. latidiscus tamsitti* Cochran and Goin, 1970, *E. lehmanvalenciae* Thornton, 1965, *E. leucopus* Lynch, 1975, *E. luteolateralis* Lynch, 1976, *E. martiae* Lynch, 1974, *E. necerus* Lynch, 1975, *E. nicefori* Cochran and Goin, 1970, *E. nyctophylax* Lynch, 1976, *E. octavioi* Bokermann, 1965, *E. orcesi* Lynch, 1972, *E. orphnolaimus* Lynch, 1970, *E. paulodutraii* Bokermann, 1974, *E. paululus* Lynch, 1974, *E. parvillus* Lynch, 1976, *E. pugnax* Lynch, 1973, *E. pulvinatus* Rivero, 1968, *E. pusillus* Bokermann, 1967, *E. quaquaversus* Lynch, 1974, *E. surdus cabrerai* Cochran and Goin, 1970, *E. thectopternus* Lynch, 1975, *E. thymalopsoides* Lynch, 1976, *E. thymelensis* Lynch, 1972, *E. trepidotus* Lynch, 1968, *E. variabilis* Lynch, 1968, *E. vinhai* Bokermann, 1974, *E. walkeri* Lynch, 1974, *Eupsophus ginesi* Rivero, 1964, *Hyla chimboe* Fowler, 1913, and *Pseudohyla nigrogrisea* Andersson, 1945.

THE INFRAGENERIC UNITS AND SPECIES GROUPS HISTORY OF THE PROBLEM

In treating the comparatively small Colombian *Eleutherodactylus* fauna, Cochran and Goin (1970) proposed four species groups. The groups were defined as follows:

“Group I: long-legged, smooth-bellied frogs with smooth heads, fairly large in size; no bony ridges on head.

Group II: Granular-bellied, shorter-legged frogs usually having a frontoparietal depression; bodies moderately long; no bony ridges on head.

Group III: Small frogs, usually with U- or)(-shaped gular folds in the male; often with pointed toes; no bony ridges on head.

Group IV: Medium-sized to large frogs, usually with bony ridges on head or some ossification of head skin and skull.”

This arrangement must be viewed as the first attempt to define species groups for the South American *Eleutherodactylus* even though the study dealt only with Colombian frogs. Cochran was the author of the leptodactylid section of the “Frogs of Colombia” and had considerable experience with *Eleutherodactylus* from all parts of the range of the genus. A number of authors have mentioned groups, listed included taxa, and in some cases defined the group(s) involved. However, these attempts dealt with restricted geographic areas and faunas (e.g., Lynch, 1968b).

The taxonomy of eleutherodactyline frogs is difficult owing to the diversity of the group and the often subtle differences evident among preserved examples of supposed different species. Many differences apparent in living or freshly preserved material are lost after relatively short periods in alcohol. The problem of species identification is not mitigated by the plethora of species group designations used by authors (including me) dealing with the genus. A recent opportunity to examine the holotypes of nearly two-thirds of the nominate South American species and the results of those studies prompts this report.

Species groups have been defined on a diverse set of characteristics. Most groups are in fact defined (or diagnosed) on single traits, e.g., the *biporcatus-cornutus* group on the basis of cranial crests, or defined on the basis of content and a general homogeneity of character states (not specified). In my own papers (1968-74) I have used the following group names with too little concern for group definition: *biporcatus*, *binotatus*, *cornutus*, *curtipes*, *fitzingeri*, *galdi*, *guentheri*, *lacteus*, *parvus*, *rugulosus*, *surdus*, and *uni-strigatus*.

As a part of my studies on the Ecuadorian species of *Eleutherodactylus*, I have examined the type specimens of 116 of the 169 names applied to frogs from South America, as well as several thousand additional specimens. Reviews of the literature, principally original descriptions or translations of original descriptions, have revealed a fair number of erroneous statements about various taxa; those statements have resulted in some erroneous conclusions being drawn. My study of these frogs and the literature has convinced me that it is desirable to define the several species groups which I have recognized for the *Eleutherodactylus* found in mainland South America. I pointed out (Lynch, 1971) the possibility of two major divisions within the genus defined on osteological grounds—an Alpha division for the species of the West Indies (exclusive of the *inoptatus* group of Hispaniola) and the genera *Sminthillus* of Cuba and *Syrrophus* and *Tomodactylus* of México and Guatemala, and the Beta division for the species in México, Central America, South America, and the Hispaniolan *inoptatus* group. I still have not acquired enough data to propose formal recognition of these two divisions.

The most recent synthesis of the species of *Eleutherodactylus* is that of Boulenger (1882) who recognized 45 species of the genus over its entire distributional area. At present, more than 400 names have been applied to the group. The genus has been defined (Lynch, 1971), although some question remains concerning the advisability of generic separation of *Syrrophus* and *Tomodactylus*, but the major question involving the genus is the definition and delineation of the units within the genus. For convenience, the genus is divided into its three geographic subunits: the West Indian section (Florida to Trinidad), the Middle American section (México to the Canal Zone in Panamá), and the South American section (Panamá east of the isthmus and mainland South America).

One hundred sixty-nine names have been proposed based on material known or thought to have originated from within the South American section. Many of these names have been synonyms in the zoological literature from essentially the time of their proposal and never have been used in the combination with *Eleutherodactylus*. Thus the spelling of names in the following account reflects their original orthography and is not necessarily in agreement in gender with *Eleutherodactylus*.

THE INFRAGENERIC UNITS

In comparing the data from original descriptions and from examinations of the type-specimens, I noted a general concordance of the character states of two characteristics among most of the South American species of the genus. Most species have the first finger shorter than the second and the skin of the venter aerolate.

The characteristics and their character states are the relative lengths of the two inner fingers (first finger longer than second / first finger shorter than second) and the texture of the skin of the venter (smooth or feebly granular / coarsely areolate). The combinations of these character states are as follows:

- 1A: first finger longer than second; skin of venter smooth or feebly granular.
- 1B: first finger longer than second; skin of venter coarsely areolate.
- 2A: first finger shorter than second; skin of venter smooth.
- 2B: first finger shorter than second; skin of venter coarsely areolate.

