

FROGS OF THE *FITZINGERI*
GROUP OF *ELEUTHERODACTYLUS*
IN EASTERN PANAMA AND
CHOCOAN SOUTH AMERICA
(LEPTODACTYLIDAE)

JOHN D. LYNCH AND CHARLES W. MYERS

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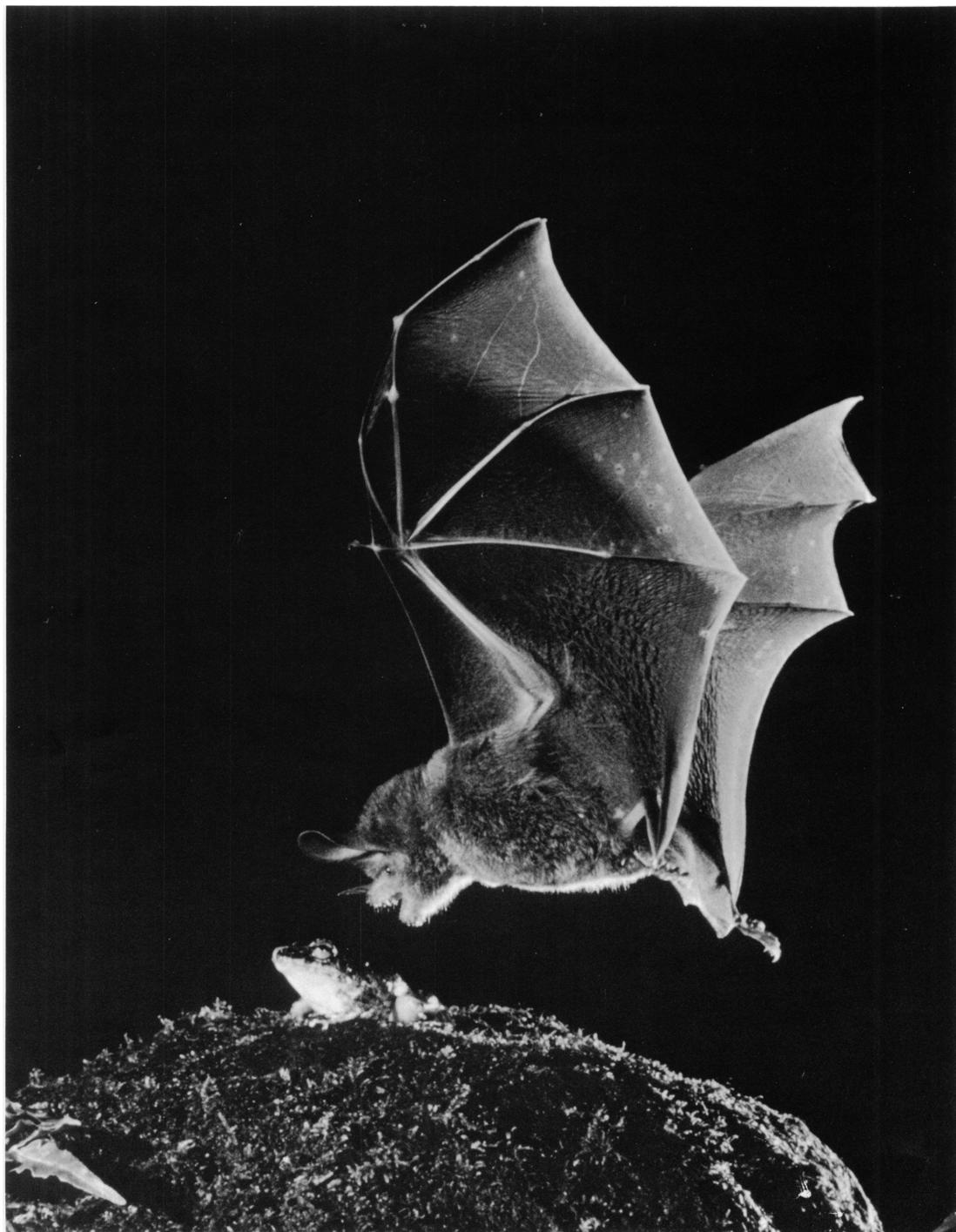
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FRONTISPIECE. A fringe-lipped bat (*Trachops cirrhosus*) about to capture an *Eleutherodactylus fitzingeri* on Barro Colorado Island, Panama. Although the frog pictured was a silent “bait” animal for photography, the bat *Trachops* is a natural predator of *E. fitzingeri* (see p. 535). Frogs of the *fitzingeri* group are abundant in many Neotropical forests and are a potentially significant food resource for a variety of predators. These frogs have vocalization characteristics that may somewhat reduce their vulnerability to sound-responsive predators such as *Trachops* (p. 566). Photograph courtesy of Merlin D. Tuttle, Milwaukee Public Museum.

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ABSTRACT

Based on field data and on examination of more than 3000 preserved specimens, species limits and distributions are defined for the frogs currently assigned to the *fitzingeri* group of *Eleutherodactylus* in the Chocoan lowlands (mainly below 1000 m. elev. in eastern Panama, western Colombia, and western Ecuador). Several of the species are abundant, ecologically important animals that have been repeatedly confused in the literature.

Nine species are treated in detail and described and illustrated from living as well as preserved material, with natural history notes added where possible. *Eleutherodactylus achatinus* (Boulenger) occurs from Panama south to southwestern Ecuador; the names *E. brederi* Dunn and *Hylodes pagmae* are assigned to its synonymy (although *brederi* might yet prove to be a valid sibling species with a different call). *Eleutherodactylus caprifer* Lynch is known from west-central Colombia and northwestern Ecuador. These two species lack appreciable toe webbing.

The following four species have moderate toe webbing: *Eleutherodactylus fitzingeri* (O. Schmidt) occurs from Nicaragua to west-central Colombia, being here treated primarily in the southern part of its range, where it has been confused with *Eleutherodactylus raniformis* (Boulenger)—a larger frog that occurs from eastern Panama south to west-central Colombia. *Eleutherodactylus longirostris* (Boulenger) occurs from the Darién highlands of extreme eastern Panama throughout western Colombia to southern Ecuador. All previous reports of *longirostris* in lower Central America

seem to have been based on specimens either of *fitzingeri* or especially of *Eleutherodactylus crassidigitus* Taylor, whose range is extended out of Costa Rica and throughout the Isthmus of Panama to the Colombian border. However, the variation of *crassidigitus* remains inadequately studied and the redefined species might be a composite. *E. crassidigitus* differs from *longirostris* in color pattern, smaller size, and in a greater extent of toe webbing, although all specimens do not show these differences to the same degree. A closer relative (sister species) of *longirostris* may be the Central American *E. talamancae* Dunn.

The remaining three species are streamside frogs having extensive toe webbing: *Eleutherodactylus anomalus* (Boulenger) is common in western Colombia and northwestern Ecuador. *Eleutherodactylus anatis*, new species, is known only from northwestern Ecuador, and *Eleutherodactylus zygodactylus*, new species, is described from west-central Colombia.

The *fitzingeri* group of *Eleutherodactylus* is especially diverse in the Chocoan lowlands. At most localities in South America, only two or three species are ever sympatric, but west of the Andes as many as seven species of the group co-occur in geographic sympatry, with species density being greatest in the region of the Río San Juan drainage of Colombia. Natural history data are fragmentary. The vocalizations and/or calling behavior of several species have characteristics that may reduce the frogs' vulnerability to sound-responsive predators.

INTRODUCTION

Much of the anuran diversity in the American tropics is vested in frogs of the leptodactylid genus *Eleutherodactylus*, an assemblage of perhaps 600 species, with major areas of differentiation in South America, the West Indies, and Middle America. In South America, the major diversity is clearly associated with the northern Andes. Frogs of the *fitzingeri* group of *Eleutherodactylus* are mostly lowland forest inhabitants, primarily below 1000 m. elevation. Species of the group are distributed from Mexico through Central America into the northern half of South America. At present, 61 species of the *fitzingeri* group *sensu* Lynch are recognized, with about half of the species occurring in South America (Lynch, 1976b, 1977, 1979a, 1980;

Hoogmoed, Lynch, and Lescure, 1977; Lynch and Hoogmoed, 1977; this paper). At most localities over the South American distribution (Lynch, 1976b, fig. 2B) of the *fitzingeri* group, one encounters only two or three sympatric members of the group, but species density is markedly higher in western Colombia and Ecuador.

Cochran and Goin (1970) included members of the group in their major treatise on Colombian frogs; it grieves us to point out that their work is markedly deficient and unreliable. Their detailed descriptions are fortunately based on single specimens, for their accounts of variation and lists of specimens examined are repeatedly confused by inclusion of more than one species under a single

name. Under valid names also treated in the present revision, Cochran and Goin listed specimens of four different species under *E. anomalus*, six species under *E. longirostris*, and seven species under *E. raniformis*; for these three names, only 24–78 percent of the specimens are correctly allocated.

A part of the confusion engendered by Cochran and Goin apparently resulted from their uncritical acceptance of old museum identifications made by others. In the case of *fitzingeri*-group frogs generally, part of the earlier systematic chaos stemmed from confusion surrounding three of the earliest named species, namely *E. conspicillatus* (Günther), *E. fitzingeri* (O. Schmidt), and *E. gollmeri* (W. Peters). Clarification of these problems was provided by Dunn and Emlen (1932) for *gollmeri*, Savage (1974) for *fitzingeri*, and Lynch (1975a) for *conspicillatus*. Savage's 1974 paper was particularly important in providing a modern descriptive account based on Emmett R. Dunn's concept of *E. fitzingeri*; Dunn had examined the holotype (now lost) of *fitzingeri* and had associated the name with many museum specimens, and thus had influenced our own working concept, although we have been aware for some time that he had confused at least one other species (*E. raniformis*) with *fitzingeri*. Savage wished to permanently stabilize his and Dunn's view of *fitzingeri* and to remove certain other old names from further consideration, but, although we sympathize with his objectives, we cannot acquiesce in his use of neotype designations that contravene the explicit requirements of the 1964 *International Code of Zoological Nomenclature* (see discussion herein under *E. fitzingeri*).

Frogs of the *fitzingeri* group of *Eleutherodactylus* are an important and obvious component of most lowland forest communities in Central America and northern South America. The taxonomy of the Central American species has been much improved with the studies by Savage (especially 1974, 1975), and here we attempt to resolve the long-standing confusion between some species in Panama and northwestern South America. We deal with those species of the *fitzingeri* group found below 1000 m. in western Ecuador and Colombia and in adjacent eastern Panama. Nine species are recognized, two of

which are described as new. In addition, we propose relegating two nominal taxa to synonymy.

We take this opportunity to make several points of critical assessment about our work: (1) The *fitzingeri* group is "defined" primarily by a suite of plesiomorphic characters and its monophyly is not assured. The present account is a partial revision primarily at the alpha taxonomic level, and phylogenetic analysis remains a task for the future. (2) We may have failed to discriminate a few sibling species (e.g., see comments under *E. achatinus* and *E. crassidigitus*). (3) In view of the foregoing criticism of the work of Cochran and Goin, it is only fair to admit that we have caught each other out in our own misidentifications. We furthermore predict that additional misidentifications remain in the appended list of several thousand specimens examined. We expect that most false determinations will prove to be of poorly preserved and/or juvenile specimens, but we hope that they are few.

ACKNOWLEDGMENTS

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Myers' recent fieldwork in Colombia, Ecuador, and Panama was supported mainly by the Lincoln Ellsworth Fund of the American Museum of Natural History, by a grant from the Camille and Henry Dreyfus Foundation, and by various contracts from the National Institutes of Health. Administrative support or other help was provided through the Museo Departamento de Historia Natural in Cali, the Gorgas Memorial Laboratory in Panama City, and the Smithsonian Tropical Research Institute in Panama. Earlier work in Panama was financed by National Institutes of Health Grant No. GM-12020 to the University of Kansas (W. E. Duellman and C. W. Myers), with laboratory facilities provided by the Gorgas Memorial Laboratory.

MATERIALS AND METHODS

We have examined more than 3000 specimens of these frogs from the area under consideration in Panama, Colombia, and Ecuador. Lynch has field experience with the five species found in western Ecuador; Myers has field experience with all eight species found in Colombia and Panama and with one of those (*E. achatinus*) in Ecuador. The extant holotypes or syntypes of all nominal species have been examined and a lectotype designated in one case (*E. raniformis*). The types of *Hylodes fitzingeri* and of several of its presumed synonyms (*Hyla grisea*, *Craugastor pulchrigulus*, *Leiyla güntherii*) are lost. Savage (1974) designated a common neotype for these four names, but, based on our understanding of the explicit wording and the intent of article 75 of the *International Code* (Internatl. Comm. Zool. Nomenclature, 1964), these designations are invalid and therefore not binding on other workers.

Measurements were made using dial calipers and recorded to the nearest tenth of a millimeter. Methods of making measurements follow Duellman (1970, p. 21), although it is well to specify that head length was measured from the posterior edge of the jaw to the level of the tip of the snout, approximating the sagittal plane of the head (rather than an oblique line from snout to jaw). The following standard abbreviations are used for convenience: SVL (snout-to-vent length¹), HW (head width), E-N (eye to naris distance), IOD (interorbital distance).

All measurements are of adult frogs unless stated otherwise. Maturity in males was judged by the presence of vocal slits, enlarged

testes, and nonspinous nuptial pads. Maturity in females was assumed if the oviducts were large and convoluted and/or if enlarged ova were evident.

Unlike most other South American species of the *fitzingeri* group, some of the Choacan species have appreciable toe webbing. Degree of webbing is recorded following the scheme proposed by Savage and Heyer (1967) for phyllomedusine hylids, with a minor modification by Myers and Duellman (1982, p. 6). Digits are represented by Roman numerals, with intervening Arabic numerals designating the number of digital segments that are free of webbing. A positive superscript indicates that the web reaches only to the proximal edge of a subarticular tubercle, whereas a negative sign shows that the web reaches the distal edge, thus encompassing the entire tubercle. See Myers and Duellman (*loc. cit.*) for a brief discussion of Savage and Heyer's useful notational device, which with slight modification can be used for all anurans.

The calls of several species had been recorded by W. E. Duellman and ourselves using various microphones and recorders (mainly Uher 4000, Report L and S models). The original tapes are on file at the University of Kansas Museum of Natural History, with copies deposited at the American Museum of Natural History. Sound spectrograms were produced on a model 6061-A Sona-Graph (Kay Electric Co.), at narrow or wide bandwidths of 45 or 300 Hertz, with the automatic gain control set at "0" (not "Off"). Calibration signals were recorded at the edge of each audiospectrogram (since these machines are subject to temporal variability), in order to allow for any necessary corrections to the pre-printed scales on which the spectrograms were to be mounted after trimming. Comparative time measurements were made from the spectrograms; pulse rates were calculated from the harmonic structure (Watkins, 1967).

¹ This is identical with "standard length," a more recent nondescriptive term that is not defined in many papers and therefore meaningless to those biologists not already well versed in the systematic literature.

TAXONOMIC CHARACTERS AND IDENTIFICATION

THE *FITZINGERI* SPECIES GROUP

DEFINITION: Lynch (1976b, p. 10) formally defined the *fitzingeri* group and listed South

American taxa then known. The group is presently defined on the basis of the following adult character states: skin of venter smooth (except *E. caprifer*); first finger longer than

second; tympanum prominent, annulus not concealed; vomerine odontophores prominent, triangular in shape; head narrow (HW/SVL 0.32–0.43 in most, 0.36–0.48 in relatively broad-headed species); unguis flap usually not indented (exceptions mainly in Central America); expanded digital discs (rarely absent on fingers); no cranial crests; nasal bones large, in median contact; frontoparietals not united synosteotically with proötics; median ramus of pterygoid abutting proötic, partially overlapping parasphenoid ala.

CONTENT: Lynch (1976b) provided only partial listing of the species of the group outside of South America, and his list of South American taxa is now out of date. We provide below a current list of the species we assign to the group; our use of these names does not constitute an opinion that all the species are valid. We include 61 nominal species in the group:

- Eleutherodactylus achatinus* (Boulenger)
E. actites Lynch
E. anatypes Lynch and Myers
E. andi Savage
E. angelicus Savage
E. anomalus (Boulenger)
E. anzuetoii Stuart
E. azueroensis Savage
E. berkenbuschii (W. Peters)
E. bransfordii (Cope)
E. brocchi (Boulenger)
E. caprifer Lynch
E. carmelitae Ruthven
E. chiastonotus Lynch and Hoogmoed
E. condor Lynch and Duellman
E. conspicillatus (Günther)
E. crassidigitus Taylor
E. cuaquero Savage
E. escoces Savage
E. fenestratus (Steindachner)
E. fitzingeri (O. Schmidt)
E. fleischmanni (Boettger)
E. gaigeae (Dunn)
E. gollmeri (W. Peters)
E. gutturalis Hoogmoed, Lynch, and Lescure
E. heterodactylus (Miranda-Ribeiro)
E. insignitus Ruthven
E. jota Lynch
E. lanthanites Lynch
E. laticeps (Duméril)
E. lineatus (Brocchi)
E. longirostris (Boulenger)
E. lymani Barbour and Noble
E. macdougalli Taylor
E. malkini Lynch
E. matudai Taylor
E. merendonensis Schmidt
E. milesi Schmidt
E. mimus Taylor
E. monnichorum Dunn
E. noblei Barbour and Dunn
E. peruvianus (Melin)
E. podiciferus (Cope)
E. punctariolus (O. Schmidt)
E. raniformis (Boulenger)
E. rayo Savage and DeWeese
E. rostralis (Werner)
E. rugulosus (Cope)
E. savagei Pyburn and Lynch
E. stantoni Schmidt
E. talamancae Dunn
E. taurus Taylor
E. terraebolivaris Rivero
E. thectopternus Lynch
E. vilarsi (Melin)
E. viridicans Lynch
E. vocalis Taylor
E. w-nigrum (Boettger)
E. werleri Lynch and Fritts
E. zeuctotylus Lynch and Hoogmoed
E. zygodactylus Lynch and Myers

We do not include *E. bilineatus* Bokermann in the group because it is imperfectly known (see Lynch, 1976b, p. 11). The frogs included in the *discoidalis* group by Lynch (*op. cit.*, p. 9) likewise are excluded from the *fitzingeri* group. Aside from having narrow digits (not expanded to form discs) and broad vomerine odontophores, these frogs are much like species of the *fitzingeri* group. Lynch (1976b) included *E. crenunguis* in the group but later (1979b) placed it in the *unistrigatus* group.