The species can be arranged into groups using other characteristics but the groups thus generated appear to be more artificial than the groupings resulting from these two characteristics. One does find a homogeneity of several character states among the groups generated by simultaneous consideration of fingers lengths and the texture of the skin of the venter. The characteristics utilized for West Indian species by Dunn (1925, 1926), Schwartz (1958, 1964), and Shreve and Williams (1963) do not result in homogeneous groups among the South American species of the genus, nor is the homogeneity amongst West Indian species high. Among the West Indian species of the genus there is considerable variation in the size and shape of the prevomerine dentigerous processes. The variation in this characteristic among South American (and Central American) species of the genus is insignificant.

These four units (1A, 1B, 2A, and 2B) are subdivided into several species groups. With the exception of a single taxon included in 2B, all species are evidently members of what I have termed the Beta division of *Eleutherodactylus*; the osteological characteristics used in defining the Alpha and Beta divisions have not been checked for each taxon but are used in the species group definitions to distinguish externally identical species groups (e.g., *auriculatus* and *unistrigatus* groups).

The four "infrageneric units" should not be viewed as more than convenient subdivisions. I do not consider the species groups included in infrageneric unit 1B to be more closely related to one another than either is to some other species group here listed in another infrageneric unit. In the accounts given below the ten species groups are listed in alphabetical order within the four infrageneric units.

THE SPECIES GROUPS *Infrageneric Unit 1A*

The 47 taxa included in this contingency include diverse types.

Ten of the 47 are considered synonyms of other taxa. Lynch (1975a) considered *brachypodius*, *ilcamazonicus*, and *rosmelinus* synonyms of *vilarsi*. Cochran and Goin (1970) considered *buergeri* a synonym of *w-nigrum*. Lynch (1969) considered *carrioni* a synonym of *lymani*. Cochran (1955) considered *divisa* a synonym of *guentheri*. Lynch (1975b) considered *napaeus* a synonym of *cornutus*. Lynch (1975a) considered *peruvianus* a synonym of *conspicillatus*. Savage (1974) made *pulchrigulus* an objective synonym of *fitzingeri* by designating a common neotype. Peters (1872) considered *rugulosus* Peters a synonym of *binotatus*.

I consider several of the 37 currently recognized taxa to be synonyms but those documentations will be dealt with separately in appropriate papers. The 37 recognized taxa are assigned here to four species groups. The name of each group is taken from the oldest species of the group. The members of all four groups share the following features: skin of venter smooth; first finger longer than second; tympanum prominent, annulus not concealed; pre-omerine odontophores prominent, triangular in shape. Those species for which skeletons are available have large nasal bones in median contact, frontoparietals not synosteotically united with the prootics, and the median pterygoid ramus overlapping the parasphenoid ala.

The *binotatus* Group

Definition.—Traits of unit 1A and the following: head narrow (HW/SVL < 0.43); no cranial crests; unguis flap indented (Fig. 1); digits bearing pads or not (*octavioi*); toes lacking webs.

Content.—*binotatus* (*rugulosus*), *galteri*, *guentheri** (*divisa*), *nasutus*, *octavioi*, and *pliciferus*.* Data are inadequate to definitely assign *henselii* and *hoehnei* to the group. The holotype of *henselii* is now lost (G. Peters, *in litt.*).

Distribution.—Coastal Brasil from Pernambuco to Rio Grande do Sul (Fig. 2).

Remarks.—The six species of the group form 3 sets. *E. octavioi* differs markedly from the other five in lacking pads on the digits. *E. guentheri* and *E. nasutus* are very similar (Cochran, 1955) with apically rounded discs; the first finger, although longer than the second, is not markedly longer. *E. binotatus* and *E. pliciferus* have pointed discs and very long first finger. Both have numerous dorsal ridges.

The *biporcatus* Group

Definition.—Traits of unit 1A and the following: head broad (HW/SVL 0.44-0.58); cranial crests present; unguis flap not indented; digits bearing narrow pads; toes lacking webs.

Content.—Lynch (1975b) recognized five species: *biporcatus*,

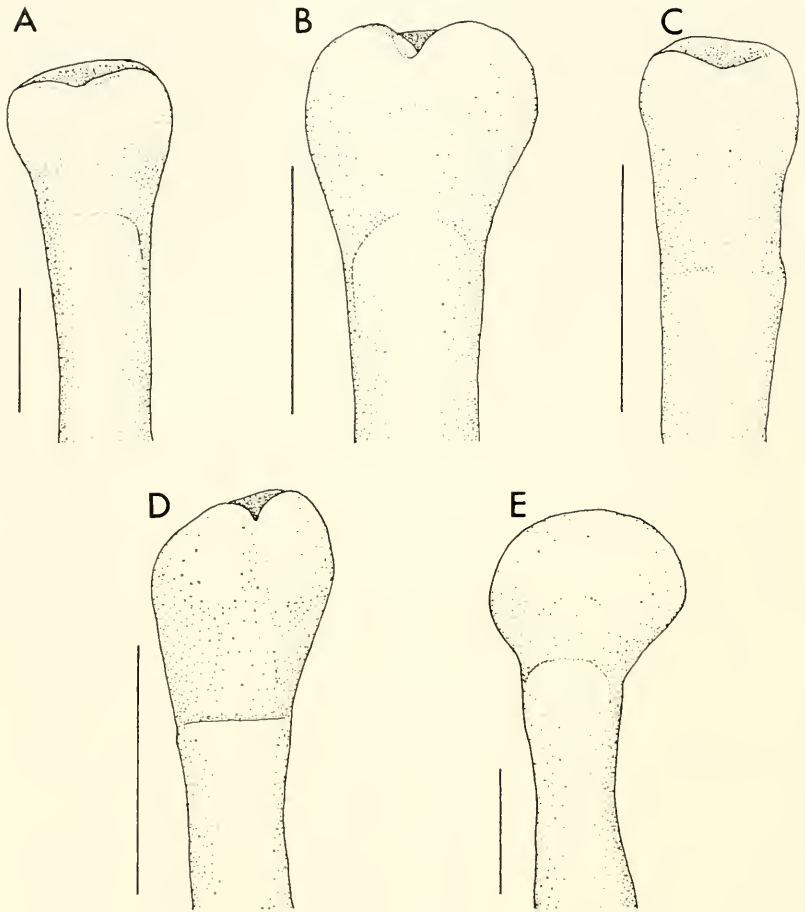


FIG. 1. Dorsal views of digital pads. A) *E. guentheri*, 3rd finger right hand, KU 92816. B) *E. nigroventris*, 4th toe right foot, KU 92734. C) *E. octavioi*, 4th toe left foot, KU 92827. D) *E. parvus*, 4th toe left foot, KU 92831. E) *E. fenestratus*, 3rd finger left hand, WACB 9841. Lines equal 1 mm. Abbreviations: KU—The University of Kansas Museum of Natural History; WACB—Werner C. A. Bokermann (private collection).

bufoniformis,^o *cerastes*,^o *cornutus* (*napaeus*), and *necerus*.^o

Distribution.—Lowlands of Central America from Honduras to eastern Panamá; Pacific lowlands and Andean versant in Colombia and Ecuador; Amazonian Andean versant in Ecuador (Fig. 2).

Remarks.—*E. anomalus* (Boulenger) is assigned to the *fitzingeri* group (see below) but approaches the *biporcatus* group in that the head is moderately broad (HW/SVL 0.42-0.48). *E. anomalus* lacks cranial crests and has fully webbed toes but is otherwise similar to *E. bufoniformis*.

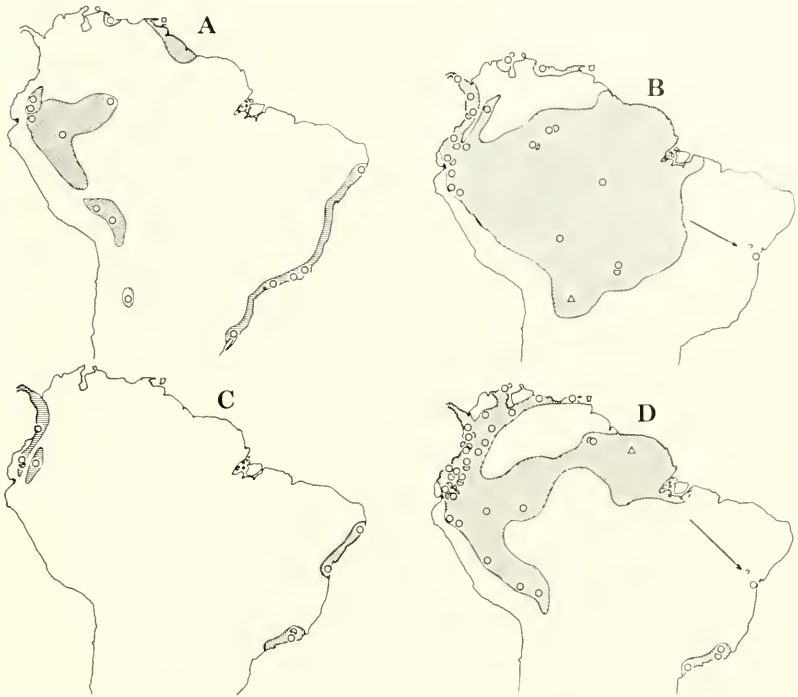


FIG. 2. Distributions of the species groups of *Eleutherodactylus* in South America. Open circles and squares denote type-localities, whereas triangles denote vague type-localities. The distribution of the group is indicated with hatching. A) *E. auriculatus* group (vertical hatching); *E. binotatus* group (horizontal hatching); *E. discoidalis* group (right oblique hatching); *E. sulcatus* group (left oblique hatching). B) *E. fitzingeri* group. C) *E. biporcatus* group (horizontal hatching); *E. parvus* group (vertical hatching); *E. ramagii* group (oblique hatching). D) *E. lacteus* group (vertical hatching); *E. unistrigatus* group (oblique hatching).

The discoidalis Group

Definition.—Traits of unit 1A and the following: head narrow; no cranial crests; unguis flap not indented; digits lacking pads; toes lacking webs.

Content.—*cruralis*,° *discoidalis*,° *elassodiscus*,° *granulosus*,° and *nigrovittatus*.°

Distribution.—Amazonian Andean versant in Bolivia and southern Perú (*cruralis* and *granulosus*) and northern Ecuador (*elassodiscus* and *nigrovittatus*); Andean foothills in northern Argentina (*discoidalis*).

Remarks.—*E. elassodiscus* and *E. nigrovittatus* have pointed discs (thus resembling *E. binotatus* and *E. pliciferus* of the *binotatus* group), whereas *E. cruralis*, *E. discoidalis*, and *E. granulosus*

have apically rounded discs. These three species resemble *E. octavioi* (*binotatus* group) in having large outer metatarsal tubercles. I consider this group annectant between the *binotatus* and *fitzingeri* groups.

The *fitzingeri* Group

Definition.—Traits of unit IA and the following: head narrow (HW/SVL 0.32-0.43 in most; 0.36-0.48 in some species, see remarks); no cranial crests; unguis flap not indented; digits bearing pads; toes lacking webs or moderately to fully webbed.

Content (South American taxa only).—*achatinus*,[°] *anomalus*,[°] *bilineatus*, *bisignatus*,[°] *brederi*,[°] *conspicillatus*[°] (*peruvianus*[°]), *crenunguis*,[°] *crepitans*, *fenestratus*,[°] *fitzingeri* (*pulchrigulus*), *heterodactylum*, *insignitus*,[°] *lanthanites*,[°] *longirostris*,[°] *lymani*[°] (*carrioni*[°]), *pagmae*,[°] *raniformis*,[°] *terraebolivaris*,[°] *thectopterus*,[°] *vilarsi*[°] (*brachypodius*,[°] *ileamazonicus*,[°] *rosmelinus*[°]), and *uigrum* (*buergeri*[°]).

Distribution.—The forested Amazon basin as far south as Mato Grosso and Bolivia; the Andean slopes in Colombia, Ecuador, and extreme northern Perú; the Pacific lowlands of Colombia and Ecuador; the Coastal Range of Venezuela. The group occurs in Central America from Panamá west and north into México (Fig. 2).