PROBLEMS: Although we can define and list the contents of the *fitzingeri* group, we are not at all convinced that the group is monophyletic. On the basis of out-group comparisons (utilizing noneleutherodactyline leptodactylids), the attributes listed above to define the group are plesiomorphic. Ontogenetic information provides a slight contradiction to that view because in the course of development the first finger grows from being shorter than the second to being greater in length, in at least *E. fleischmanni*, *E. lymani*, and *E. rugulosus*.

Savage (1980a [and in earlier editions of the included "Handlist"]) placed the various

Costa Rican species listed above in his *fitzingeri*, *gaipei*, *gollmeri*, and *rugulosus* groups. The first three of Savage's groupings so far are defined solely by the included species. The *rugulosus* group, however, was defined and revised in one of the best treatments available for an assemblage of *Eleutherodactylus* (Savage, 1975). Savage and DeWeese (1979) later described a species (*E. rayo*) sharing features of Savage's *rugulosus* and *fitzingeri* groups and stated (p. 113) that "there can be little doubt that the two groups . . . are closely allied," providing new data on musculature and karyotypes in support of the relationship. Savage and DeWeese stated (p. 107) that their new species "belongs to the *fitzingeri* group *sensu* Lynch," but they criticized Lynch's (1976b) preliminary species groupings as being (p. 112) "based on 'key' characteristics of external and skeletal morphology that are of dubious evolutionary cogency." Savage (1980a) placed *E. rayo* Savage and DeWeese without further comment in the *fitzingeri* group *sensu* Savage, and later (1980b, p. 18) dismissed Lynch's grouping as being based on "trivial external features."

Judging from Savage and DeWeese (*op. cit.*, p. 112), examples of nontrivial characters apparently would include those of jaw musculature (but perhaps not osteology), serum proteins, and karyology—from which "It is clear . . . that a series of at least six major evolutionary lineages are subsumed under the genus *Eleutherodactylus*." Reference is made to three unpublished Ph.D. dissertations completed in 1968, 1973, and 1976; dissertation citation unfortunately tends to be a rather one-sided affair (Myers, 1982, p. 31), although perhaps this should not be so. In any case we do agree that various approaches are bound to elucidate the evolution and systematics of *Eleutherodactylus*, and we eagerly await the extension of such techniques to appreciable geographic areas and sections of the genus, as well as publication of completed studies. However, *Eleutherodactylus* is a very large genus and meaningful taxonomic divisions must of course be based on *comparative* data. Since we wish to see some progress within our own working life time, we cannot agree with Savage and DeWeese (1979, p. 112) that "the time is premature for an attempt to establish higher-level divisions based

solely on traditional taxonomic (key) characters" nor are we willing to dismiss *any* character out of hand, without some analysis as to why it should be considered "trivial" or noninformative in a given context.

After the above paragraphs were written we read a second paper by Savage and DeWeese (1981) repeating much of their previous discussion but with additional information from the earlier cited dissertations. They point (p. 941) to the dilemma of a "frog that in external and skeletal morphology clearly belongs with one major section of the genus . . . but in extremely important features of jaw musculature and karyology belongs elsewhere . . . !" We agree with them (p. 940) that there may be a "complex mosaic of superficial morphological characteristics that have been combined over and over again in distantly related species of *Eleutherodactylus*," and would only suggest that the other "extremely important" characters mentioned may be subject in some degree to the same problem. Savage and DeWeese (1979, 1981) appear to believe that Savage and Lynch separately established species groupings in some fundamentally different way, but it seems to us that both have been using essentially a phenetic approach that differs only in, respectively, lesser or greater geographic coverage, and in differential sampling of the suite of available characters. Considering the alpha nature of much of the work to date, the phenetic approach is not to be faulted on grounds of convenience, whether the objective is a faunal study of Costa Rica or a mutual groping toward definition and preliminary grouping of species. But we suggest that substantial progress toward unraveling evolutionary lineages does not so much depend on waiting for more data (*vide* Savage and DeWeese) as in recognizing the perils of plesiomorphy and in establishing a schema of synapomorphies that results in testable groupings. This admittedly will not be easy considering the size and geographic range of *Eleutherodactylus* and the difficulty in obtaining critical material, for which reason morphological characters accessible in preserved material will remain important. Although the developing science of assessing immunological distance has its own problems (Farris, 1981), we hope that this technique also will be useful as an

independent test at least of major lineages, notwithstanding that some tropical-forest species are likely to be extinct before they can be sampled for that purpose.

Following is a discussion of the principal morphological, color pattern, and bioacoustical characters that are useful in differentiating the species covered in this paper. Some of the characters also point to relationships at least between pairs of species, although extralimital taxa will have to be considered before possible synapomorphies can be properly evaluated.

MORPHOLOGY

TOE WEBBING: Chocoan frogs of the *fitzingeri* group readily fall into four groupings on the basis of toe webbing.

Webbing absent or basal. Toes bearing narrow lateral fringes or keels that may coalesce at the bases of the toes to form a basal web. When present, the web does not encompass the basal subarticular tubercle on toes I–IV but usually encompasses the basal tubercle on toes IV–V (fig. 1B). (Some non-Chocoan members of the group lack the lateral fringes as well as webbing [fig. 1A].)

Moderate webbing. Toes bearing more pronounced lateral fringes and increased webbing. The web encompasses most or all the basal subarticular tubercle of all toes (fig. 1C) and in specimens of some species reaches or encompasses the second subarticular tubercle of toes III–V (fig. 18B). Outer edges of toes I and V with or without narrow lateral fringes.

Extensive webbing. Web encompasses all subarticular tubercles except the distal-most one on toe IV, often extending to disc on toe V. Lateral fringes on unwebbed portions of digits, including outer edges of toes I and V (fig. 1D).

Very extensive webbing. Web reaching or virtually reaching discs on toes I–III and V, with only the penultimate phalange of toe IV being free of web. Heavy lateral fringes on unwebbed portion of toe IV and on outer edges of toes I and V (fig. 1E).

The only Chocoan species lacking webbing is *Eleutherodactylus caprifer*, and the only

one with basal webbing is *E. achatinus* (including *brederi* and *pagmae*). Most species of the *fitzingeri* group from other parts of South America also have minimal or no webbing, as do some Central American species.

The included species having moderate webbing are *Eleutherodactylus crassidigitus*, *E. fitzingeri*, *E. longirostris*, and *E. raniformis*, although these species can be discriminated to some degree by the extent of such webbing (e.g., fig. 18). Possible ontogenetic changes have not been properly documented, although there seems to be an intraspecific size-correlated increase in the relative amount of web. The only other South American species having moderate webbing is the Amazonian *E. malkini*, although a number of Middle American species show this condition (Savage, 1975).

The only Chocoan species having extensive webbing is the streamside *Eleutherodactylus anomalus*. Savage (1975) described nearly as great webbing in some Middle American species.

The fourth category—very extensive webbing—includes only the two new streamside species described herein, *E. anatipes* and *E. zygodactylus*. Comparable webbing in *Eleutherodactylus* seems to occur only in the Puerto Rican *E. karlschmidti* Grant.

FINGER DISCS: The Chocoan species fall into two groups on the basis of development of the disc apparatus, including the subdigital pad.² *Eleutherodactylus anomalus* has the terminal phalanges of the fingers unexpanded, with poorly developed subdigital pads. The other species have noticeably expanded

² In this paper we use the terms *disc* and subdigital *pad* in the same way as the few other authors who have had occasion to study or comment on the specialized region of adhesive epithelium on the ventral surface of the expanded portion of the digit. Most herpetologists concerned with frog systematics have not involved themselves with the components of the disc apparatus, and have used either disc (or disk) or pad for the expanded terminal segment in its entirety. For much of the past decade, the senior author has made the distinction in print but in precisely the opposite way as used herein (i.e., disc *sensu* Lynch = subdigital pad, and pad *sensu* Lynch = disc). It remains to be seen which usage will become standard and workers will have to be aware of the potential for confusion.

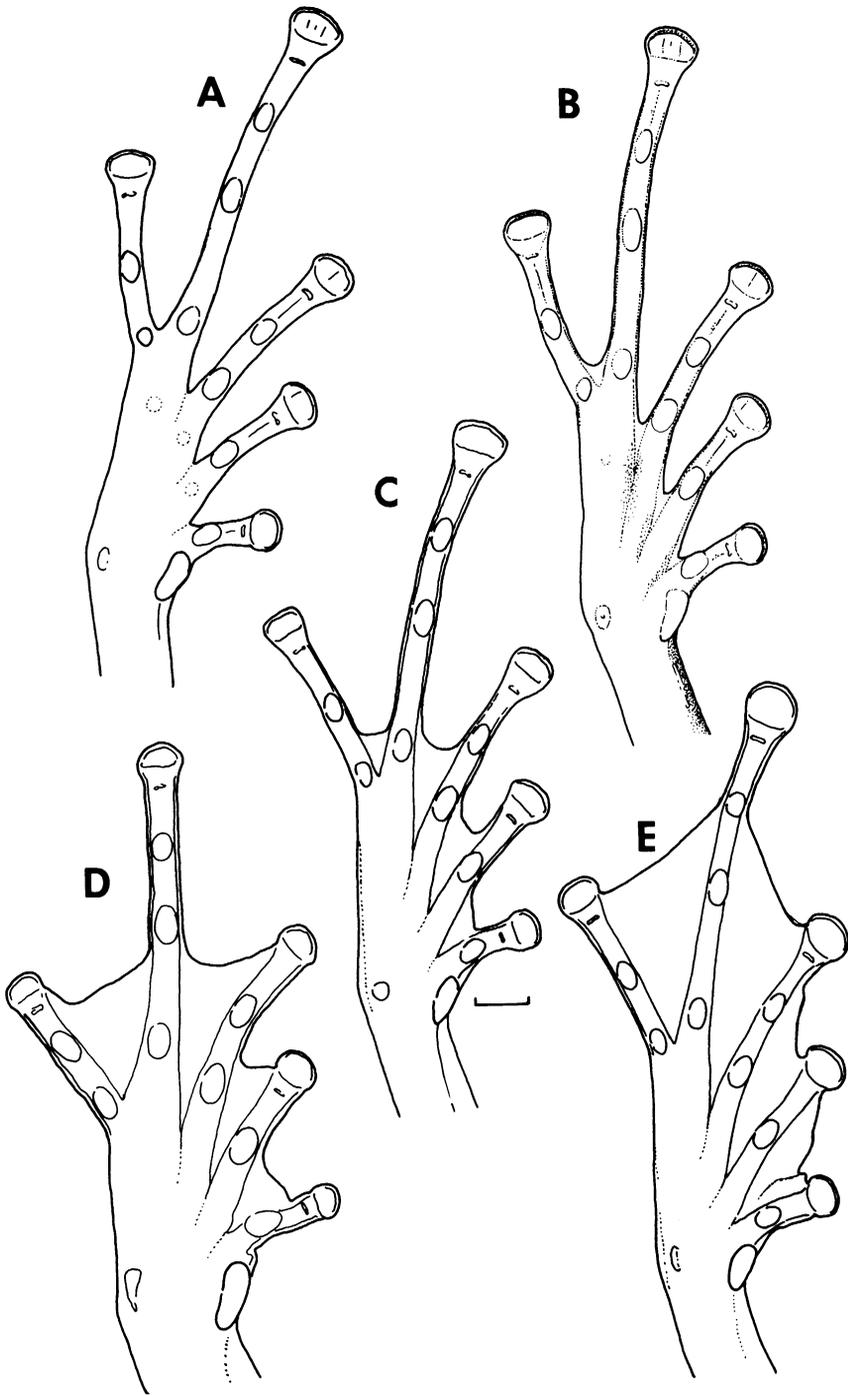


FIG. 1. Variation in toe webbing among frogs of the *fitzingeri* group of *Eleutherodactylus*; line equals 2 mm. A. No webbing or fringe (*E. lanthanites*, KU 104548). B. Basal webbing and narrow fringe (*E. achatinus*, UIMNH 55720). C. Moderate webbing (*E. fitzingeri*, LACM 73062). D. Extensive webbing (*E. anomalus*, CAS-SU 10467). E. Very extensive webbing (*E. anatipes*, new species, USNM 233093). Note that toes I through IV are shown from right to left (right foot, plantar view). Relative toe length in species treated herein is IV > V <> III > II > I.

discs (and better defined pads) on fingers III and IV, with those on the first two fingers being much narrower, only slightly wider than the penultimate segments (fig. 2).

NUPTIAL PADS: No adult males are available of the new species from Ecuador (*E. anatipes*), but they probably have white non-spinous excrescences on the thumb, as do all other species of the group in the Chococoan lowlands except *Eleutherodactylus caprifer*. Nuptial pads are present in males of most species of the group, although some Middle American taxa lack them (Savage, 1975).

CONDITION OF THE TARSUS: The inner edge of the tarsus bears a low tubercle or is relatively smooth in *E. achatinus*, *E. anatipes*, and *E. caprifer*. But in *E. anomalus*, *E. crassidigitus*, *E. fitzingeri*, *E. longirostris*, *E. raniformis*, and *E. zygodactylus* there is a pungent fold or ridge extending along approximately the distal two-thirds of the tarsus.

VOCAL SLITS AND SACS: Among the treated species, only *Eleutherodactylus anomalus* is known to lack vocal slits and hence a vocal pouch. It is often assumed that such species are voiceless, which, however, is not necessarily true, since anuran vocalization is not dependent on the presence of a vocal sac (as evidenced for example by the well-developed call of male *Dendrobates reticulatus* and the piercing distress scream given even by juvenile *Leptodactylus pentadactylus*). The presence or absence of a vocal sac was not determined for *E. anatipes* because adult males were unavailable.

Calling males of *E. achatinus* and *E. caprifer* have relatively conspicuously distensible vocal sacs that tend to remain evident in preserved specimens, whereas *E. crassidigitus*, *E. fitzingeri*, *E. longirostris*, *E. raniformis*, and *E. zygodactylus* have shallower vocal sacs that usually are externally inconspicuous in preserved specimens. Frogs showing these extremes are often described as having either "external" or "internal" vocal sacs, but these terms are a bit misleading.

EAR SIZE: In *Eleutherodactylus anomalus* the tympanum is relatively obscure dorsally and its length no more than about a third that of the eye. *E. anatipes*, *E. caprifer*, and *E. zygodactylus* have prominent but also rela-

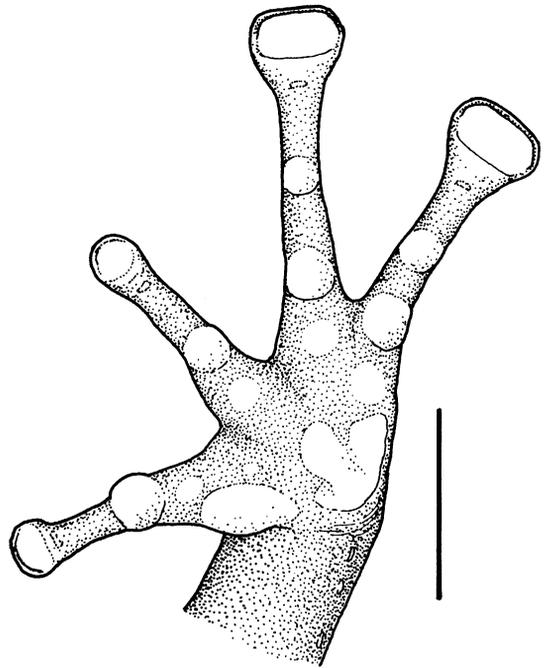


FIG. 2. Left hand of *Eleutherodactylus achatinus* in palmar view (KU 119468); line equals 5 mm. Note expanded discs and subdigital pads on fingers III and IV (this condition characterizes all species in the present account except *E. anomalus*).

tively small tympana, about one-fourth to one-third of eye length. The tympanum is prominent and its length at least one-half that of the eye in *E. achatinus*, *E. crassidigitus*, *E. fitzingeri*, *E. longirostris*, and *E. raniformis*. The tympanum may be noticeably larger in males of the last four species, particularly in *fitzingeri* (see individual accounts), which is suggestive that their calls may have a strong territorial component.

SNOUT SHAPE: As seen from above, the snouts of the Chococoan frogs are either subacuminate or rounded (fig. 3B–D). The color pattern on the subacuminate snouts may accentuate the pointedness, but none of these frogs approaches the acuminate condition such as in *E. chiastonotus* (fig. 3A). All species having subacuminate snouts also have sharp canthi rostrali (*E. achatinus*, *E. caprifer*, *E. crassidigitus*, *E. fitzingeri*, *E. longirostris*, *E. raniformis*, and *E. zygodactylus*). Frogs with

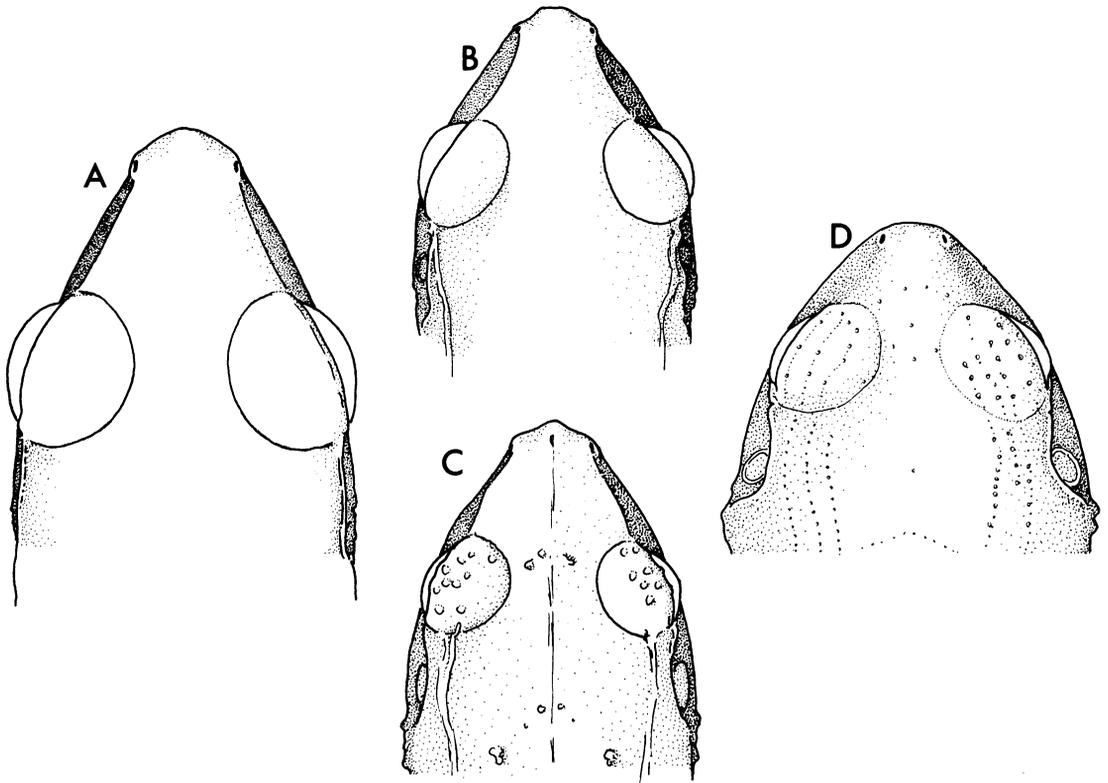


FIG. 3. Snout shapes among frogs of the *fitzingeri* group of *Eleutherodactylus*. A. Acuminate (*E. chiastonotus*, WCAB 2311). B. Subacuminate, with concave canthus rostralis (*E. conspicillatus*, KU 110785). C. Subacuminate, with convex canthus rostralis (*E. lanthanites*, KU 123892). D. Rounded, with indistinct canthus rostralis (*E. anomalus*, LACM 73254).

rounded snouts have round or obtuse canthi rostrali (*E. anatises*, *E. anomalus*).