Remarks.—I tentatively include the Central American frogs placed in the *gollmeri* group in this group as well as the frogs Savage (1975) considered to be members of the *rugulosus* group. The several groups of Mexican *Eleutherodactylus* recognized by Smith and Taylor (1948) include some representatives of the *fitzingeri* group as used here (*viz.*, *laticeps* group, in part; *rhodopis* group, in part; *rugulosus* group). The Mexican and Guatemalan species previously assigned to the *laticeps* and *rhodopis* groups but here considered *fitzingeri* group frogs include *E. anzuetoi* Stuart, *E. laticeps* (Duméril), *E. lineatus* (Brocchi), *E. macdougalli* Taylor, *E. rostralis* (Werner), *E. stantoni* Schmidt, and *E. werleri* Lynch and Fritts. These seven nominate taxa are closely allied to the Middle American *E. gollmeri* (Peters), *E. minus* Taylor, and *E. noblei* Barbour and Dunn.

E. anomalus is perhaps the most divergent member of the group in having no pads on the fingers with very poorly developed discs and having nearly fully webbed feet. *E. fitzingeri*, *E. longirostris*, and *E. raniformis* have appreciable webbing of the toes as well but presently I am not willing to separate these four species from the other 17 on the basis of toe webbing. I am aware of one or two undescribed taxa from the upper Amazon basin (Colombia, Ecuador, and Perú) having nearly as great but observably less webbing. Additionally, Savage's (1975) studies of Central American species

suggest that variation in toe webbing is not a desirable base for species group separations.

Bokermann's (1974) *E. bilineatus* is placed here only tentatively. On the basis of the description and illustrations, the frog is similar to a frog now under study by M. S. Hoogmoed; if *E. bilineatus* is congeneric with Hoogmoed's frog, it is not a member of the genus *Eleutherodactylus*.

Infrageneric Unit IB

The seven nominate species of this contingency readily fall into three groups. Lynch (1975b) considered *koki* and *macrocephalus* synonyms of *sulcatus*.

Cochran (1956) described *E. beebei* from Kartabo, British Guiana (= Guyana) noting that the frog was similar to the Haitian *E. inoptatus*. I re-examined the unique holotype (USNM 129526) and found a number of discrepancies with the original description. The holotype is an adult female containing ovarian eggs (not a male with vocal slits as reported by Cochran). Cochran cited the presence of dermal appendages on the upper eyelid, elbow, knee, and heel and illustrated a tarsal fold. Although dermal horns are present on the upper eyelid no trace of such structures are found on the elbow, knee, or heel; likewise no tarsal fold is present. Lastly, the illustration of the holotype shows vertical pupils; the pupils of the holotype are horizontal.

The holotype of *E. beebei* is not distinguishable from equal-sized adult females of *E. inoptatus*; in the absence of differences, *E. beebei* Cochran is referred to the synonymy of *E. inoptatus* (Barbour). I seriously doubt that the holotype originated from Guyana in spite of the notes of William Beebe (quoted by Cochran, 1956:12). The frogs of the *E. inoptatus* group (*E. chlorophenax*, *E. hypostenor*, *E. inoptatus*, *E. nortoni*, and *E. ruthae*) are restricted to Hispaniola (Schwartz, 1965, 1976) and although the Kartabo region has not been so extensively collected as some areas in South America it seems unlikely that so large a frog would continue to escape notice.

The ramagii Group

Definition.—Skin of venter areolate; first finger longer than second; tympanum prominent, annulus not concealed; prevomerine odontophores small, oblique; head narrow; no cranial crests; unguis flap not indented; digits bearing large pads; toes lacking webbing. No osteological data available.

Content.—*paulodutraii*, *ramagii*.^o

Distribution.—Extreme eastern Brasil (Bahia, Pernambuco).

Remarks.—These two species differ from all other South American *Eleutherodactylus* in having a long first finger and large pads

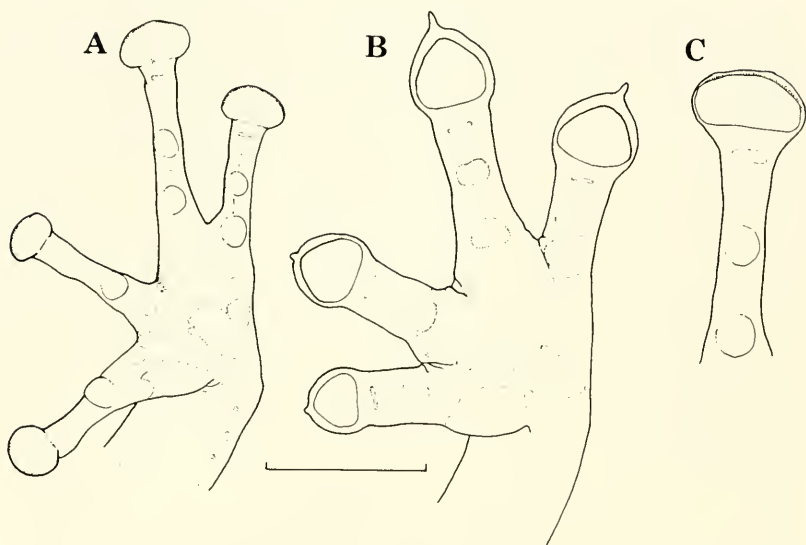


FIG. 3. Palmar views of hands and digits of *Eleutherodactylus*. A) *E. ramagii*, KU 137752. B) *E. gularis*, LACM 73239. C) *E. altamazonicus*, 3rd finger left hand, KU 148772. Line equals 2 mm. Abbreviations: KU—The University of Kansas Museum of Natural History; LACM—Los Angeles County Museum.

and discs on the innermost digits (Fig. 3). These traits in combination with the insignificant prevomerine odontophores are suggestive of an affinity with West Indian *Eleutherodactylus* but until osteological data are available I am reluctant to assert a West Indian affinity for the group.

The sulcatus Group

Definition.—Skin of venter coarsely areolate; first finger longer than second; tympanum prominent, annulus not concealed; prevomerine odontophores prominent, arch-like; head broad (HW/SVL 0.44-0.55); cranial crests present; unguis absent or not indented; fingers lacking pads; toes lacking webbing; nasal bones large, in median contact; frontoparietal not fused to prootic; median ramus of pterygoid overlapping parasphenoid ala.

Content.—Lynch (1975b) recognized two species: *maussi*,^{*} *sulcatus*^{*} (*koki*,^{*} *macrocephalus*^{*}).