SKIN TEXTURE: The belly is smooth in all species except *Eleutherodactylus caprifer*, which seems unique in the *fitzingeri* group in having a coarsely areolate venter (Lynch, 1977). The skin of the dorsum is coarsely tuberculate with numerous short ridges and folds in *E. anomalus* (fig. 14); this texture extends onto the upper eyelid which bears pungent tubercles. The only other frog whose skin could be described as tuberculate is *E. fitzingeri*, but the tuberculation is much less pronounced and is somewhat variable in life (compare the two frogs in fig. 5B); the tuberculation also frequently tends to be obliterated in preservative; the tuberculation extends onto the upper eyelid in *fitzingeri*, which bears pungent warts. The few available sub-adult males of *E. anatises* have small spi-

nules on the dorsal skin and a pair of sinuous postocular ridges. Females of *anatises* and both sexes of the remaining species have smooth or shagreened dorsal skin, which may bear pungent warts and low ridges.

SIZE AND PROPORTIONS: Although there is geographic variation in body size of some species (table 1), *E. achatinus*, *E. caprifer*, *E. crassidigitus*, *E. fitzingeri*, and *E. longirostris* are all moderate-sized frogs of nearly comparable size. *Eleutherodactylus raniformis* is a significantly larger frog over most of its distribution, with interspecific size discrimination being most apparent in females. As is the general rule in *Eleutherodactylus*, the females are larger than the males in all species; sexual size dimorphism is sometimes very striking (fig. 4) and collectors often mistake adult males for juveniles. The three stream-side species (*E. anatises*, *E. anomalus*, and

TABLE 1
Sizes (Snout-to-vent Lengths in Millimeters) of Adult Frogs of the *fitzingeri* Group in Lower Central America and Northwestern South America
(Range above, mean \pm 1 S.E., and sample size below)

Sample	Males	Females
<i>E. achatinus</i> (eastern Panama)	28.8–36.2 32.0 \pm 0.6 (14)	40.0–41.2 (2)
<i>E. achatinus</i> (Río San Juan, W Colombia)	26.7–33.2 29.7 \pm 0.4 (24)	33.0–45.2 38.1 \pm 0.9 (15)
<i>E. achatinus</i> (NW Ecuador)	23.9–31.6 29.0 \pm 0.4 (26)	33.6–45.0 39.4 \pm 0.6 (22)
<i>E. achatinus</i> (Pacific slopes of Ecuador)	24.4–34.2 28.8 \pm 0.3 (42)	37.0–46.1 42.1 \pm 0.4 (33)
<i>E. achatinus</i> (W Ecuador)	23.0–35.1 28.2 \pm 0.6 (18)	40.3–45.4 42.3 (5)
<i>E. anatis</i> (Ecuador)	[>33]	[>73]
<i>E. anomalus</i> (Ecuador-Colombia)	31.5–61.0 47.0 \pm 1.4 (46)	76.5–92.4 85.4 \pm 1.5 (10)
<i>E. caprifer</i> (Ecuador)	21.0–30.4 25.8 \pm 1.1 (9)	40.5–43.8 42.7 (3)
<i>E. crassidigitus</i> (Bocas del Toro, W Panama)	25.2–28.0 26.1 (6)	41.7 —
<i>E. crassidigitus</i> (Chiriquí, W Panama)	20.2–27.0 24.2 \pm 0.4 (21)	38.9–44.7 41.2 \pm 0.6 (12)
<i>E. crassidigitus</i> (Los Santos, W Panama)	23.5–28.1 25.7 \pm 0.3 (16)	36.6–40.0 38.5 \pm 0.4 (10)
<i>E. crassidigitus</i> (central Panama)	23.8–30.2 26.8 \pm 0.6 (11)	34.3–44.1 38.0 \pm 1.0 (10)
<i>E. fitzingeri</i> (Nicaragua and Costa Rica)	24.9–29.1 27.1 \pm 0.6 (8)	36.5–43.5 40.1 (5)
<i>E. fitzingeri</i> (western Panama)	25.5–30.5 27.7 \pm 0.4 (14)	38.1–52.5 43.3 \pm 0.5 (35)
<i>E. fitzingeri</i> (eastern Panama)	25.9–34.9 29.4 \pm 0.8 (9)	42.9–52.2 47.3 (5)
<i>E. fitzingeri</i> (Colombia)	26.3–35.0 29.7 \pm 0.4 (26)	38.2–44.0 41.3 \pm 0.4 (18)
<i>E. longirostris</i> (eastern Panama)	31.2 —	40.9–47.1 44.1 (3)
<i>E. longirostris</i> (northern Chocó, Colombia)	27.3–37.2 33.6 \pm 0.3 (56)	44.5–53.2 48.3 \pm 0.4 (30)
<i>E. longirostris</i> (central Chocó, Colombia)	28.7–39.2 35.0 \pm 0.2 (68)	46.5–58.5 51.6 \pm 0.4 (28)
<i>E. longirostris</i> (Ecuador)	28.8–34.4 31.9 \pm 0.5 (14)	43.1–59.6 48.2 \pm 1.1 (15)
<i>E. raniformis</i> (Pearl Islands, Bay of Panama)	— —	45.3–53.0 49.5 \pm 1.0 (7)
<i>E. raniformis</i> (eastern Panama)	31.5–43.1 36.2 \pm 0.4 (64)	52.0–70.0 59.5 \pm 1.2 (41)
<i>E. raniformis</i> (northern Chocó, Colombia)	27.2–40.0 35.1 \pm 1.0 (17)	53.9–61.9 57.9 \pm 1.0 (8)
<i>E. raniformis</i> (central Chocó, Colombia)	31.7–40.6 36.4 \pm 0.4 (30)	54.2–74.0 62.4 \pm 0.9 (30)
<i>E. raniformis</i> (Ríos Cauca and Magdalena, Colombia)	35.5–43.2 39.7 \pm 0.6 (10)	55.8–61.1 58.4 \pm 0.6 (8)
<i>E. zygodactylus</i> (Colombia)	39.6–54.1 48.4 \pm 1.3 (12)	76.5–83.8 79.7 (6)

TABLE 2
 Proportions of Frogs of the *fitzingeri* Group in Pooled Samples from Eastern Panama, Western Colombia and Ecuador
 (Range above, mean in boldface type, and sample size below)

Sample		Tibia/SVL	HW/SVL	Eyelid/IOD	Tymp./Eye	E-N/Eye
<i>E. achatinus</i>	♂	50.6–67.5 60.4 (74)	33.5–41.8 37.3 (74)	78.2–114.2 94.0 (68)	40.8–63.2 53.2 (74)	86.4–117.5 103.1 (74)
<i>E. achatinus</i>	♀	52.6–67.3 60.7 (46)	35.6–42.2 38.8 (46)	78.2–116.7 91.5 (41)	40.0–59.6 53.0 (46)	93.0–127.4 103.6 (46)
<i>E. achatinus</i> juv.	♀	58.1–69.9 63.6 (36)	35.4–43.2 38.4 (36)	75.0–100.0 90.0 (28)	44.9–59.1 53.1 (36)	100.0–123.5 106.5 (36)
<i>E. anatypes</i> 2 juv.	♂	56.6–57.7	39.9–40.5	158.3–182.4	21.4–27.1	66.6–66.7
<i>E. anatypes</i> 2 juv.	♀	63.4–65.1	39.0–40.8	160.0–163.3	26.9–27.7	93.6–95.2
<i>E. anomalus</i>	♂	49.5–61.2 54.4 (12)	42.6–47.6 44.9 (18)	118.9–183.8 159.6 (5)	37.1–43.9 41.0 (12)	81.5–94.9 87.9 (12)
<i>E. anomalus</i>	♀	50.0–57.8 53.6 (9)	41.8–48.3 45.4 (10)	161.8–173.3 166.5 (4)	34.1–43.9 39.0 (9)	75.7–85.7 82.3 (9)
<i>E. caprifer</i>	♂	51.3–57.7 54.4 (7)	33.1–35.9 34.4 (7)	96.3–113.3 101.6 (6)	23.5–30.0 26.8 (6)	77.4–85.3 80.3 (6)
<i>E. caprifer</i>	♀	48.5–57.1 52.9 (5)	33.4–36.3 34.9 (5)	100.0–110.3 105.8 (5)	23.1–35.1 28.3 (5)	82.5–90.7 87.2 (5)
<i>E. crassidigitus</i> ^a	♂	59.9–70.0 64.9 (12)	35.5–41.0 38.1 (10)	87.5–114.3 105.4 (12)	51.6–66.7 59.9 (12)	77.4–100.0 88.4 (12)
<i>E. crassidigitus</i> ^a	♀	64.1–73.2 66.7 (17)	35.6–39.9 38.2 (17)	85.7–112.5 98.2 (16)	45.3–60.5 53.4 (17)	87.0–121.4 105.6 (17)
<i>E. fitzingeri</i>	♂	61.3–64.0 62.8 (5)	35.2–37.5 36.0 (4)	116.7–129.2 123.6 (4)	64.9–77.9 71.0 (5)	76.7–98.8 90.4 (5)
<i>E. fitzingeri</i>	♀	59.3–64.6 61.2 (6)	34.0–37.0 35.2 (6)	100.0–131.2 118.9 (6)	42.3–59.2 50.1 (6)	94.2–106.5 101.3 (6)
<i>E. longirostris</i>	♂	59.5–70.6 63.7 (28)	32.7–38.5 36.4 (28)	97.1–131.0 116.2 (28)	53.1–75.0 62.8 (28)	81.2–108.7 98.2 (28)
<i>E. longirostris</i>	♀	59.6–66.4 62.8 (16)	35.4–41.2 37.4 (16)	92.2–148.6 113.0 (15)	43.0–57.6 49.4 (16)	86.1–115.2 100.2 (16)
<i>E. raniformis</i>	♂	56.7–68.7 62.0 (28)	34.7–39.0 36.8 (27)	111.5–152.2 131.5 (20)	52.2–77.4 64.0 (27)	76.4–104.3 92.6 (27)
<i>E. raniformis</i>	♀	59.0–65.5 62.4 (20)	35.6–38.8 37.2 (20)	112.0–137.8 121.2 (9)	45.2–62.7 52.0 (19)	91.9–117.9 103.8 (19)
<i>E. zygodactylus</i>	♂	55.5–62.0 59.2 (12)	37.1–39.0 38.2 (12)	137.1–196.7 171.7 (12)	30.7–51.5 42.8 (12)	75.6–100.0 88.6 (12)
<i>E. zygodactylus</i>	♀	54.8–59.5 57.7 (6)	38.8–39.7 39.2 (6)	140.0–160.0 148.2 (6)	31.1–40.9 34.8 (6)	86.4–100.0 95.7 (6)
<i>E. zygodactylus</i> juv.	♀	59.8–62.6 61.8 (7)	37.8–40.3 39.0 (7)	121.8–169.2 142.6 (6)	30.6–40.0 34.8 (7)	94.8–106.8 101.9 (7)

^a Western and central Panamanian specimens.

E. zygodactylus) seem nearly equal in size and are considerably larger than the other six species.

Most variations in proportions seem minor (table 2) with a few exceptions. *Eleutherodactylus anomalus* has a distinctly wider

head than does any other member of the *fitzingeri* group and approaches the condition termed broad-headed for species in other groups (Lynch, 1975b). *Eleutherodactylus anomalus* and the other two streamside species (*E. anatypes*, *E. zygodactylus*) have

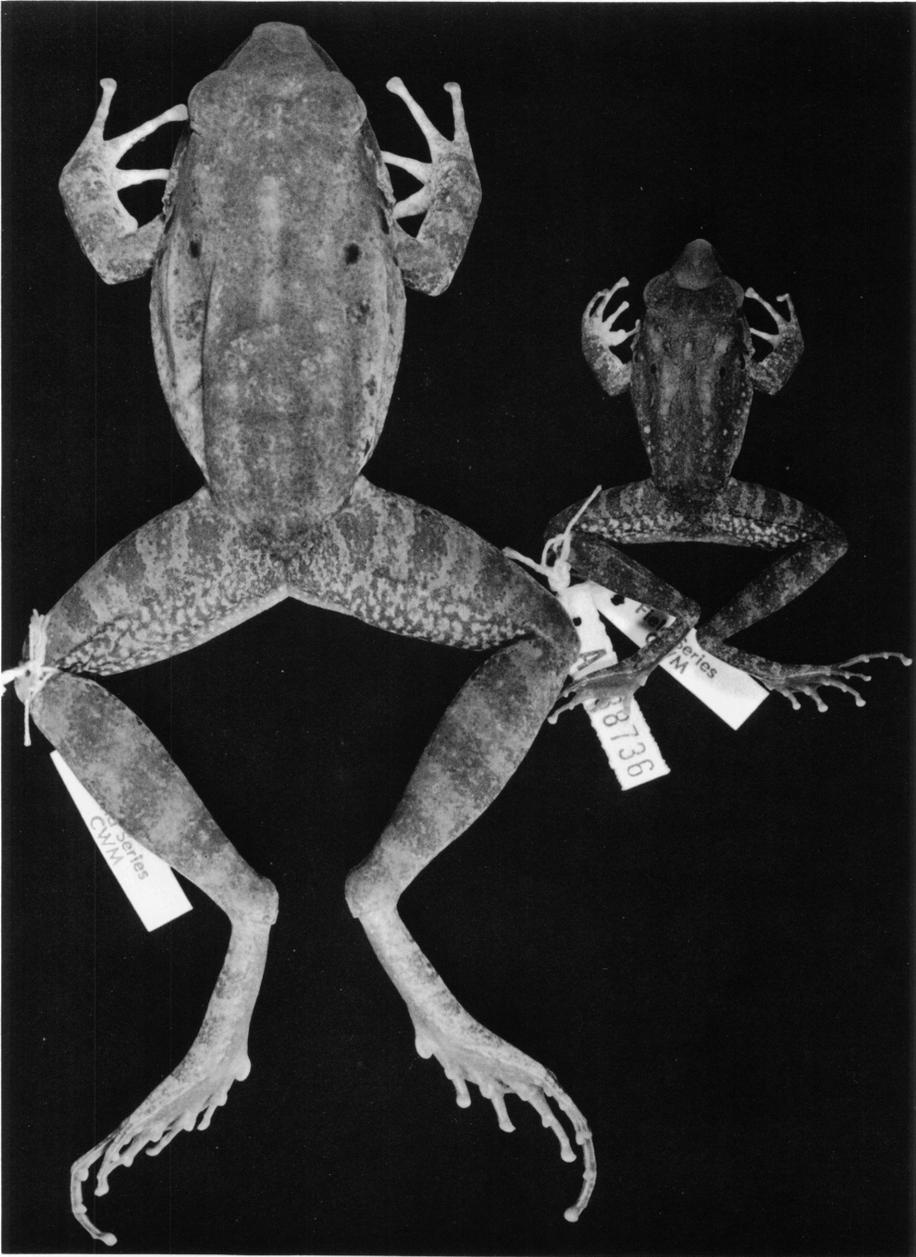


FIG. 4. Sexual dimorphism in size, as illustrated by a pair of *Eleutherodactylus raniformis* from the same population (Altos de Majé, Panamá Prov., Panama). *Left*: Adult female, 70 mm. SVL (AMNH 88720). *Right*: Adult male, 37 mm. SVL (AMNH 88736). Approximately natural size.

narrower interorbital spaces (eyelid/IOD ratios large) compared with the other Chocoan species; these high ratios are, however, approached by *E. fitzingeri* and *E. raniformis*. *Eleutherodactylus anomalus* and *E. caprifera*

have relatively shorter legs than do the other seven species, and they and *E. anatis* and *E. zygodactylus* have relatively short snouts. Interspecific and sexual differences in tympanum size have already been mentioned.

COLOR AND COLOR PATTERN

DORSAL SURFACES: The dorsal ground color is fundamentally brown in all species, but with a variational range from yellowish and greenish brown through medium brown and orange- or red-brown to grayish or blackish brown. Much of this variation may occur within single species or even single populations. Some variation is attributable to metachromatism, as noted for the ground color of individual *E. achatinus* (changeable from bright orange to dark brown) and for the mid-dorsal stripe of one *E. raniformis* (from reddish orange at night to light tan by day). Nonetheless, individual frogs of markedly different color may be found together and may maintain their different hues over a period of confinement, indicating that not all intrapopulation variation can be associated with simple changes in temperature or light.

Dorsal patterns are mostly vague but usually include an interorbital bar or triangle, and dark limb bands, and sometimes a few conspicuous black spots (especially in scapular region) enclosing warts. A dark face mask and/or labial bars are present or absent. *Eleutherodactylus crassidigitus*, *E. fitzingeri*, *E. longirostris*, and *E. raniformis* often have at least a trace of a dark hourglass, or scapular butterfly-shaped or W-shaped marking, although some individuals or populations of these species are virtually patternless. At least some populations of these four species also contain morphs having a vivid tan, yellow, or reddish middorsal stripe (figs. 5, 19, 22, 25, 28), with such polymorphism being most common in *crassidigitus* and *fitzingeri*, relatively uncommon in *raniformis*, and rare in *longirostris*. Some populations of *E. crassidigitus* contain at least four pattern morphs, including "normal," striped, light unicolor middorsum, and one with a poorly defined dorsal light area that is somewhat intermediate between the striped and light-backed conditions (fig. 19).

Eleutherodactylus achatinus and *E. caprifer* have dorsolateral dark lines and a dorsal pattern of dark chevrons (figs. 12, 16), which in some *achatinus* are beautifully set in light halos. Many specimens of *E. longirostris* have a few dark chevrons on the rear of the body—posterior to the dark hourglass marking, an

unusual combination of dorsal patterns that is also shared with some individuals of the Central American *E. talamancae* (fig. 26).

The three streamside species with extensive foot webbing (*E. anatises*, *E. anomalus*, *E. zygodactylus*) lack any indication of the aforementioned hourglass markings or dark chevrons, having at most a body pattern of poorly defined dark blotches and short lines. The Middle American streamside species of the *fitzingeri* group (the *rugulosus* group of Savage) are somewhat similarly patterned, although some individuals of these species have a median light line or even a broad middorsal light stripe (Savage, 1975, p. 260), a variation that we have not recorded in the Chococoan streamside species.

VENTRAL COLOR AND THROAT PATTERN: The overall ventral color varies from white to yellow in living specimens, often with a posterior suffusion of green or occasionally (in a few species) of orange. Often the throat and chest are white, with the belly and undersides of the hind limbs being yellow or greenish. In some species, perhaps all, the appearance of the brighter ventral hues seems to be related to size and/or sex. In life, the male vocal sac is differently colored from the throat of females in *E. achatinus* and *E. caprifer*, which are the only species having moderately distensible sacs.

The underside of the head tends to be basically white or yellow like the chest, as mentioned, but usually there is a weak to strong suffusion of melanophores that may be either uniformly distributed or arranged in definite patterns (fig. 6). In species or populations having uniformly distributed melanophores (e.g., fig. 6C, D), the throat in life varies from a pale color to relatively dark gray or brown depending on intensity of the pigmentation, which may also extend posteriorly onto the chest.

Eleutherodactylus fitzingeri is characterized by an unpigmented median white gular stripe, the distinctness of which depends on the number and distribution of melanophores on either side (fig. 6A, B); if melanophores are few the stripe may be inconspicuous, but at least a hint of it is always present. The pale gular stripe is present in various other species of the *fitzingeri* group, but, among the species treated here, it ap-

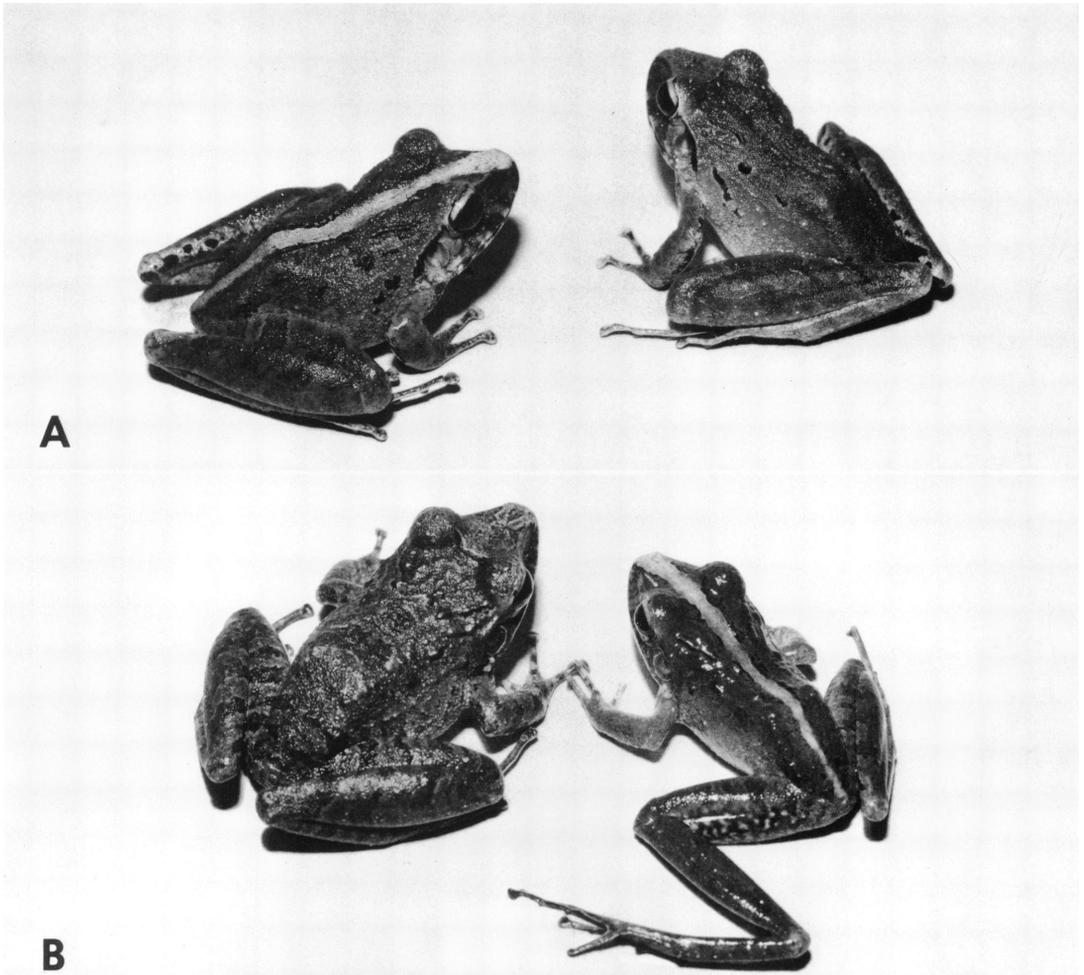


FIG. 5. Similar color-pattern polymorphism in two species. A. *Eleutherodactylus crassidigitus* (KU 114647–114648, Camp Summit, 300–400 m., San Blas, Panama). B. *Eleutherodactylus fitzingeri* (KU 114570–114571, 4 km. SE Puerto Pilón, 190–240 m., Colón, Panama).

pears as a sharply defined stripe normally only in some individuals of some populations of *Eleutherodactylus crassidigitus*, in which throat pattern is polymorphic (fig. 19). A pale gular streak is present in many *E. zygodactylus*. Only very rarely can a faint indication of a gular stripe be perceived in *E. raniformis* or *E. longirostris*, which usually can be separated from *E. fitzingeri* (but not *E. crassidigitus*) by the absence of this marking. In *E. longirostris* the melanophores are usually faintly to heavily clumped, forming a spotted pattern that often includes a close-spaced pair of spots or short lines slightly anterior to a

more widely spaced pair of markings high on the chest (figs. 6E, 24A–C), although some specimens or populations of *longirostris* are characterized by nearly uniform pigmentation on the throat (fig. 24D). A median gular stripe may well be primitive in the *fitzingeri* group, being present and well defined in virtually all specimens of some species, completely lost in other species, and appearing vaguely or distinctly in the variational repertory of the remaining species. *Eleutherodactylus caprifer* usually has a pair of longitudinal brown stripes on the throat; judging from their position, these stripes probably

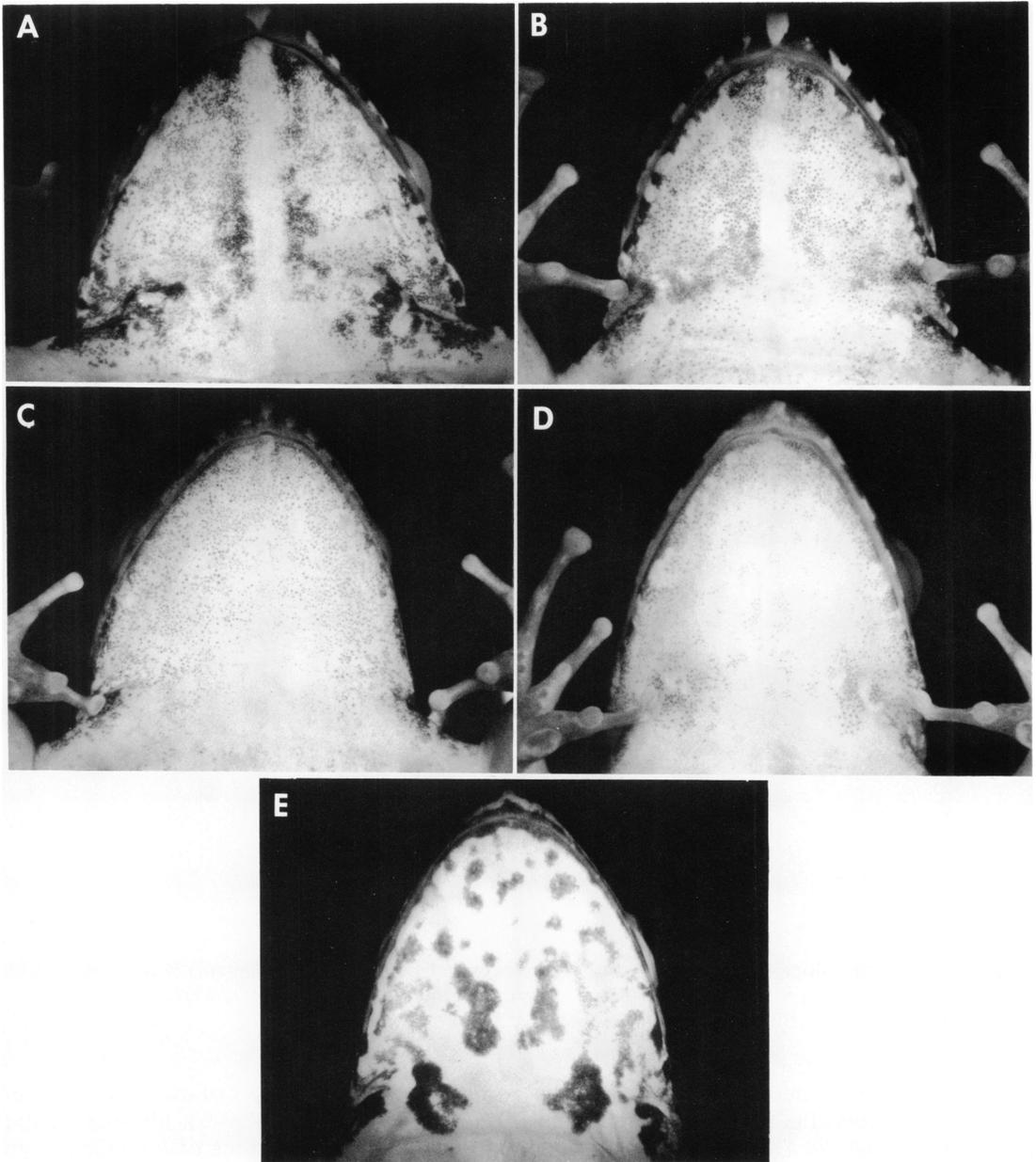


FIG. 6. Pigmentation on throats of three sympatric, frequently confused species of *Eleutherodactylus* (not to scale). A, B. *E. fitzingeri* (AMNH 88706, 88708, Altos de Majé, 100 m., Panama). C, D. *E. raniformis* (AMNH 88728, 88737, from same locality as A, B). E. *E. longirostris* (AMNH 86364, Quebrada Guanguí, 100 m., Cauca, Colombia).

Another frequently confused species is *E. crassidigitus*, which may resemble either A and B or C and D above (see fig. 19). See figure 24 for variation in *E. longirostris* (E above).

represent the dark edges of a median pale gular stripe in the primitive pattern.

REAR OF THIGH, AND GROIN: The pattern

or lack of one on the posterior face of the thigh (fig. 7) is diagnostically important in *Eleutherodactylus*, being often one of the least

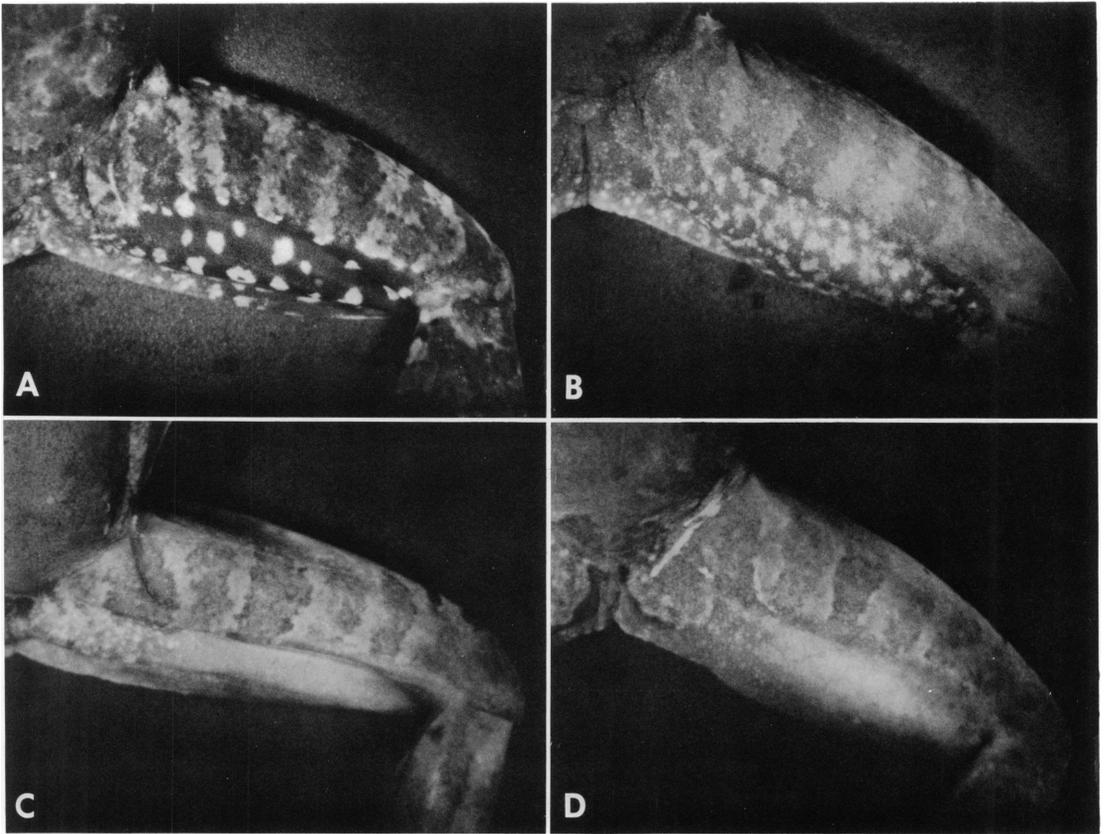


FIG. 7. Pigmentation on posterior surface of thigh in four sympatric, frequently confused species of *Eleutherodactylus* (not to scale). A. *E. fitzingeri* (AMNH 88706). B. *E. raniformis* (AMNH 88725). C. *E. crassidigitus* (AMNH 88703). D. *E. longirostris* (AMNH 88959).

Specimens of the three species in A–C all from Altos de Majé, about 100 m. (now an island in man-made Bayano Lake), Panamá Prov., Panamá. Specimen D from Quebrada Guanguí, 100 m., Cauca, Colombia.

variable aspects of the color pattern. Some of the Chocoan species have essentially uniform brown or gray thighs (in life sometimes with an orange, red, or yellow cast); species described as having uniformly colored thighs may in fact have minute pale flecks (usually unpigmented areas), especially proximally, but these are inconspicuous and do not suggest a definite pattern (fig. 7C, D). The Chocoan species having uniform thigh coloration are *E. anatipes*, *E. caprifer*, *E. crassidigitus*, and *E. longirostris*. Some individuals or populations of *E. achatinus* also have virtually uncolored thighs, but in others there is a broad distribution of pale flecks or spots; some geographic correlation is evident in this variation.

The remaining four species have pale markings (usually tan or yellowish) on the rear of the thigh. These markings are fairly dense but small and inconspicuous in *E. zygodactylus*. The pale markings tend to be small also in *E. raniformis*, but in this species the crowded markings are frequently clumped, imparting a somewhat mottled pattern (figs. 4, 7B, 29). The thigh markings are larger and better defined spots in *E. anomalus* and adult *E. fitzingeri* (fig. 7A). The thigh markings are an important diagnostic aid in separating specimens of sympatric *E. fitzingeri* and *E. raniformis* (compare fig. 7A with B) so long as it is realized that small *fitzingeri* may have relatively small and/or inconspicuous thigh markings (see fn. 12 and fig. 22 bottom). Col-

or of the markings in life also is useful, since *raniformis* has tan flecks or mottling, whereas in *sympatric* populations of *fitzingeri* the larger spots are normally greenish yellow.

The groin is described as mottled or not mottled in the species accounts, and this feature may be of some use in identifying specimens. Groin mottling is fairly conspicuous in *E. anomalus*, in which the dark brown or black mottling is sharply set against a background of pale yellow or pink. When present, the mottling tends to be vague and less conspicuous in other species.

EYE: The bright coloring of the iris is a conspicuous feature of these frogs in life, but, as indicated in the descriptions, individual and ontogenetic variation within species tends to be greater than most differences between species. The pupil is usually set in a brown or reddish brown horizontal stripe or between the wings of a brown or reddish butterfly-shaped marking; the upper part of the iris most often is a bright bronze or golden color, with fine black venation; the lower part of the iris may be similarly colored but often differs in having a pronounced gray aspect. The upper edge of the dark stripe or butterfly mark is sharply defined, but the lower edge often is less well demarcated. In larger specimens of some species (e.g., *E. raniformis* but not *E. fitzingeri*) there is an ontogenetic darkening of the lower half of the eye, which consequently becomes sharply bicolored, usually pale golden or bronze on the upper third and dark brown on the lower two-thirds. *Eleutherodactylus anomalus* has the most distinctively patterned iris among the Chocoan species, with a conspicuous butterfly mark that is always sharply defined above and below and with some vague dark lines radiating ventrad from the pupil and sometimes with a vertical dark line above the pupil (fig. 14). This pattern is similar to that of some other large streamside *Eleutherodactylus*, including *E. bufoniformis* and some other members of the *fitzingeri* group, and so the question arises as to possible adaptive significance (see fn. 6).

VOCALIZATIONS

Sympatric species of frogs usually have distinctive vocalizations that obviously have great ecological and behavioral significance

at the community and species levels. But the application of bioacoustical data in phylogenetic studies has so far been rather unconvincing. There is some belief (more often spoken than published) that such data *should* be useful in systematic studies at the generic level and above, but only occasionally have bioacoustical data been explicitly used in assessing relationships (vs. differences) even within subgeneric groups of closely related species. Vocalizations seem remarkably diverse among species in some medium-sized and large genera of anurans, whereas there may be remarkable similarity among the calls of ecologically similar but geographically separated species in different families. Comparative functional morphology of the vocal apparatus may prove taxonomically more revealing than the sounds alone. Nonetheless, frog vocalizations are of unquestioned systematic importance at least for the purposes of characterizing species, for discriminating sibling species, and sometimes for corroborating hypothesized relationships between allopatric (rarely sympatric) species. The minimal data presented here primarily serve the purpose of characterization but may have broader application in the future.

Many *Eleutherodactylus* are sporadic callers that are recorded only fortuitously or with considerable expenditure of time and patience. Our field observations on the Chocoan species of the *fitzingeri* group have been incidental to other studies, and we have notes on the calls of only five of the nine species, of which recordings were obtained for four. Some observations on calling activity are given in the species accounts (under Ecological Notes) and in the Discussion; the following paragraphs are confined to descriptive analyses of the known calls.