Distribution.—Coastal Range of Venezuela and upper Amazon basin in western Brasil and eastern Ecuador and Perú (Fig. 2).

Remarks.—The frogs of the *sulcatus* group are quite similar to those of the *biporcatus* group but, perhaps, are most closely related to the eleutherodactyline genus *Amblyphrynus*. In spite of the similarities of the *biporcatus* and *sulcatus* groups, I am reluctant

to combine the two groups or to advocate generic separation from *Eleutherodactylus*.

Infrageneric Unit 2A

Nine nominate species are included in this contingency and are separable into two species groups. One of the included species, *E. racenisi* Rivero, is probably incorrectly referred to Unit 2A but until the holotype is re-examined and the inadequate original description verified, the species is included here; it is not assigned to either the *lacteus* group or *parvus* group.

Of the eight other names, Cochran (1955) considered *gehrtii* a synonym of *bolbodactyla*. Lynch (1968b) assigned *nanus* and Heyer (1972) assigned *pumilio* to the synonymy of *parvus*.

In addition to having the skin of the venter smooth and the first finger shorter than the second these five species have indented unguis flaps (as in the *E. binotatus* group). Those species for which skeletal data are available have large nasal bones, frontoparietals not fused to the prootics, and the median ramus of the pterygoid overlapping the parasphenoid ala.

The *lacteus* Group

Definition.—Traits of unit 2A (except that *E. nigroventris* has an areolate venter) and the following: digits bearing large pads and apically rounded discs; tympanum prominent, annulus not concealed; prevomerine odontophores low, oblique; nasal bones in median contact.

Content.—*bolbodactyla* (*gehrtii*), *lacteus*, *nigroventris* (*holtii*^o), *venancioi*.

Distribution.—Mountains of southeastern Brasil (Fig. 2).

Remarks.—*E. nigroventris* (Lutz) [and its synonym, *E. unistri-gatus holti* Cochran (*vide* Bokermann, 1966)] differs from the other species of the group in having areolate skin on the venter. In spite of this difference I consider *nigroventris* a member of the *lacteus* group because of the agreement in digit morphology, prevomerine dentition, and the visibility of the tympanum.

The *parvus* Group

Definition.—Traits of unit 2A and the following: digits bearing narrow pads and apically pointed discs; tympanum indistinct or concealed, annulus not or only partially visible; prevomerine odontophores prominent, triangular in outline. Nasal bones narrowly separated.

Content.—*parvus* (*nanus*,^o *pumilio*^o), *pusillus*.

Distribution.—Mountains of southeastern Brasil (Fig. 2).

Remarks.—These frogs once were confused with *E. rhodopis*

(Miranda-Ribeiro, 1926); the similarity largely stems from the pointed discs in each group. The pointed discs of the frogs of the *E. parvus* group are also shared with *E. nigrovittatus* (an Ecuadorian frog of the *discoidalis* group) and *E. stenodiscus* (a Venezuelan frog of the *unistrigatus* group). Neither of the last two species has indented unguis flaps.

The coincidence of notched or indented unguis flaps in all three groups found in southeastern Brasil is suggestive that they not be separated. All three also share smooth skin on the venter and the osteological traits cited above for unit 2A but vary in relative lengths of the first two fingers, prominence of the prevomerine odontophores, and prominence of the tympanum. I place little significance on the last trait but consider finger lengths and prominence of prevomerine odontophores relatively important features.

Infrageneric Unit 2B

This is the largest of the four contingencies, including 104 nominate species. The 104 taxa are here assigned to two groups: *urichi* is placed in the *auriculatus* group and the other 103 in the *unistrigatus* group. Eleven of the 104 are considered synonyms of other names. Lynch (1974) considered *anderssoni* a synonym of *ockendeni* and *brevicrus* a synonym of *altamazonicus*. Lynch and Schwartz (1972) considered *bufonius* a synonym of *diadematus*. Barbour and Noble (1920) consider *equatorialis* a synonym of *unistrigatus*. Dunn (1944) considered *fasslianus* a synonym of *bogotensis*. Lynch (1974) considered *Hylodes festae* a synonym of *galdi* and pointed out (1975c) that *Paludicola festae* was identical to *trepidotus* but as a secondary homonym of *Hylodes festae* was not available. Dunn (1944) considered *fulhmanni* a synonym of *elegans*. Savage (1968) considered *lehmanvalenciae* a synonym of *moro*. Lynch (1969) considered *margaritifera* a synonym of *galdi*.

Dunn (1942) considered *gularis* and *huigrae* synonyms of *diastema* but both differ from *diastema* in having papillae at the digit tips. Although I here remove them from the unjustified synonymy with *diastema* I consider *huigrae* a synonym of *gularis*.

The remaining 93 names are here treated as valid although some surely are not. My use of *chimboe*, *grandoculis*, *melini*, *ventrivittatus*, and *whymperi* is tentative; these names will be placed in the synonymies of other species in appropriate papers.

The 93 species here recognized include one (*urichi*) placed in the West Indian *auriculatus* group by Schwartz (1967) as well as the frogs Cochran and Goin (1970) placed in groups II and III. Their group III is equivalent to a sometimes recognized Central American species group, the *diastema* group (Table 1).

In addition to having the skin of the venter coarsely areolate

and the first finger shorter than the second, these frogs have narrow heads (HW/SVL 0.30-0.42) and the unguis flap is not indented. Compared to the other infrageneric units, 2B is heterogeneous. The tympanum is prominent (annulus not concealed) in many species but an equal number have partially or entirely concealed tympana and in three species (*anotis*, *pugnax*, and *surdus*) the tympanic annulus, cavum tympanicum, and plectrum are absent. The pre-omerine odontophores range from prominent, triangular-shaped structures (e.g., *erythropleurus*, *quaquaversus*) to obscure, thin, oblique structures (e.g., *curtipes*, *nigrogriseus*, *ockendeni*, *unistrigatus*). In *coeruleus* and *orcesi* odontophores are absent and those of *areolatus* are nearly indistinguishable. Cranial crests usually are lacking in these frogs but are well developed in *buckleyi*, *curtipes*, *devillei*, *galdi*, and *surdus* and prominent, although less well developed in *chloronotus*, *glandulosus*, and *vertebralis*. Many species have very slight upturning of the lateral edges of the frontoparietals which might be termed incipient or poorly-developed cranial crests.