Eleutherodactylus achatinus

Recordings made in northwestern Ecuador and eastern Panama reveal interesting differences between populations assigned to this species. The Ecuadorian and Panamanian samples are described separately and then compared.

ECUADOR: Lynch recorded two specimens (KU 177609, 177611) at an elevation of 1410 m. at Maldonado (near Colombian border), Carchi Province, in May 1977, at air tem-

peratures of 16° and 18°C. (KU tape nos. 1358–1359, copies on AMNH reel 225).

The call is a rather nasal-sounding *kree*, which may be given in short trains of from three to at least six notes (fig. 8A), but which also is often given as an isolated pair of close-spaced notes (fig. 8C, D) or as isolated single notes. Tape segments of 1.0 and 2.5 min. contained *kree* notes given at respective rates of 0.4 notes/sec. (mostly in short trains; at 18°C.) and 0.2 notes/sec. (mostly double and single notes; 16°C.). Isolated *chirp* notes (fig. 8B, E) are interspersed between some of the *kree* notes, but there is no obvious pattern on these recordings. Chirp notes are given at the same fundamental and dominant frequencies as *krees* but are of much shorter duration (0.04–0.09 sec., \bar{x} = 0.06 sec., N = 6 notes).

The *kree* notes are 0.15–0.45 sec. in duration (\bar{x} = 0.32 sec., N = 36 notes); the interval is 0.07–0.35 sec. between calls of a group (\bar{x} = 0.17 sec., N = 23 intervals). Sound spectrograms (fig. 8) and sections (not shown) of 41 notes show a strongly emphasized fundamental at usually about 1500 or 1600 Hz (range about 1300–1800 Hz), and one to several strongly emphasized harmonics in the region of 2600–3600 Hz. The calls of one specimen consistently show a single dominant harmonic, most often at 3100 Hz in a range of 3000–3400 Hz (fig. 8E, F); the calls of the other individual (fig. 8A–D) consistently were less well tuned, with three to five emphasized harmonics that were shown by sectioning to be co-dominant in energy output. These individual differences are real³ but might have a very simple basis (e.g., a difference in vocal sac inflation). Pulse rate calculated from spectrograms of the calls having several harmonics is about 200–215/sec.

PANAMA: Expeditions by Myers and Duellman in 1965, and by Myers in 1967, resulted in recordings from two localities roughly 100 km. apart in Darién Province, extreme east-

³ Harmonic structure is sometimes over interpreted on sound spectrograms, at least for taxonomic purposes. Depending on original recording level and gain level of the sound spectrograph, harmonics supplemental to the dominant may appear present or absent in certain calls, and distortion may appear owing to the magnetic recording system. Caution must therefore be used in ascribing taxonomic significance to this character.

ern Panama. (1) Cerro Quia, 740 m., near Colombian border at 77°30'W longitude. Four specimens (KU 113767–113770); recorded in July at temperatures of 24° and 25°C. (KU tape nos. 750–753). (2) Northeast slope of Cerro Sapo, 560 m. on the ridge La Jarcia. A specimen (KU 115722) recorded in May at 23°C. (KU tape no. 754). Copies of these tapes are filed on AMNH reel 235.

There are no obvious call differences between the two populations sampled in Panama. *Eleutherodactylus achatinus* in Panama produce various noises that sound like *ribits*, *bleeps*, *chirps*, and *clicks*. The most characteristic call is the *ribit* (*ri·bit'*)—a sound of 0.13–0.18 sec. duration (\bar{x} = 0.15 sec., N = 20) that is irregularly repeated at intervals from 0.30 sec. to over 1.3 sec., at average rates of about 1.0–1.8 *ribits* per second (fig. 9A). The tape segments contain up to 44 calls in a 39-second period, so the calls are not confined to short trains but are given rather continuously albeit with irregular spacing as already stated. A *ribit* is comprised of two notes that are very closely spaced, with a separation of about 0.01–0.05 sec. (\bar{x} = 0.03 sec., N = 18). Spectrograms show several emphasized frequencies in the region of 2000–4000 Hz, but with sections showing one harmonic tending to be slightly dominant, usually at 2400 to 3300 Hz.

Bleep notes (fig. 9B) seem to represent a short *ribit*, the two parts of which are run together. The two *bleeps* in figure 9B occupy about 0.12 sec. of the spectrogram; insertion of the missing interspace (0.01–0.05 sec.) would make each *bleep* as long as a *ribit* call. These two kinds of calls are similarly pulsed at about 250/sec. Transformation of *ribits* into shorter *bleeps* conceivably might be temperature-related (since call length is sometimes negatively correlated with temperature), but, based on the present recordings, the infrequent *bleeps* can only be regarded as atypical *ribits* without evident significance.

Chirp notes (fig. 9C) are only about 0.04–0.20 sec. duration (\bar{x} = 0.11 sec., N = 9), with a dominant frequency at about 2400–2800 Hz. They are produced while the vocal sac is kept apparently fully inflated; *chirps* may be given independently or occasionally as a series of soft sounds following a normal call.

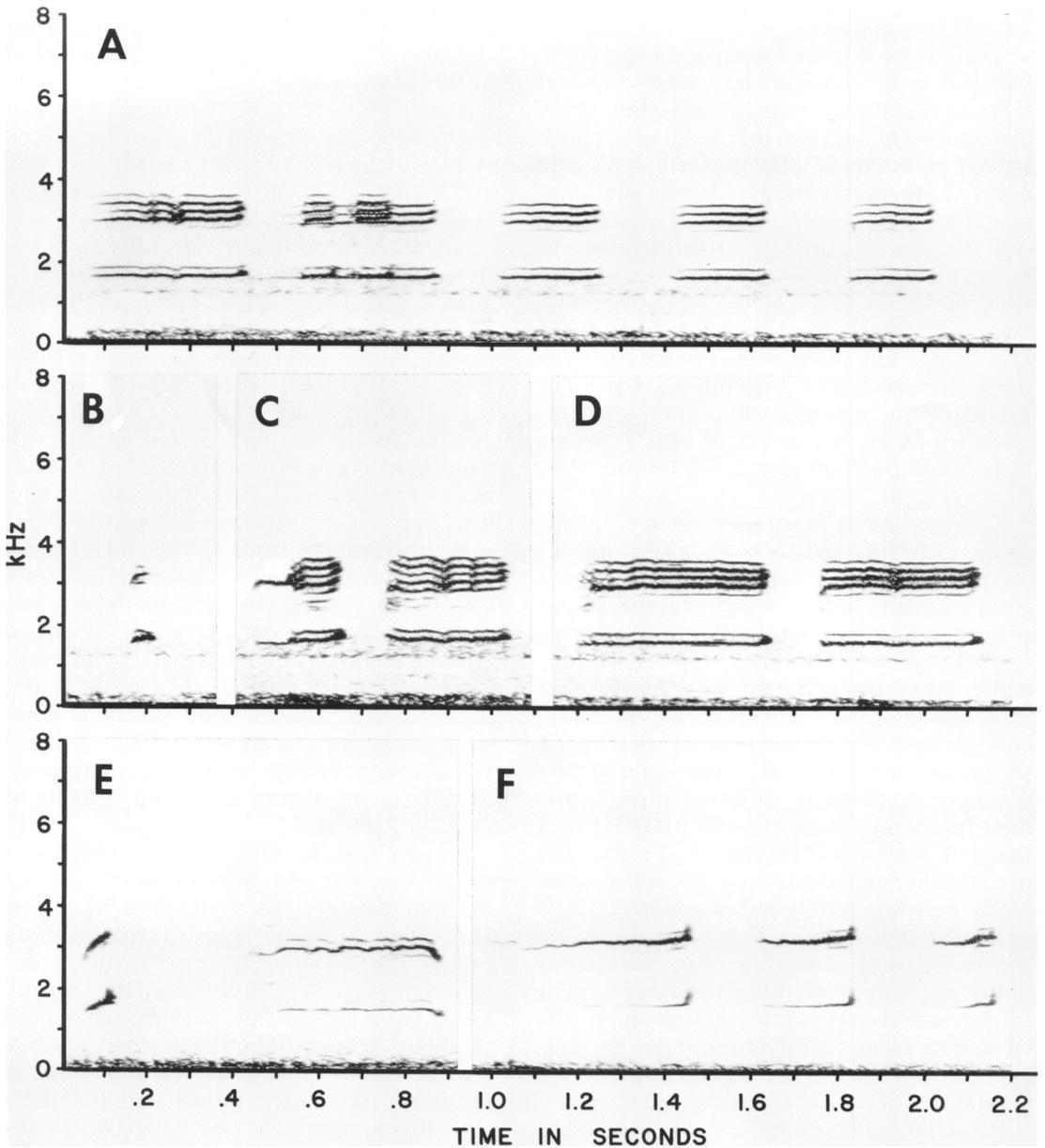


FIG. 8. Vocalization of *Eleutherodactylus achatinus* in Ecuador (narrow-band, 45-Hz filter; data in text). A-D. Variability in calls of single frog (KU 177609), as follows: A, train of 5 *kree* notes; B, isolated *chirp* note; C and D, double *kree* notes of different duration. E, F. Calls from a single frog (KU 177611) as follows: E, single *chirp* followed by *kree* note; F, train of 3 *kree* notes (the *kree* calls of this specimen consistently had fewer emphasized harmonics than produced by the frog in A-D).

Chirps evidently have a territorial function since they are the primary sounds made during agonistic behavior, although some unanalyzed (unrecorded) *clicking* noises also have been heard (see Aggressive Behavior in

species account). Chirps are the only vocalizations on KU tape 751, which sounds as if two frogs might have been recorded unknowingly.

COMPARISONS: Based on the above descrip-

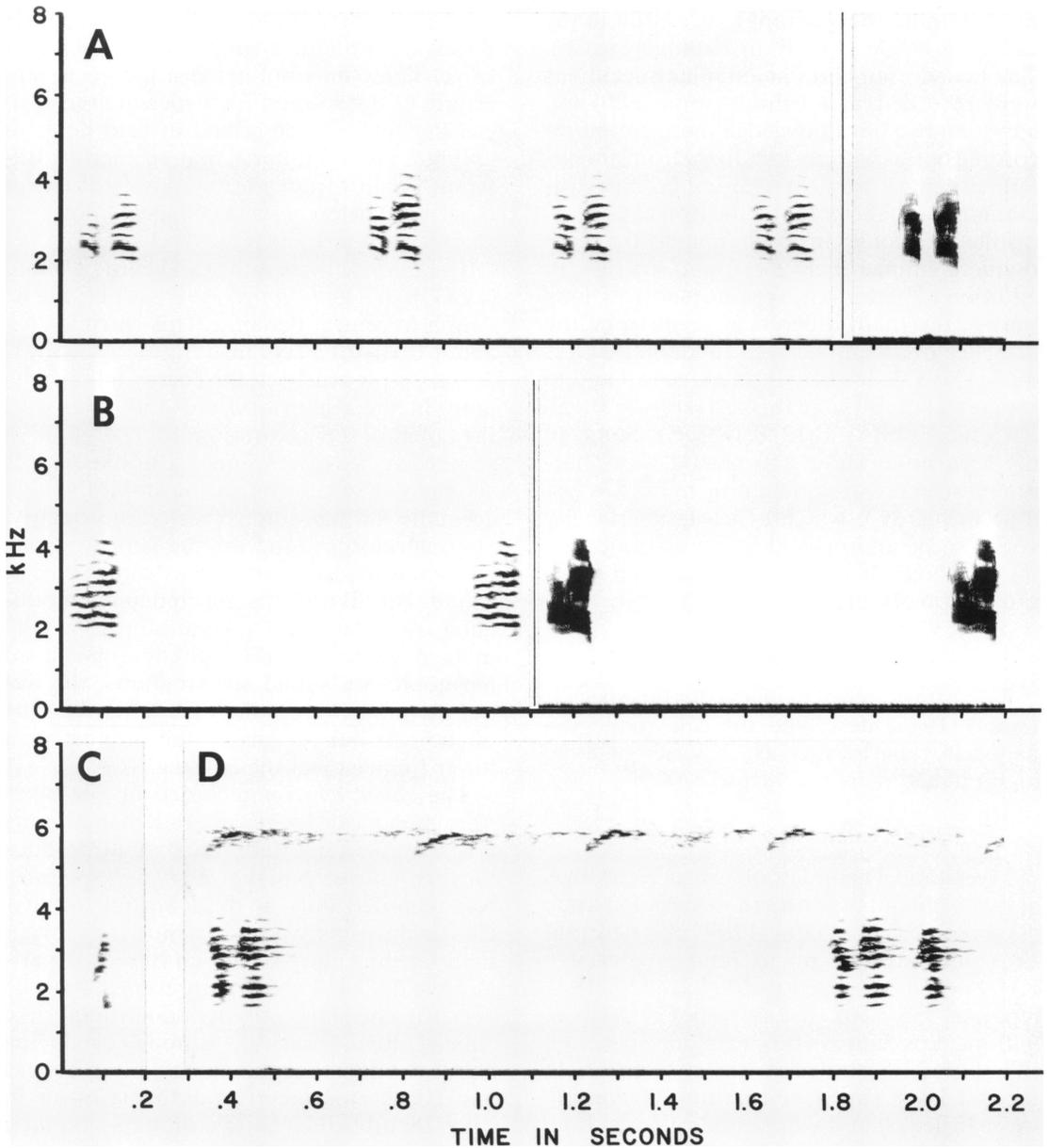


FIG. 9. Vocalization of *Eleutherodactylus achatinus* in Panama (narrow-band, 45-Hz filter unless stated otherwise; data in text). A. Four typical *ribit* notes from a longer train; last note also shown graphed with wide-band, 300-Hz filter. B. Two atypical *ribit* (*bleep*) notes, narrow-band on left, wide-band on right. C. Isolated *chirp* note. D. A *ribit* note followed by atypical tripartite note. (Calls in A and B produced by KU 113770; C and D by KU 115722.)

tions of *kree* (fig. 8) and *ribit* (fig. 9) calls, the intuitively obvious conclusion is that two species are involved, for which the name *E. achatinus* is available for Ecuadorian populations and *E. brederi* for the Panamanian

frogs. If true, this is a problem that will have to be resolved by future work, since we have failed to find other supporting differences and therefore cannot define geographic ranges (see Remarks in *E. achatinus* account).

However, we cannot dismiss out of hand the possibility of geographic variation in the call of a single, widely distributed species. The Ecuadorian and Panamanian specimens were recorded at localities some 700 km. apart, and to our knowledge there are no recordings of *achatinus*-like frogs from the intervening territory in Colombia. Spectrograms of both the kree and the ribit calls show distinct harmonics in approximately the same frequency range (between 2 and 4 kHz). In addition to patterns of spacing (short vs. long trains), the main differences seem to be the presence of an emphasized fundamental frequency at 1.3–1.8 kHz in the kree call and in the greater duration of this call (krees = 0.15–0.45 sec.; ribits = 0.13–0.18 sec.). Some of the kree notes show a tripartite wavy harmonic structure (e.g., first note in fig. 8A, last note in fig. 8C), which at least superficially seems to be approached by an aberrant “ribit” of three closely spaced notes and a duration of 0.30 sec.

Eleutherodactylus caprifer

Recordings are not available for this species. Lynch (1977) described the call at the Ecuadorian type locality as “a series of 8–10 high pitched piercing chirps.”

Eleutherodactylus crassidigitus

Myers and Duellman obtained recordings at two highland localities in western Panama. (1) Finca Santa Clara, 1200 m., Chiriquí Province; two specimens (one preserved = KU 114676) recorded in May at 20°C. (KU tape nos. 755–756). (2) East slope Cerro Hoya, 940 m., Los Santos Province; one specimen (KU 114622) recorded in May at 20.5°C. (KU tape no. 794). Tape speed at time of recording was a little fast at the first locality (as audibly indicated by the voice documentation), but the spectrograms do not appear distorted when compared with those from the Cerro Hoya locality and provide some useful information. Copies of these tapes are filed on AMNH reel 235.

Eleutherodactylus crassidigitus produces a short single or sometimes double note at sporadic intervals. Although these notes sound varied to the human ear, there seem to be

only two basic types in the populations sampled in western Panama, namely a single *birdlike chirp* and a single or double *chuck chirp*. These may not exhaust the vocal repertoire of the species, for a specimen in eastern Panama was described in field notes as giving a sporadic *aaah* that seemed of different quality from the two kinds of chirps described below (see Ecological Notes in species account).

The *birdlike chirp* is the call heard by Dunn (1933, p. 67, as *E. longirostris*) at El Valle de Antón in central Panama. This chirp is only about 0.10–0.12 sec. in duration (\bar{x} = 0.11, N = 8), with nearly all the energy falling variably in the region of 1400–4500 Hz, with the greatest concentration of energy in a somewhat narrower zone. Birdlike chirps show good separation of harmonics, which accounts for their almost melodious quality, although chirps even from the same frog may be somewhat differently pulsed and varied in sound. Birdlike chirps are frequency modulated, resolving into several almost basally merged but distally distinct chevron-shaped harmonics on sound spectrograms; the frequency momentarily increases after the start of the call but returns to the original or a lower frequency at the end (fig. 10A).