The variation in digit morphology ranges from those lacking pads (e.g., *ginesi*, *myersi*, and *trepidotus*) to those having greatly dilated pads (e.g., *diadematus*, *latidiscus*, and *rubicundus*) with a complete array of intermediates. In those having digital pads, the pads on the inner fingers are smaller than those of the outer fingers. Two species (*areolatus*, *gularis*) have triangular discs (apex distal) with prominent papillae above the disc (Fig. 3). In most species the discs are much broader than long (Fig. 3) but in the species lacking pads as well as those having triangular discs the disc length is equal to or exceeds disc width. However, disc shape (i.e., length vs width) is a continuous variable.

Most frogs of this group lack toe webbing but many have lateral fringes on the toes. One (*pugnax*) has appreciable webbing but the extent of the web is much less than that seen in certain species of the *fitzingeri* group.

I have examined skeletons of only 17 of the named species in unit 2B (*acuminatus*, *altamazonicus*, *areolatus*, *bogotensis*, *cajamarcesis*, *chloronotus*, *croceinguinis*, *curtipes*, *devillei*, *galdi*, *lacrimosus*, *nicefori*, *ockendeni*, *riveti*, *stenodiscus*, *surdus*, *thymelensis*, *trepidotus*, *unistrigatus*, and *variabilis*). The frontoparietals are fused to the prootics in *curtipes* and *thymelensis* and may be fused in *riveti* and *trepidotus* but the specimens examined do not permit definite characterization. The median ramus of the pterygoid overlaps the parasphenoid ala in all except *acuminatus* and *cajamarcesis*. The nasals are large and in median contact in all species although one might describe the nasals of *bogotensis*, *riveti*, *thymelensis*, *unistrigatus*, and *variabilis* as narrowly separated. The nasals of these five species are less separated than are those of *E. parvus* (*parvus* group, unit 2A).

Lynch (1971) suggested dividing *Eleutherodactylus* into Alpha and Beta divisions on the basis of three osteological features. The Alpha division was characterized in having the frontoparietals and prootics fused, the median pterygoid ramus not overlapping the parasphenoid ala, and the prevomers small and separated medially. At least two of the 17 species in unit 2B have frontoparietal-prootic fusions but also have pterygoid-parasphenoid contact. Two others present the inverse character states. In view of the variability in osteological characteristics, separation of the South American and West Indian species of unit 2B as distinct species groups is difficult to defend. That skeletal data of only 17 South American and 16 Antillean species currently are available also renders any such separation tenuous. Osteological preparations are not available for *E. urichi* (putative *E. auriculatus* group member) or for most species in unit 2B from Venezuela. However, until more species of unit 2B are known osteologically, I propose to recognize Antillean and mainland groups.

The *auriculatus* Group

Definition.—skin of venter coarsely areolate; first finger shorter than second; heads narrow; unguis flap not indented; frontoparietal bone fused to prootic; median ramus of pterygoid not overlapping parasphenoid ala; large nasal bones in median contact or narrowly separated; prevomerine odontophores narrow (patch-like, not arched).

Content.—39 species (see Schwartz, 1969, 1973); *urichi* occurs on Trinidad and the adjacent mainland (Venezuela, Guyana).

Distribution.—Throughout the Antilles possibly excepting Jamaica (Schwartz, 1969).

The *unistrigatus* Group

Definition.—skin of venter coarsely areolate; first finger shorter than second; heads narrow; unguis flap not indented; frontoparietal bone rarely fused to prootic; median ramus of pterygoid usually overlapping parasphenoid ala; large nasal bones in median contact or narrowly separated; prevomerine odontophores narrow (not arch-like).

Content.—92 species having South American type-localities; the type-locality for *moro* is extra-limital: *acuminatus*,[°] *affinis*, *altamazonicus*[°] (*brevicrus*), *anonymus*, *anotis*,[°] *appendiculatus*,[°] *areolatus*,[°] *bicumulus*,[°] *bogotensis* (*fasslianus*), *boconoensis*, *bokermanni*, *briceni*,[°] *buckleyi*,[°] *cabrerai*,[°] *cajamaricensis*,[°] *calcaratus*,[°] *calcarulatus*,[°] *carmelitae*,[°] *carvalhoi*, *celator*,[°] *chalcus*, *chimboe*,[°] *chloronotus*,[°] *coeruleus*,[°] *croceinguinis*,[°] *crucifer*,[°] *curtipes*,[°] *delicatus*,[°] *devillei*,[°] *diadematus* (*bufonius*[°]),

elegans (*fuhrmanni*), *erythropleurus*,[°] *frater*, *galdi* (*festae*,[°] *margaritifera*,[°]), *ginesi*, *glandulosus*,[°] *grandoculis*, *gularis*[°] (*huigrae*,[°]), *inguinalis*,[°] *lacrimosus*, *lancinii*, *latidiscus*,[°] *lehmanni*, *leucopus*,[°] *luteolateralis*,[°] *marmoratus*,[°] *martiae*,[°] *megalops*,[°] *melini*, *moro* (*lehmanvalenciae*,[°]), *myersi*,[°] *nicefori*,[°] *nigrogriseus*,[°] *nyctophylax*,[°] *ockendeni*[°] (*anderssoni*,[°]), *orcei*,[°] *ornatissimus*, *orocostalis*, *orphanolaimus*,[°] *palmeri*,[°] *parvillus*,[°] *pastazensis*,[°] *paululus*,[°] *platydactylus*,[°] *pseudoacuminatus*,[°] *pugnax*,[°] *pulvinatus*,[°] *quaquaverus*,[°] *reticulatus*,[°] *riveti*,[°] *roseus*,[°] *rozei*, *rubicundus*, *sanctaemartae*,[°] *stenodiscus*,[°] *subsigillatus*,[°] *surdus*,[°] *taeniatas*,[°] *tamsitti*, *thymalopsoides*,[°] *thymelensis*,[°] *trachyblepharis*,[°] *trepidotus*[°] (*Paludicola festae*,[°]), *turumiquirensis*,[°] *unistrigatus*[°] (*equatorialis*,[°]), *variabilis*,[°] *ventrimarmoratus*,[°] *ventrivittatus*, *vertebralis*,[°] *vinhai*, *walkeri*,[°] *whymperi*,[°] and *williamsi*.