The *chuck chirp* is recorded on the tapes from both localities in western Panama, being given by the same individuals that produce birdlike chirps, but the *double chuck chirp* was recorded only at the Chiriquí locality. Chuck chirps may be either shorter or longer than birdlike chirps, with an observed variation of 0.02–0.13 sec. in duration (\bar{x} = 0.05, N = 10); the shortest notes sound more like “clicks” than “chucks.” Although occupying about the same frequency range the chucks and clicks are perceived as being lower in pitch than birdlike chirps, probably because they are less loud. Chuck chirps do not resolve into harmonic bands on sound spectrograms and are nonmelodious; spectrograms made with a wideband filter show that the pulse rate is slow at the beginning of the chuck and speeded up at the end, at least in the longer notes (fig. 10B). Three double chucks are comprised of two short notes having a 0.10–0.16 sec. separation, with the entire call group being about 0.2 sec. from start

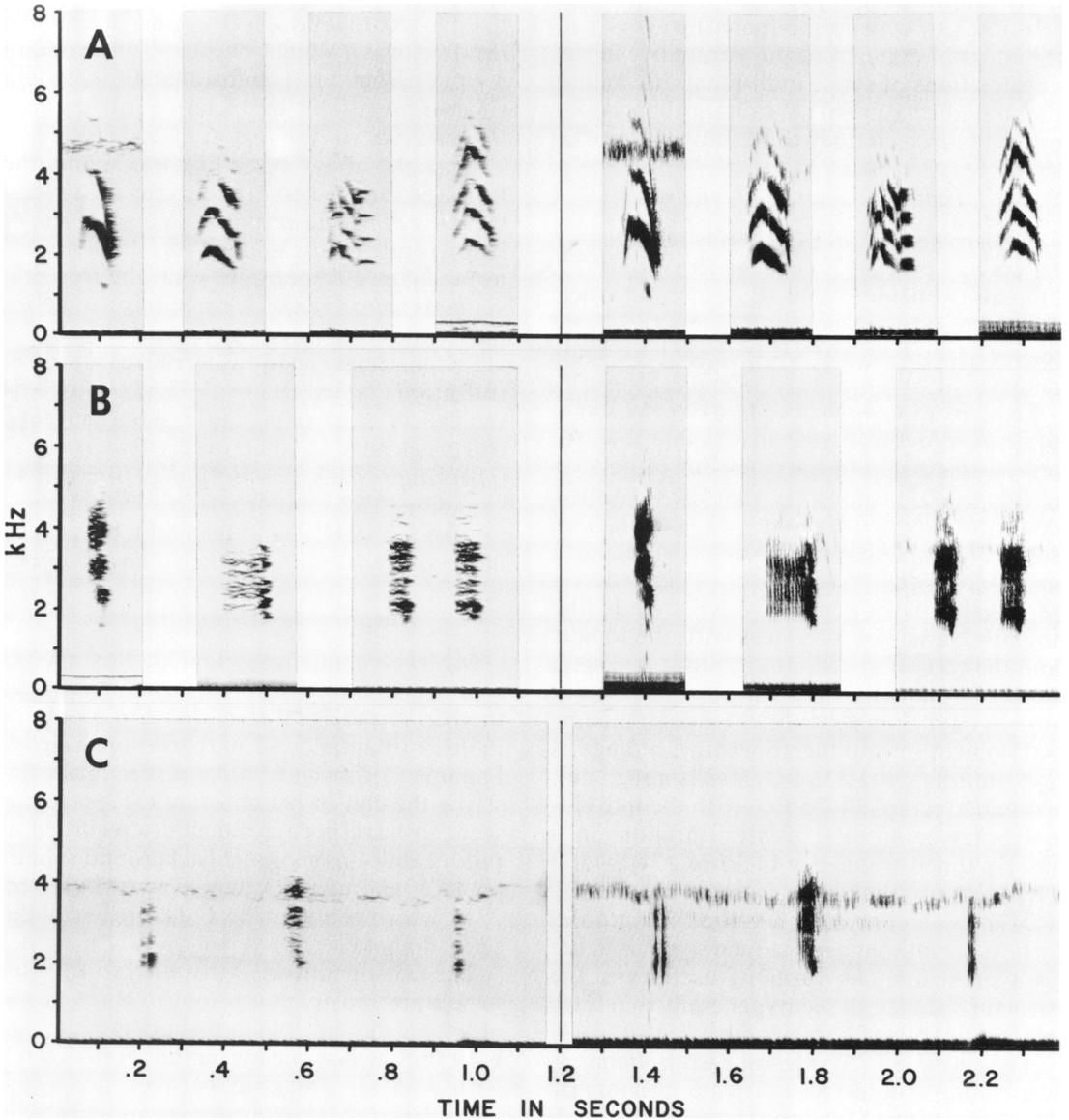


FIG. 10. Variability in calls of *Eleutherodactylus crassidigitus* from western Panama. Calls left of center graphed with narrow-band, 45-Hz filter; same notes repeated on right side, with wide-band, 300-Hz filter. Other data in text.

A. Four birdlike chirp notes (note 1 = KU 114622, notes 2 and 3 = unpreserved specimen [KU tape 755], note 4 = KU 114676). B. Two single chuck chirps and one double chuck chirp (note 1 = KU 114676; note 2 and double-note 3 = unpreserved specimen [KU tape 755]). C. Short train of three brief chuck chirps (unpreserved specimen [KU tape 755]).

to finish. Unlike birdlike chirps, single chuck chirps are sometimes given in a short train of several notes (fig. 10C).

We have no observational evidence to suggest that the variability in the call of *E. crassidigitus* is related to intraspecific interac-

tions, although we expect that there are vocal responses to conspecific male intruders and to potential mates. But the variability in the vocalizations of single individuals, as well as the sporadic nature of the calls, probably does make the frogs harder to find by predators.

Eleutherodactylus fitzingeri

A specimen (KU 114498) was recorded by Myers in April 1967, near the Río Jaqué, 1.5 km. above Río Imamadó, 50 m., Darién Province, extreme eastern Panama (KU tape no. 793 [copy on AMNH reel 235]; air temperature at calling site 23°C.).

Calls from a single *E. fitzingeri* are likely to be so sporadic or well spaced that they are tediously difficult to trace, leading Fouquette (1960, p. 207) to observe that the frustrated collector may perceive the call as a laughing sound. Fouquette also well described the call as "a rather quiet series of short, harsh notes, repeated rapidly, each of which sounds like the noise a person produces with the tongue and the roof of the mouth in order to coax a horse." Fouquette's (*op. cit.*, p. 204) tabulation of data from recordings made in the Canal Zone of central Panama shows a range of 2–12 notes (\bar{x} = 4.5 notes [*N* calls not given]; estimated temp. 24–25°C.), with the individual notes being of 0.02 sec. duration, in a poorly tuned frequency band of 1700–4400 Hz. His published spectrogram (*op. cit.*, fig. 1D) shows a complete (?) call of seven notes in 0.9 sec.; although reproduction of his figure as a small line cut limits its usefulness, the structure of the call seems generally to resemble the one described below.

The specimen recorded in eastern Panama was calling at intervals at least 5 min. apart. The one "normal" call recorded is of 2.6 sec. duration and may approach the maximum length, being in any case longer than suggested by Fouquette's data from central Panama (see above). This call (a portion shown in fig. 11A) consists of 18 short nonmusical notes of about 0.01–0.02 sec. duration, in the frequency range of 1500–4000 Hz. Intervals between notes are 0.17 sec. at the start and 0.12–0.13 sec. toward the end of the call, which speeds up slightly from start to finish. (On the recording, the call also increases greatly in loudness from start to finish, but

study of overlapping spectrograms indicates that the record level was being increased while the frog was calling. The best spectrogram segments [fig. 11A] unfortunately include a superimposed call of an unidentified *Eleutherodactylus* in the region of 3 kHz.)

After the above recording was made, the frog was induced to give a series of several creaking chirps in response to a playback of its own call. These sounds (fig. 11B) are interpreted as a response to what the frog presumably perceived as a conspecific male intruder in its territory.

Perhaps it was an intraspecific response vocalization that led Dunn (1933, p. 67) to liken the call of *E. fitzingeri* to a "short birdlike chirp" similar to that of *E. "longirostris"* (*crassidigitus*). A description of the call as sounding "like sand or grit in a casting reel" (Swanson, 1945, p. 211) might have been based on some animal other than *fitzingeri*.

Eleutherodactylus raniformis

Myers saw an individual of this species calling on a branch 2 m. up in a sapling, near the Río Jaqué, 1.5 km. above the mouth of the Río Imamadó, 50 m. elevation, Darién, Panama. Although he did not specifically describe the call in his notes, other specimens seem to have been accidentally recorded at this locality—as sporadic background sounds on KU tape no. 793 (copy on AMNH reel 235), which contains the *E. fitzingeri* call described above.

The calls tentatively attributed to *E. raniformis* are mostly comprised of three notes, of which the first two are short (about 0.03 sec.) and the last one longer (about 0.14 sec.), with 0.05 sec. intervals between notes (fig. 11C). Narrow-band spectrograms show harmonic separation, with sections showing about eight co-dominant peaks in the range of 1400–3300 Hz. A few calls show only one short note before the long one, and one faint spectrogram shows three short notes preceding the long note. The call sounds very much like a short burst of laughter (*ha-ha-ha*), with the notes given in rapid succession.

Charles M. Breder described the call of a Panamanian specimen of *E. raniformis* as "ha,ha,ha,ha" (on field tag attached to AMNH 40741♂ from Río Chucunaque, Darién),

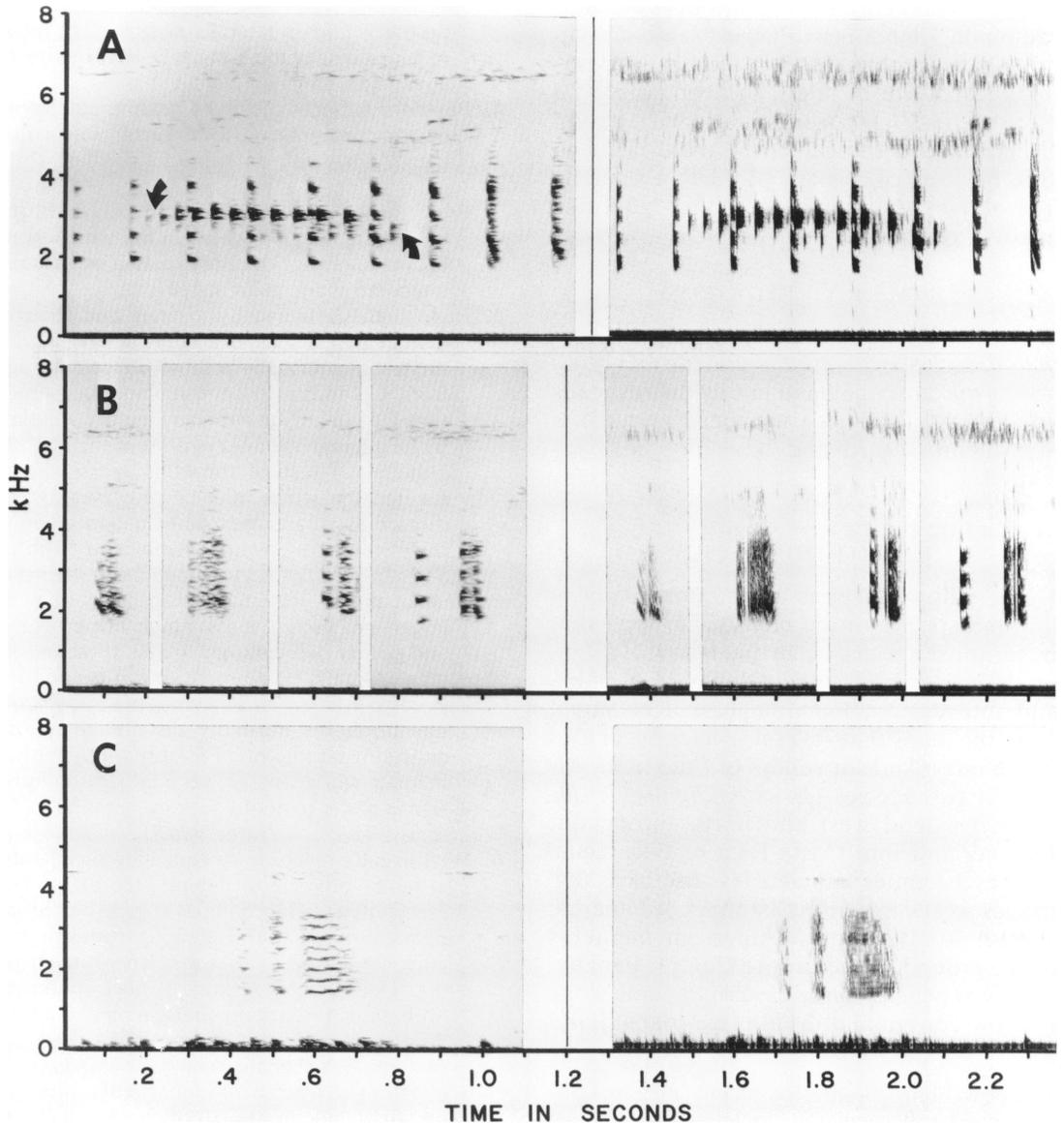


FIG. 11. Vocalizations of *Eleutherodactylus fitzingeri* (A, B) and presumed *Eleutherodactylus raniformis* (C). Calls on left side graphed with narrow-band 45-Hz filter; same calls repeated on right side, with wide-band, 300-Hz filter. Other data in text.

Eleutherodactylus fitzingeri: A. Portion of 2.6-seconds-long normal call showing short notes spaced at intervals of about 0.12–0.13 sec. (NB. The notes superimposed [arrows] at about 3 kHz are of unidentified frogs calling close by.) B. Four variable chirp calls given by frog in response to playback of its normal call above; the last call is audibly broken. *Eleutherodactylus raniformis*: C. Three-note laughter call (*ha-ha-ha*) provisionally attributed to *E. raniformis*, recorded on same tape as *E. fitzingeri* above.

which seems to support the provisional identification of the calls described above. (In a published report, Breder erroneously asso-

ciated this call with a species of hylid that sounds quite different; see under Ecological Notes in species account.)

Lynch and Pedro Ruiz found *E. raniformis* calling on June 5 near Puerto Valdivia, Antioquia, Colombia; the frogs were calling during a rainstorm at night, in deep grass in a pasture 10–20 m. from a wooded stream. Lynch likened the call in his field notes to “the bleating of a goat.” Breder in Panama (see above) also mentioned the “goat-like quality” of the call.

FEMALE VOCALIZATION

The females (and males?) at least of *Eleutherodactylus crassidigitus* and probably *E. raniformis* are capable of giving distress calls (see species accounts), but these sounds are infrequently heard and have not been recorded.

KEY TO THE SPECIES

The following key is for the trans-Andean lowland species of the *fitzingeri* group—that is, for those species occurring below 1000 m. on the western side of Ecuador and Colombia and into eastern Panama. It will be noted from the maps that several species occur also in the inter-Andean valleys of Colombia. Although two species (*E. crassidigitus*, *E. fitzingeri*) extend west and north throughout Panama and into Costa Rica or Nicaragua, the key becomes less and less useful as one moves westward on the Isthmus of Panama; several strictly Central American members of the group range east into Central Panama and a few penetrate into eastern Panama along the low continental divide (see maps 7 and 9).

- 1. Toe webbing absent or basal, not encompassing basal subarticular tubercles unless between toes IV and V (fig. 1A, B) 2
 - Toe webbing moderate to extensive, at least encompassing basal subarticular tubercles on all toes 3
- 2. No webbing; skin of venter coarsely areolate or granular; throat sometimes bearing two dark stripes *Eleutherodactylus caprifer*
 - Basal webbing at most; venter smooth; throat never striped *Eleutherodactylus achatinus*
- 3. Moderate webbing, never extending past second subarticular tubercle on toe V, usually not extending past second tubercle on lateral side of toe III (figs. 1C, 18A, B) 4
 - Extensive to very extensive webbing, with web

- extending past second subarticular tubercle on toe V and on lateral side of toe III, often reaching disc of toe V (fig. 1D, E); principally streamside frogs 7
- 4. Posterior surfaces of thighs bearing pale spots or pale mottling on a darker ground color (fig. 7A, B); with or without a median white gular stripe 5
 - Posterior surfaces of thighs virtually uniform brown (fig. 7C, D), which in life varies from brown to orange or reddish; with or without a median white gular stripe 6
- 5. Rear thigh spots usually discrete and sharply demarcated, at least in adults (fig. 7A); in life, thigh spots normally yellowish green in frogs from Colombia to central Panama, sometimes tan or gray in western Panama; median white gular stripe always present (fig. 6A, B) although if rest of throat is sparsely pigmented the stripe may be only weakly indicated as an area devoid of melanophores; males to about 35 mm., females to 53 mm. SVL *Eleutherodactylus fitzingeri*
 - Rear of thighs with many pale flecks or with larger, coalescing spots which are crowded and poorly defined (figs. 4, 7B); these markings normally pale brown or tan in life (not yellowish green as in sympatric *fitzingeri*); melanophores normally distributed across entire throat (fig. 6C, D), only rarely with a median white line or very faint ill-defined stripe; males to about 43 mm., females to 74 mm. SVL *Eleutherodactylus raniformis*
- 6. Web usually reaching or enclosing distal subarticular tubercle on lateral side of toe III, especially in adult females (fig. 18B); throat pigmentation variable, ranging from white to gray, sometimes with a median white stripe (fig. 19); never two pairs of dark markings on base of throat and chest; males to about 30 mm., females to 45 mm. SVL *Eleutherodactylus crassidigitus*
 - Web failing to reach distal subarticular tubercle on lateral side of toe III, often ending closer to the proximal tubercle (fig. 18A); throat variably whitish to gray but often irregularly spotted with gray or brown, and often with at least a hint of a pair of close-spaced dark markings on base of throat above a more widely spaced pair on chest (figs. 6E, 24); males to about 39 mm., females to 60 mm. SVL *Eleutherodactylus longirostris*
- 7. Toe webbing not approaching distal subarticular tubercle of longest toe (fig. 1D); skin of dorsum coarsely tuberculate or heavily spinulate, bearing pungent ridges and folds; head width greater than 41% of SVL *Eleutherodactylus anomalus*

- Toe webbing reaching or closely approaching distal subarticular tubercle of longest toe (fig. 1E); skin of dorsum not tubercular with sharply raised ridges; head width less than 41% of SVL 8
8. No tarsal fold; canthus rostralis rounded; posterior surfaces of thighs uniform brown; dorsal skin of males spinulate
 *Eleutherodactylus anatipes*
- Tarsal fold present; canthus rostralis sharp; posterior surfaces of thighs brown with cream flecks; both sexes having smooth dorsal skin with flattened warts
 *Eleutherodactylus zygodactylus*

ACCOUNTS OF SPECIES

Eleutherodactylus achatinus (Boulenger)

Figures 1B, 2, 8, 9, 12; Map 1

Hylodes achatinus Boulenger, 1898, p. 120 (holotype, BMNH 98.4.28.106 [reregistered as 1947.2.15.69], an adult female taken at Cachabé [=Cachabí, see fn. 5], Prov. Esmeraldas, Ecuador, by Mr. Rosenberg).

Hylodes pagmae Fowler, 1913, p. 162 (holotype, ANSP 18244, a juvenile female taken in the Pagma forest in the Chanchan River basin, Prov. Chimborazo, by S. N. Rhoads). NEW SYNONYMY.

Eleutherodactylus brederi Dunn, 1934, p. 1 (holotype, AMNH 40523, an adult female taken at Chalichiman's Creek, Prov. Darién, Panama, by C. M. Breder, Jr.). NEW SYNONYMY.