Distribution.—Throughout forested Colombia and Ecuador as well as into the high altitude grasslands; along the western edge of the Amazon basin in Perú and adjacent Bolivia; the northern Amazon basin in Brasil and Venezuela; Guyanas; Mérida Andes and the Coastal Range of Venezuela (Fig. 2). Species of the group occur in Central America at least to eastern and southern México. Insofar as I can judge from the description (Bokermann, 1974), *E. vinhai*, in eastern Brasil, is a member of this group.

Remarks.—As noted above, the *unistrigatus* group may not prove separable from the Antillean *auriculatus* group. Likewise, some of the species listed above may be *auriculatus* group species (i.e., those from the Coastal Range of Venezuela and the Sierra Nevada de Santa Marta in Colombia).

The *unistrigatus* group has its center of diversity in the Andes of Colombia and Ecuador. The distributional rami of this group extending south along the east face of the Andes and east across the northern Amazon basin contain few (3-4) species. The ancient Guyana highlands have produced only 2 species. The Coastal Range of Venezuela and the Santa Martas of Colombia each have a half-dozen species. Savage's (1973) checklist includes fewer than a dozen species in Costa Rica. By way of contrast, the region about Santa Cecilia in eastern Ecuador harbors 12 species of this group. Most localities on the Andean slopes of Ecuador support 5-8 species of the *unistrigatus* group.

COMPARISONS WITH ANTILLEAN GROUPS

Schwartz generally has recognized 6 species groups for Antillean *Eleutherodactylus* even though a number of species has not been assigned to any species group. By and large, he used the same features E. R. Dunn proposed to separate groups. Shreve and Williams (1963) proposed using some additional features (i.e.,

webbing, body glands) but Schwartz (1966, 1967) has objected adequately to the use of such features. Neither Dunn nor Schwartz proposed using finger lengths as a means of distinguishing groups, perhaps because all Cuban forms are identical with regard to this feature. In perusing Cochran's (1941) Hispaniolan herpetology, Stejneger's (1904) and Schmidt's (1928) Puerto Rican studies, Lynn and Grant's (1940) Jamaican study, as well as the many papers by Schwartz I noted that only 5 West Indian *Eleutherodactylus* have the thumb longer than the second finger. Schwartz (1965, 1976) proposed separating these from the *auriculatus* group as the *inoptatus* group and in so doing noted that the frogs of this group were quite dissimilar to all other Antillean *Eleutherodactylus*. That dissimilarity is reflected osteologically as well; unlike all other Antillean *Eleutherodactylus*, the frontoparietal and prootic bones are not fused in frogs of the *inoptatus* group (Lynch, 1971).

As already noted, the Antillean *auriculatus* group is very similar to the mainland *unistrigatus* group. The Antillean equivalent to the *unistrigatus* group includes the *auriculatus* and *varleyi* groups of Dunn and Schwartz. Schwartz (1969) termed the digits of *E. flavescens* and *E. poolei* "notched" suggesting a possible relationship of these otherwise normal *auriculatus* group frogs to some southeastern Brazilian groups (e.g., *lacteus* and *parvus* groups). The digital pads of *E. flavescens* and *E. poolei* are not notched in the same way that the pads are notched in the southeastern Brazilian frogs but are more appropriately termed emarginate and thus resemble the pads of certain Mexican frogs (*alfredi* group) as well as some members of the *unistrigatus* group (i.e., *E. anotis* of Venezuela and *E. latidiscus* of Colombia and Ecuador).

The other four groups currently recognized by Schwartz (*in litt*: *emiliae*, *gossei*, *ricordi*, and *symingtoni*) do not have readily identified South American equivalents. The four groups are distinguished in the breadth of the prevomerine odontophores (very broad in *gossei* and *ricordi* groups, patch-like in *emiliae* and *symingtoni* groups), texture of the skin (smooth in *emiliae* and *gossei* groups, rugose in *ricordi* and *symingtoni* groups), and body size (*symingtoni* group frogs are quite large). The only South American groups having broad prevomerine odontophores (some *biporcatus* and *sulcatus* group species) are markedly different large frogs having broad heads, prominent cranial crests, and the thumb longer than the second finger. The South American *ramagii* group reminds me of some *ricordi* group frogs until the prevomerine dentitions are compared.

The Antillean *inoptatus* group resembles the South American *sulcatus* group in having broad prevomerine dentition (slightly narrower than those of frogs of the *emiliae*, *gossei*, and *ricordi* groups), long first fingers, cranial crests, and lack of frontoparietal-

prootic fusion. The groups differ in that the *sulcatus* group frogs have broad heads, markedly (rather than feebly) areolate skin on the venter, and contact between the pterygoid and parasphenoid bones.

COMPARISON WITH MEXICAN AND CENTRAL AMERICAN GROUPS

As mentioned above, the *biporcatus*, *fitzingeri*, and *unistrigatus* groups extend easterly and northeasterly into Central America. The *biporcatus* group is represented in Central America by two species also found in Colombia (*E. biporcatus* and *E. bufoniformis*). The *fitzingeri* group includes Central American frogs placed in the *gollmeri* and *rugulosus* groups of Savage (1973, 1975) and Smith and Taylor (1948) as well as some species previously placed in the *rhodopis* group (*E. anzuetoi*, *E. lineatus*, *E. macdougalli*, *E. rostralis*, and *E. werleri*) and *laticeps* group (*E. laticeps* and *E. stantoni*). The *unistrigatus* group includes Savage's (1973) *crucentus*, *diastema*, and *melanostictus* groups as well as some species previously placed in the *alfredi* group (*E. batrachylus* Taylor and *E. glaucus* Lynch) and *mexicanus* group [*E. greggi* Bumzahem and *E. omiltemanus* (Günther)].

For the present, the remaining species of Smith and Taylor's (1948) *alfredi* group are left in that group. I am not convinced that these remaining eleven species are closely related. The *alfredi* group is partially characterized in having smooth skin on the venter, the first finger shorter than the second, and large, emarginate digital pads. The species of the group occur in southern México and Guatemala.