DIAGNOSIS: A moderate-sized species (adult males 24.4–36.2 mm. SVL, adult females 36.7–46.1 mm. SVL) of the *fitzingeri* group; measurements and proportions in tables 1 and 2. Skin of dorsum shagreened, with occasional larger tubercles, and bearing low, granular dorsolateral folds; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid about as wide as IOD, lacking pungent tubercles; tympanum prominent, its length two-fifths to two-thirds of eye length; snout of moderate length, E–N \geq eye length; vomerine odontophores separated on midline by space equal to odontophore width; males with vocal slits and a large, externally obvious subgular vocal sac; HW 33.5–43.2 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers I and II round, those on fingers III and IV truncate; adult males bearing non-spinous nuptial pad on thumb; toes bearing expanded discs; toes not or only basally webbed (web not encompassing basal subarticular tubercles except between toes IV and V), bearing narrow lateral fringes or keels; no

inner tarsal fold but usually a small inner tarsal tubercle; no calcar on heel; in preservative, dorsum usually tan or pale brown with brown interorbital bar, dorsal chevrons, narrow brown stripes along dorsolateral folds, canthal and supratympanic stripes, and labial bars; posterior surfaces of thighs tan with or without minute cream flecks or (in southwestern Ecuador) small spots; groin not mottled; venter cream to white; throat suffused with gray; undersides of limbs white with some gray mottling laterally.

Eleutherodactylus achatinus bears a resemblance to the sympatric but less common *E. caprifer*, since both share a variable pattern of dorsal chevrons and, unlike other members of the group, the males have externally conspicuous vocal sacs. But body colorations are usually quite different in life (*achatinus* usually reddish to orangish brown or brown, *caprifer* usually with a greenish or yellowish aspect), and the two species are readily separated by ventral skin texture (smooth in *achatinus*, areolate in *caprifer*).

Eleutherodactylus achatinus is similar to two Amazonian species, *E. conspicillatus* (Günther) and *E. peruvianus* (Melin), and to *E. terraebolivaris* Rivero from the Coastal Range in Venezuela. The Amazonian species have more pronounced lateral fringes on the toes and large pale spots on the posterior surfaces of the thighs. Also, *E. conspicillatus* has a dark face mask obscuring the labial bars, and *E. peruvianus* has cream spots on the dusky ventral surfaces of the shank and a spotted venter. In *E. terraebolivaris*, the throat is moderately (females) to heavily (males) flecked with brown pigmentation defining a narrow white gular stripe. *Eleutherodactylus terraebolivaris* has narrow lateral keels on the toes and dorsolateral folds are scarcely detectable.

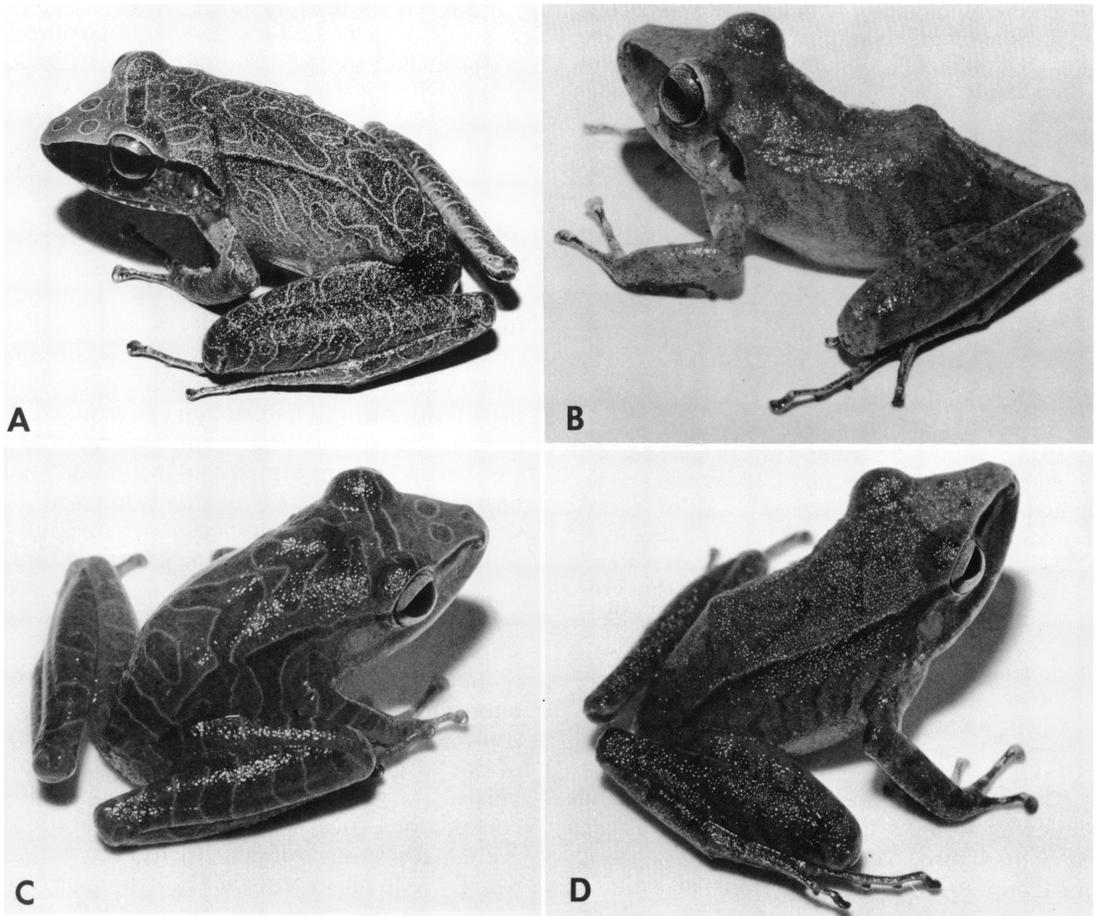


FIG. 12. Color pattern variation in *Eleutherodactylus achatinus* (not to scale). A. Camp Summit, 300–400 m., San Blas, Panama (KU 113786). B. 7 km. SSW El Corazón, 800 m., Bolívar-Cotopaxi border, Ecuador (AMNH 104960, juvenile). C, D. Quebrada Vicordó, 80–110 m., middle Río San Juan, Chocó, Colombia (AMNH 87021–87022).

DESCRIPTION: Published descriptions by Boulenger (1898), Dunn (1934), and Fowler (1913) are brief. Both Boulenger and Fowler provided illustrations of holotypes. Cochran and Goin's (1970) description (as *E. brederi*) is detailed and accompanied by photographs of a described individual, but their account is based on material from the eastern base of the Cordillera Oriental in Colombia—well removed from the rest of the known range (see map 1)—and we are not positive that the specimens are correctly assigned to *achatinus*. Therefore, *Eleutherodactylus achatinus* is redescribed here on the basis of material from western Ecuador. A discussion of geo-

graphic variation in coloration follows the standard description.

Head as wide as body (less so in gravid females), slightly wider than long. Snout subacuminate in dorsal view, rounded in lateral profile; snout long, E–N \geq eye length; nostrils weakly protuberant, directed laterally; canthus rostralis sharp, nearly straight (feebly sinuous in large females); loreal region flat, sloping abruptly to lips; lips not flared. IOD of moderate width, no cranial crests. Supratympanic fold distinct, ending well above arm insertion, obscuring upper edge of tympanic annulus. Tympanum superficial, fully exposed, annulus raised, round in males but

slightly higher than long in many females; tympanum separated from eye by distance equal to one-half to two-thirds of tympanum length. Postrictal tubercles subconical, not prominent. No enlarged tubercles on head.

Choanae oval, longer than wide, relatively large, not concealed by palatal shelf of maxillary arch. Vomerine odontophores prominent, elevated, median and posterior to choanae, each slightly larger than a choana, bearing a row of five to nine teeth across posterior border; odontophores triangular in outline, separated medially by distance equal to one-half to two-thirds the width of an odontophore. Tongue slightly longer than broad, its posterior border not or feebly notched, posterior third not adherent to floor of mouth. Males with large, externally evident, subgular vocal sac.

Skin of head and dorsum finely shagreened but also bearing scattered larger warts (especially laterally). Indistinct dorsolateral folds, rarely reaching so far as groin. Skin of limbs generally more smooth than dorsum. No anal sheath. Skin of throat and venter smooth but some encroachment by granules on posterolateral edges of venter. Discoidal folds prominent. Undersides of thighs areolate.

Antebrachial tubercle small, no other ulnar tubercles. Palmar tubercle bifid, larger than oval thenar tubercle. Four to five supernumerary palmar tubercles, all smaller and less pungent than subarticular tubercles which are nearly round (more distal tubercles smaller than basal ones). Lateral keels on fingers. First finger longer than second; when I and II are equally adpressed, tip of II reaches base of disc of I. All fingers bearing discs and pads, the subdigital pads broader than long. Discs of I and II small, those of III and IV large (broader than length of inner metatarsal tubercle but smaller than tympanum). Discs not emarginate.

No tubercles on knee, heel, or outer edge of tarsus. An indistinct tubercle (or short fold) on inner edge of tarsus. Inner metatarsal tubercle three times as long as wide, not compressed, at least four times size of low, round outer metatarsal tubercle. One small supernumerary plantar tubercle below subarticular tubercle of toe IV. Subarticular tubercles longer than wide, pungent, subconical, di-

minishing in size distally, but basal tubercle on toe V minute. Lateral keels on toes but no webbing (coalesced fringes not reaching base of subarticular tubercles [except between toes IV and V]). Toes bear broad subdigital pads on dilated discs (fig. 2). Toe discs as large as those of fingers. Heels of flexed hind legs overlapping.

Brown above becoming more pale on flanks, thighs, and hands and feet. Darker brown interorbital bar, chevrons, and limb bars. Supratympanic stripe black; canthal stripe and labial bars brown. Limb bars oblique on shanks, much narrower than interspaces which are subdivided by thin bars. Posterior surfaces of thighs brown with minute cream spots. Groin and anterior surfaces of thighs brown. Ventral surfaces cream with brown flecking on thighs, throat, and breast.

COLOR IN LIFE: *Eleutherodactylus achatinus* exhibits some geographic variability in aspects of its coloration, although analysis is complicated by individual and temporal variation in hue. Individual frogs can change their basic dorsal color at least from bright orange through dark brown,⁴ but it must be emphasized that this is not a simple temperature- or light-associated change, inasmuch as frogs of markedly different color may be found together and may maintain their different hues over long periods in the same environment (e.g., see under Aggressive Behavior).

The ground color of the body and dorsal limb surfaces is most commonly some shade of bright orangish or reddish brown, in a total range of yellowish brown–orange–orangish brown–reddish brown–brown–greenish brown–grayish brown–blackish brown. There seems a tendency for the average ground color to be a rather bright orangish to reddish brown at the northern end of the range, in Panama, whereas at the extreme southern end, in the lowlands of southwestern Ecuador (El Oro Prov.), most of 15 specimens seen alive were dull grayish to greenish brown, with only a few having a slight orangish aspect. The markings on the dorsum and limbs may be

⁴ Some potential for metachromatism is assumed for individuals throughout the range, although it was specifically noted only at one locality (Quebrada Vicordó, Chocó, Colombia).

either a darker shade of the ground color or of some contrasting color (e.g., grayish brown on orange-brown), and are often conspicuously outlined in light yellow or pale creamy yellow (fig. 12). The side of the head is darker than the dorsum, but the labial bars are easily seen through the ground color; frequently there is a diffuse yellow spot (highlight) below the eye. The canthal and supratympanic stripes are nearly black and grade ventrally into the ground color, and there is often a brown or blackish streak along the lower edge of the weak dorsolateral fold. The vocal sac is usually pale yellow, in a range from greenish white through light orange; in females, the throat varies from white to pale yellow and is finely to heavily stippled or splotched with gray or brown. The venter, which lacks dark stippling, varies from white to creamy yellow, occasionally with an orange suffusion.

The coloring of the posterior surfaces of the thigh is geographically variable: In Panama and northwestern Colombia, it is orange or reddish brown, and the undersides of the hind limbs are similarly colored; pale flecks on the thighs are absent or inconspicuous. On the Pacific slopes of Ecuador (e.g., fig. 12B), the rear thigh surfaces are reddish brown with red flecks (these frogs also may have red flecks in the groin). There is no bright coloring on the hind limbs in lowland populations in southwestern Ecuador, where the rear thigh surfaces vary from light to pale brown, with a sparse to heavy flecking of light tan.

Throughout the geographic range, the iris of *E. achatinus* is usually bright gold or golden bronze above the pupil and pale gray or grayish bronze below, all finely reticulated in black, with the pupil lying in a reddish brown horizontal stripe that separates the golden and grayish parts of the eye. In some specimens, the lower part of the iris may resemble the upper part instead of being grayish, or, in some Panamanian populations, it may even be a bright and contrasting reddish orange or pinkish bronze. The transverse reddish area may be in the form of a streak or narrow stripe having parallel edges, or else in the shape of a butterfly owing to expansion toward the ends of the stripe, these variations occurring within single populations throughout the range. Two local northern samples differed in having a *brown* stripe or *blackish*

brown line through the pupil, with no hint of red, and with the rest of the eye also being relatively dull and nearly the same color below the pupil as above (NE slope Cerro Sapo, Darién, Panama, and 13 km. W Dagua, Valle, Colombia).

ECOLOGICAL NOTES: *Eleutherodactylus achatinus* is an "edge" species that attains higher densities in disturbed areas than in mature forest, where it is seldom found. It is in many places a common nocturnal frog in moist pasture land, along roadcuts, in forest clearings, and in groves and plantations of cacao, bananas, and oranges. Unlike some edge species, it is not particularly likely to be encountered along forest streams or rivers unless the bordering forest has been cut.

A clear example of the propensity of this species for disturbed areas was noted on Cerro Sapo in the Darién of Panama: Earlier in this century, the lower reaches of Cerro Sapo were exploited for its dense stands of ivory nut palm (*tagua*), but, with the growth of the plastics industry, the mountain reverted to relatively mature forest, and the forest on the upper slopes probably never had been seriously disturbed—except on the 1080 m. summit, where a small area of elfin woodland was cleared by a geodetic field crew. In May 1967, when the grassy clearing seemed no more than a few years old (no sapling growth), there was an established colony of *E. achatinus* in and about the edges of the small clearing, as evidenced by their calls at dusk (a single voucher, KU 113774, was taken). But not one was heard calling in the dense forest adjacent to the clearing. In nine collecting days above 500 m. elevation, the only other calls heard and specimens found were at 540–560 m. on a ridge in the more open evergreen seasonal forest (habitat descriptions and photographs in Myers, 1969, but note that figs. 6, 7 are reversed). Despite the lack of records between 560 and 1080 m., it seems most likely that the mountaintop colony of *E. achatinus* was founded from a lower-density population already in place, rather than suppose that there was relatively long-distance dispersal. But our main point is that *E. achatinus* finds its optimal ecology in disturbed areas rather than in forest climax.

By day, individuals are found in and under ground litter and sometimes beneath rocks

and logs. At night, they sit on the ground and on low perches in vegetation (including grass) or on tree roots or rocks, usually less than a meter aboveground. Males have been noted as calling in January, March, April, May, June, and July; possibly they call throughout the year, at least in the wetter parts of their range. Calling is more frequent in rainy weather; a heavy afternoon rain has been noted to stimulate calling the same night, in places where few or no calls were heard on dry days preceding or following the rain. The most intense calling activity in Panama occurs during a brief period at dusk, although a few individuals may continue to call well into the night, and some calling also occurs on rainy, overcast days. There is either geographic variation in the "normal" call (see figs. 8, 9 and associated text under Vocalizations) or we have included two similar species under the name *E. achatinus* (see Remarks following). There also is a short chirp call made at various times, as for example during the following instance of male combat.

AGGRESSIVE BEHAVIOR: A prolonged "combat" between two males was observed in an overgrown banana grove on the upper Río Jaqué in Darién, Panama. The activity took place on the leaf litter and about 15 cm. aboveground on the broad leaves of a small plant, within a total area no greater than about 45 cm. in diameter. Observations were made by keeping the frogs in the dim periphery of a headlight beam, but they did not appear disturbed by occasional direct light. The individuals were fortunately easily kept track of because of different colorations; one (KU 113779) was a bright brownish orange frog of 32.3 mm. SVL, whereas the other (KU 113780) was grayish brown and smaller, 31.0 mm. SVL.

A basic aspect of the behavior involved mutual kicking. As the frogs approached one another in short hops, one or both would turn to back into contact with the other's side or hind limbs, after which one or the other would deliver a sharp kick by an abrupt extension of either hind leg. Hindquarter contact might be maintained for several seconds before a kick was given. The kick frequently was sufficient to send its target sprawling a few centimeters away or even to knock it off the leaf on which much of the action occurred. After

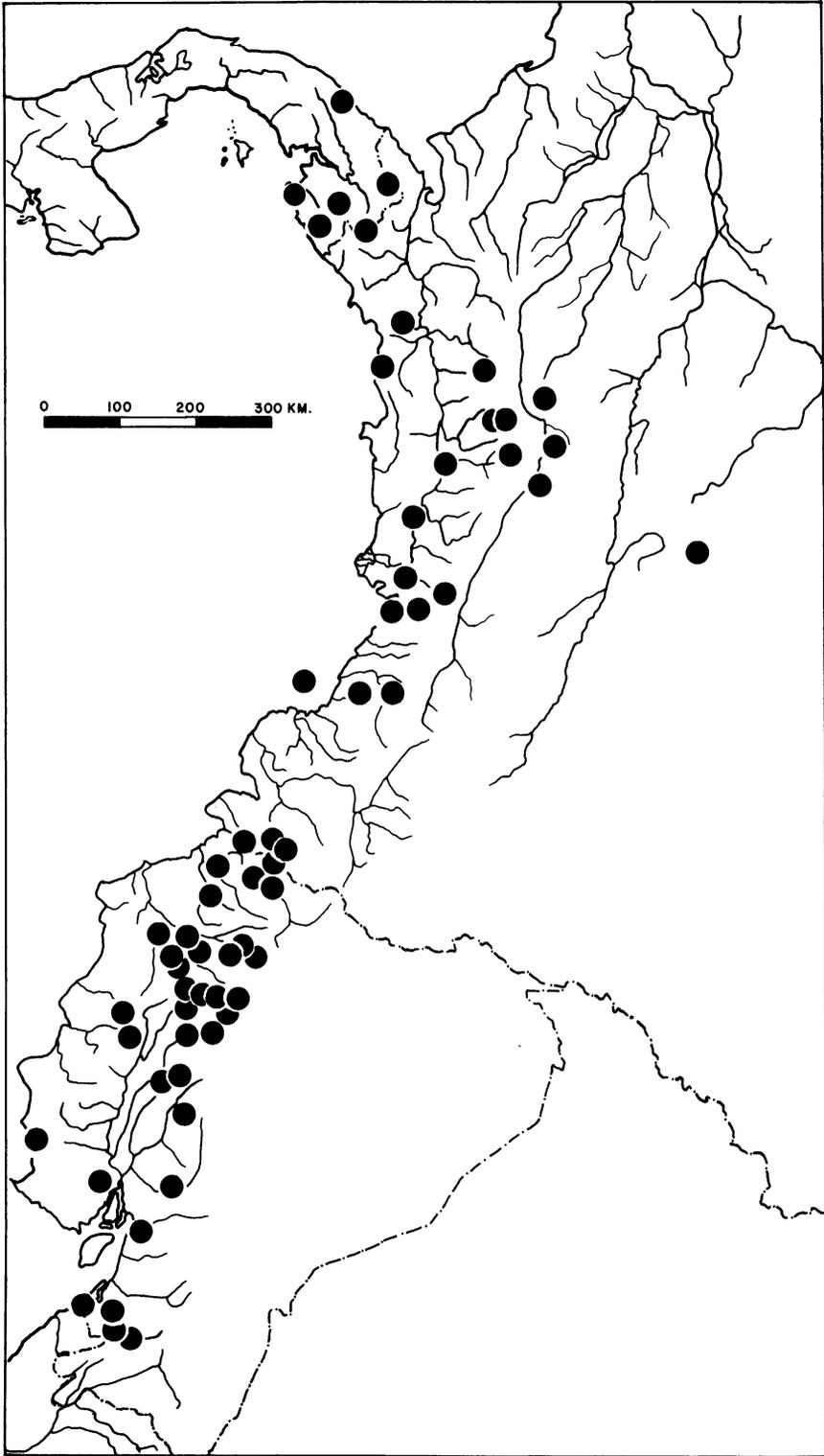
varying intervals of usually less than a minute, this kicking behavior would be repeated.