In the *rhodopis* group I include the species Lynch (1970) placed in the *mexicanus* and *pygmaeus* groups (except for *greggi*, *occidentalis* and *omiltemanus*) as well as most species Smith and Taylor (1948) included in their *rhodopis* group. Frogs of this group have smooth skin on the venter, the first finger as long as the second, small digital pads, and lack discs on the innermost fingers and toes. Males have markedly larger tympana (nearly as large as or larger than the eye) than do females. These seven species occur in southern México and Guatemala and along the Pacific versant to Nicaragua (Stuart, 1963). *Eleutherodactylus bransfordi* of Nicaragua, Costa Rica, and Panamá also appears to belong to this group.

The *alfredi* and *rhodopis* groups superficially resemble the Antillean *dimidiatus*, *ricordi*, and *symingtoni* groups but differ in lacking the frontoparietal-prootic fusion and in having longer median pterygoid rami. The southeastern Brazilian *parvus* group superficially resembles some *rhodopis* group members. The peculiar digital structure of *parvus* group frogs does not suggest a close

relationship. At least for the present, it appears that the two endemic Middle American groups are distinguishable from the 9 South American and 6 Antillean groups.

TABLE I.—Summary of Species-Group Arrangements for *Eleutherodactylus*

MÉXICO ¹	COSTA RICA ²	COLOMBIA ⁴	SOUTH AMERICA ⁵	WEST INDIES ⁶
<i>alfredi</i>				
[<i>mexicanus</i> <i>pygmaeus</i> <i>rhodopis</i>]	²			
	<i>laticeps</i>	<i>gollmeri</i>		
	<i>rugulosus</i>	<i>rugulosus</i>	} Group I	} <i>fitzingeri</i>
	<i>fitzingeri</i>			
	<i>gaigeae</i>			
	<i>bufoniformis</i>	} <i>biporcatus</i>		
	<i>biporcatus</i>			
	<i>cruentus</i>	} Group II	} <i>unistrigatus</i>	
	<i>melanostictus</i>			
	<i>diastema</i>	Group III		
		Group IV	<i>sulcatus</i>	
			<i>binotatus</i>	
			<i>discoidalis</i>	
			<i>lacteus</i>	
			<i>parvus</i>	
			<i>ramagii</i>	
			<i>auriculatus</i>	<i>auriculatus</i>
				<i>emiliae</i>
				<i>gossei</i>
				<i>inoptatus</i>
				<i>ricordi</i>
				<i>symingtoni</i>
				<i>varleyi</i>

¹ Modified after Smith and Taylor (1948). ² Combined herein; see text.

³ After Savage (1973). ⁴ After Cochran and Goin (1970). ⁵ Proposed herein.

⁶ Following Schwartz.

SUMMARY

The South American species of the genus *Eleutherodactylus* are partitioned into 10 species groups. Three groups are centered in southeastern Brasil (*binotatus*, *lacteus*, and *parvus* groups). The *ramagii* group is found in extreme eastern Brasil. The *discoidalis* group occurs on the interior Andean slopes in Ecuador, southern Perú and Bolivia, and northern Argentina. The *fitzingeri* group is the most widespread species group; frogs of this group are primarily lowland species and range throughout the forested Amazon basin, the Guianas, and the Chocó as well as into Central America as far as México. The *biporcatus* group occurs in lower Central America, western Colombia, and Ecuador. The *sulcatus* group occurs in the Coastal Range of Venezuela and the upper Amazon basin. The *unistrigatus* group occurs primarily in Colombia and Ecuador but species are also found along the northern and western edges of the Amazon basin and the Coastal Range of Venezuela. Also the group is moderately well represented in lower Central America; four species occur in Guatemala and México. The *auriculatus* group occurs over most of the West Indies and is represented in South America by *E. urichi* in Guyana and Venezuela.

One hundred and forty-one species are currently recognized based on 169 names proposed for South American *Eleutherodactylus*. The numbers of species in each of the 10 species groups are: *auriculatus* (1), *binotatus* (6), *biporcatus* (5), *discoidalis* (5), *fitzingeri* (21), *lacteus* (4), *parvus* (2), *ramagii* (2), *sulcatus* (2), and *unistrigatus* (92).

The approximately 340 recognized species of *Eleutherodactylus* are currently placed in 6 primarily Antillean groups, 9 groups in Central and South America, and 2 groups in Guatemala and México.

RESÚMEN

Las especies sudamericanas del género *Eleutherodactylus* están repartidas en 10 grupos de especies. Tres grupos se encuentran ubicados en el sudeste brasileño (*binotatus*, *lacteus*, y *parvus*). El grupo *ramagii* se encuentra en el extremo este del Brasil. El grupo *discoidalis* ocurre en el interior de las laderas andinas en Ecuador, sur del Perú y Bolivia, y norte de Argentina. El grupo *fitzingeri* es el de mas amplia distribución entre todos; los sapos de esta grupo son primariamente de tierras bajas y se extienden a lo largo de la cuenca amazónica, las Guayanas, y el Chocó (colombiano) así como también en Centroamérica hasta México. El grupo *biporcatus* se encuentra en las partes bajas de América Central, en el oeste de Colombia, y en Ecuador. Al grupo *sulcatus* se lo encuentra en la región costera de Venezuela y en el Alto Amazonas. El grupo *unistrigatus* ocurre primariamente en Colombia y Ecuador pero

también sus especies se encuentran a lo largo de los bordes norte y oeste de la Cuenca Amazónica y en zonas costeras de Venezuela; este grupo está también presente en los bajíos de la América Central. El grupo *auriculatus* se dispersa sobre la mayor parte de las Indias Occidentales y está representado en Sud-América por *E. urichi* en Venezuela y Guyana.

Para este grupo de anfibios actualmente se reconocen 141 especies basadas en 169 nombres propuestos para los *Eleutherodactylus* sudamericanos. El número de especies en cada uno de los diez grupos (incluyendo un grupo de las Indias Occidentales) son: *auriculatus* (1), *binotatus* (6), *biporcatus* (5), *discoidalis* (5), *fitzingeri* (21), *lacteus* (4), *parvus* (2), *ramagii* (2), *sulcatus* (2), and *unistrigatus* (92).

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