Between kicking episodes, the frogs hopped about one another while exhibiting *differential and constant behavior*, suggesting that one might have been an intruder in a defended territory. The smaller brown frog performed frequent, jerky push-ups, in which the body was raised by abrupt straightening of the forelimbs and just as abruptly lowered. The larger orange frog did none of that but emitted a nearly constant flow of soft chirping and clicking sounds, while keeping its vocal sac apparently fully inflated. The brown frog was thought to emit an occasional and much softer noise, but its vocal sac was inflated only slightly.

A frog displaced off the leaf by a kick usually jumped back up immediately, but on a few occasions the smaller brown frog took the better part of a minute in returning. When this happened, the orange frog noticeably increased the rate and volume of his calls, and, if the brown frog was particularly long in returning (as once when it was startled by a passing cricket and leaped temporarily outside of the arena), the orange one would give a few searching hops in the direction of the sluggard. Sometimes one frog hopped atop the other and then slithered forward and off to deliver a quick backward kick. Occasionally, one frog leaped completely over the other, calling to mind the name of a children's game.

The components of the behavior described above were repetitive and the combat seemed interminable after 1 hr., 5 min. continuous observation late on the night of April 10, 1967. A failing headlight battery and an oncoming electrical storm caused the specimens to be collected before the combat had reached a conclusion. They were kept in an inflated plastic bag with leaf litter through the following night, but nothing of further note was seen.

DISTRIBUTION: *Eleutherodactylus achatinus* occurs from extreme eastern Panama south through the Chocóan lowlands to El Oro Province in southern Ecuador, at elevations ranging from sea level to 2330 m. We have seen specimens from the valley of the Río Cauca and from the eastern base of the Cordillera Oriental in Colombia (map 1). We



MAP 1. Distribution of *Eleutherodactylus achatinus* (eastern Panama to southwestern Ecuador).

have not seen the specimens reported by Cochran and Goin (1970) from the lower Magdalena (El Centro, Depto. Santander) in Colombia. *Eleutherodactylus achatinus* is uncommon above 1500 m.

REMARKS: We relegate the nominal *E. brederi* Dunn and *E. pagmae* (Fowler) to the synonymy of *E. achatinus*. Fowler (1913) recognized that *achatinus* and his *pagmae* were similar but separated them because the tongue of the holotype of *achatinus* is feebly notched posteriorly and because the figured pattern of *achatinus* lacks the pale halos on the markings. We have not directly compared the holotypes but the supposed differences are bridged in various samples of *E. achatinus*. Lack of a tongue notch is probably a preservation artifact. The pattern difference is a product of ontogenetic and individual differences. Large females (such as the holotype of *E. achatinus*) rarely exhibit the pale halos on the body or limb markings, but the smaller males and juvenile females frequently do. In naming *E. brederi*, Dunn (1934) compared it with and distinguished it from the Central American *E. gollmeri* (Peters) and *E. noblei* Barbour and Dunn. Cochran and Goin (1970) pointed out the similarities between *E. achatinus* and *E. brederi* as well as differences they tabulated from the original descriptions. They did not examine either holotype. Both holotypes are adult females and the differences in the original descriptions (snout length, interorbital distance, tympanum size, and toe disc size) exaggerate the differences between the two specimens (there are no proportional differences). Boulenger (1898) reported the toes of *achatinus* as unwebbed in contrast to the basal webbing in *brederi*; however, the toes of the holotype of *achatinus* are basally webbed. Although we have not directly compared the three holotypes (each has been examined separately), we consider the differences between the three to not be of taxonomic significance and view all three specimens as representing a single species that ranges from extreme eastern Panama to southwestern Ecuador. Within this range, there is relatively little interpopulational variation in size (table 1), although geographic variation in some aspects of color is noteworthy (see Color in Life).

However, our decision to relegate Panamanian *E. brederi* Dunn to the synonymy of Ecuadorian *E. achatinus* on morphological grounds is not corroborated by our analysis of vocalizations (see figs. 8, 9 and associated text under Vocalizations). Panamanian frogs give a characteristic *ribit* or *bleep* call (fig. 9) that sounds quite unlike the longer *kree* call of Ecuadorian frogs (fig. 8). Because of morphological similarity and because of the 700 km. gap between populations for which recordings are available, we have not been able to decide whether this is an instance of geographic variation in the call or whether two species are actually represented. It is a problem that will have to be resolved with more recordings and possibly by a critical reappraisal of morphological features. It is worth noting that the Ecuadorian recordings represent one of the Pacific slope populations characterized by small red spots on the rear of the thigh, but, inasmuch as Lynch believes that he has heard the same type of call (*kree*) at lowland localities in Ecuador, we assume that the name *achatinus* will continue to apply at least to all the southern populations. The *kree* recordings were made at Maldonado, near the Colombian border in Carchi Province. Maldonado is in the same region as the type locality of *E. achatinus*, but at an elevation (1410 m.) some 1200 m. higher.⁵

Cochran and Goin (1970) did not report *E. achatinus* from Colombia, and the spec-

⁵ The type specimen of *Eleutherodactylus achatinus* (Boulenger) was obtained by Mr. W. F. H. Rosenberg at "Cachabé, a small village on the river of that name . . . Prov. Esmeraldas . . . about 500 feet [152 m.] above the sea" (Boulenger, 1898, p. 107). "Cachabé" and "Cachaví" are old spellings for the Río Cachabí of modern maps and gazetteers. We have not found the village Cachabí on recent maps, but entomological and ornithological gazetteers (Brown, 1941; Paynter and Traylor, 1977) place it on the upper Río Cachabí, and Peters (1955, p. 339) more specifically places it as a "small town about 10 miles [16 km.] southeast of Concepción, on the Río Cachabí," at about "200 meters." Thus, Cachabí should not be confused with the railroad town of San Javier de Cachabí, at a much lower elevation on the same river. The matter is of some importance, since Rosenberg's "Cachabé" is the shared type locality for 10 taxa described by Boulenger, including *E. achatinus*, *E. anomalus*, and *E. longirostris* of the present paper.

imens that they listed under the synonymous name *E. brederi* include examples of at least three species. We have seen 28 of the 54 examples they reported: 16 specimens are assigned (tentatively in a few cases) to *E. achatinus*, 11 are *E. w-nigrum* (Boettger), and one is *E. conspicillatus* (Günther). Other specimens of *E. achatinus* were reported by these authors as *E. conspicillatus*, *E. longirostris*, and *E. raniformis*.

***Eleutherodactylus anatipes*, new species**

Figures 1E, 13; Map 2

HOLOTYPE: KU 177626, a subadult female taken at Maldonado, Prov. Carchi, Ecuador, 1410 m., on May 20, 1977 by Thomas Berger (field no. JDL 8664).

PARATYPES: KU 177625, taken syntopically with the holotype, and USNM 233092, 233093, collected 2 km. S of junction of Río Lita and Río Mira, Prov. Esmeraldas, Ecuador, 520 m., on November 27, 1958 by James A. Peters.

ETYMOLOGY: The specific epithet is a noun in apposition, being a compound of the Latin *anatis* (of a duck) + *pes* (foot), in reference to the extensive foot webbing of the species.

DIAGNOSIS: A large species (adult males > 33 mm. SVL, adult females > 73 mm. SVL) of the *fitzingeri* group. Skin of dorsum in males bearing numerous pimblelike spinules and a pair of sinuous postorbital ridges; dorsum in females smooth with low tubercles, short ridges, and postorbital ridges; snout round in dorsal view; canthus rostralis rounded; upper eyelid much broader than IOD, lacking enlarged tubercles; tympanum small, obscure, its length one-fourth eye length; snout short, E-N < eye length in males, nearly equal eye length in females; vomerine odontophores separated on midline by distance equal to one-third to one-half of odontophore width; HW 39.0–40.8 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers round; toes bearing expanded discs; toes very extensively webbed, web nearly reaching subdigital pads on discs of toes I–III and V; web reaching distal sub-articular tubercle of toe IV; prominent lateral fringe on unwebbed portion of toes and along outer margins of toes I and V; no tarsal fold;

no calcar on heel; dorsum brown with darker brown markings; posterior surfaces of thighs brown; groin brown; throat finely stippled with brown; venter cream; undersides of limbs gray, flecked with gray.

Because of its extensive toe webbing, *E. anatipes* requires comparison only with the Colombian *E. zygodactylus*. Both have only two phalanges of toe IV free of webbing and differ from all other species of the *fitzingeri* group of *Eleutherodactylus* in this feature. *Eleutherodactylus anatipes* differs from *E. zygodactylus* in lacking an inner tarsal fold, in having rounded canthi rostrali, in having many small spinules on the skin of the dorsum in males, and in the short snout of the male. They resemble one another in large body size, in having small tympana, and narrow IOD (also shared with *E. anomalus*), the extent of toe webbing, size of the digital discs, and in coloration.

DESCRIPTION: Head as wide as body, wider than long. Snout round in dorsal view, truncate in lateral profile; snout very short in males, E–N nearly as great as eye length in females; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis rounded, very weakly defined; loreal region concave, sloping to lips; lips not flared. IOD very narrow, low cranial crest palpable. Supratympanic fold prominent, concealing upper edge of tympanum. Tympanum small, round, more distinct in males than in females; tympanum separated from eye by distance equal to twice tympanum length in males, by only one and one-half tympanum diameter in females. Postrictal tubercles coalesced forming ridge. No enlarged tubercles on head.

Choanae small, oval, not concealed by palatal shelf of maxillary arch. Vomerine odontophores five to seven times size of a choana, median and posterior to choanae; odontophores triangular in outline, elevated, each bearing five to nine teeth in a transverse row along posterior border. Tongue as long as wide, its posterior border shallowly notched, posterior border not adherent to floor of mouth. Both males are immature (no vocal slits, no nuptial pads).

Skin of top and sides of head, upper surfaces of limbs, dorsum, and upper flanks bearing numerous minute spinules in males; in females, dorsum smooth with many low



FIG. 13. *Eleutherodactylus anapipes*, new species. The holotype (KU 177626), slightly larger than life.

warts (and short ridges). A pair of sinuous ridges runs from eyes to middle of back. Skin over rest of body smooth. Anal opening not extended in sheath. Discoidal folds prominent, especially posteriorly, well anterior to groin.

Forearm lacking ulnar tubercles. Palmar tubercle bifid, larger than oval thenar tubercle. Very indistinct supernumerary palmar tubercles. Basal subarticular tubercles round or longer than wide, not pungent; distal subarticular tubercles low, obscure. Traces of lateral fringes at bases of fingers, otherwise no lateral fringes on fingers. Fingers bearing relatively narrow discs, all with round subdigital pads; finger discs as large as tympanum. First finger longer than second.

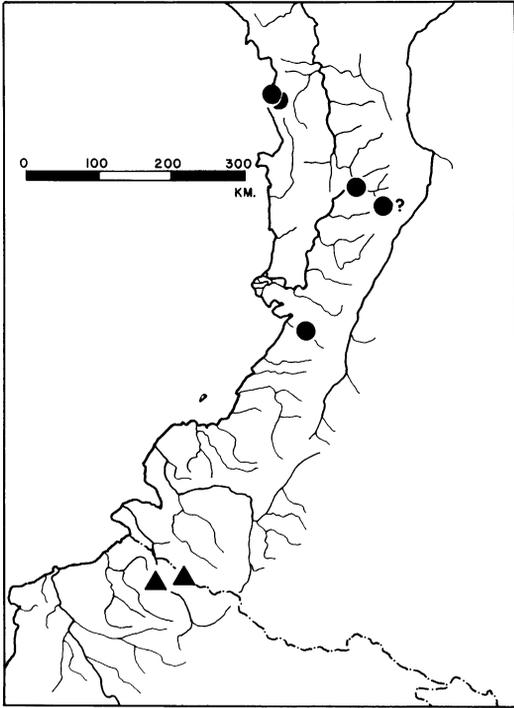
No tubercles or folds on knee, heel, or tarsus. Inner metatarsal tubercle oval, its length twice its width, not compressed. Outer metatarsal tubercle low, scarcely evident, less than one-sixth size of inner. No supernumerary plantar tubercles. Subarticular tubercles longer than wide, weakly pungent. Toes fully webbed except on toe IV (fig. 1E), bearing strong lateral fringes along unwebbed portion

and along outer edges of toes I and V; no fold along outer edge of foot. Heels of flexed hind legs touch; heel of adpressed hind leg reaches to tip of snout or just beyond.

Reddish brown above with darker brown markings (interorbital triangle, pair of lines posterior to eyes on back, transverse bar in scapular region, another above sacrum, and one or two bars between sacrum and vent). Labial bars and ill-defined canthal and supratympanic stripes dark brown. Limb bars dark brown, about as wide as interspaces; those on shank oblique. Anal triangle brown, ill-defined. Anterior and posterior surfaces of thighs brown. Undersides of shanks dull brown, flecked with darker brown. Throat finely stippled with brown. Flanks rapidly grade from brown above to cream below. Venter cream.

MEASUREMENTS OF HOLOTYPE (IN MM.): SVL 73.1; shank 47.6; HW 28.5; head length 25.9; upper eyelid width 8.0; IOD 4.9; tympanum length 2.3; eye length 8.3; E-N 7.9.

COLOR IN LIFE: Dorsum greenish brown with orangish warts and ridges. Groin, anterior and posterior surfaces of thighs dull



MAP 2. Locality records for *Eleutherodactylus anatypes* in northwestern Ecuador (▲) and *Eleutherodactylus zygodactylus* in western Colombia (●). Questioned locality is Pueblorrico (fn. 18).

yellow reticulated with black. Throat white with brown vermiculations. Venter and undersides of limbs yellow. Iris bright copper with black flecks and a brown horizontal streak.

VARIATION: Body ratios are summarized in table 2. The female paratype (KU 177625) has slightly less webbing than the female holotype or the male paratypes. The skin of the larger individuals, both females, is more warty than in the two males. The color pattern described above is more evident in the males than in the females.

ECOLOGICAL NOTES: The late James A. Peters found the two male paratypes "under bark in the woods along a small stream." The two females were sitting on rock exposures just above a small stream (Quebrada Huagambi) 1–2 m. wide and less than 0.5 m. deep. The rock exposures were at the base of steep, undercut banks about 1.5–2 m. high. Roots and branches partially obscured the under-

cut. The stream was heavily shaded by trees. The only other frog found in this microhabitat was *Eleutherodactylus necerus* Lynch, a large, broad-headed species.

DISTRIBUTION: The only known specimens are the holotype and paratypes, which come from two localities less than 30 km. apart in the drainage of the Río Mira in extreme northern Ecuador (map 2), at elevations of 520 and 1410 m. The foothills of the Andes in northern Ecuador and for a considerable distance northward into Colombia are poorly explored herpetologically, whereas the adjacent lowlands are better known.

REMARKS: *Eleutherodactylus anatypes* is probably most closely related to *E. anomalus* (Boulenger) and *E. zygodactylus*, new species. This group of three species conceivably may prove to be more closely related to certain broad-headed species [*E. bufoniformis* (Boulenger) and *E. necerus* Lynch] than to other species of the *fitzingeri* group where presently placed.

Eleutherodactylus anomalus (Boulenger)

Figures 1D, 3D, 14, 15; Map 3

Hylodes anomalus Boulenger, 1898, p. 119 (three syntypes, BMNH 98.4.28.98–98.4.28.100 [re-registered as 1947.2.16.8–1947.2.16.10], collected at Cachabé [=Cachabí, see fn. 5], Prov. Esmeraldas, Ecuador, by Mr. Rosenberg).

DIAGNOSIS: A large species (adult males 31.5–61.0 mm. SVL, adult females 76.5–92.4 mm. SVL) of the *fitzingeri* group; measurements and proportions in tables 1 and 2. Skin of dorsum coarsely tuberculate with many short ridges and folds but no complete dorsolateral folds; snout round in dorsal view; canthus rostralis obtuse or rounded; upper eyelid much broader than IOD, bearing pungent warts; tympanum relatively obscure, small, its length one-third of eye length; snout short, E–N < eye length; vomerine odontophores nearly in contact medially, broad, extending laterally to beneath choanae; males lack vocal slits; HW 41.8–48.3 percent SVL; fingers lack enlarged discs, subdigital pads very poorly defined proximally; adult males bearing nonspinous, glandular nuptial pads on thumbs; toes bearing expanded discs; toes extensively webbed, no more than 3¼ phalanges of toe IV free of web; modal webbing



FIG. 14. *Eleutherodactylus anomalus* (AMNH 88969) from 13 km. W Dagua, 820 m. elev. in Río Anchicayá drainage, Valle del Cauca, Colombia.

formula I $1\frac{1}{2}$ –2 II 1 – $2\frac{2}{3}$ III $1\frac{1}{2}$ – $3\frac{1}{4}$ IV $3\frac{1}{4}$ –1 V; heavy lateral fringes on unwebbed portions of toes and on lateral edges of toes I and V; inner tarsal fold extending along distal two-thirds of tarsus; no calcar on heel; dorsum dark brown with indistinct darker brown blotches; posterior surfaces of thighs brown with cream spots (or cream with brown reticulation); groin marbled; throat brown with diffuse pale spots; venter cream; undersides of limbs cream with some brown mottling.

Eleutherodactylus anomalus is similar to *E. bufoniformis* in size, skin texture, in having small tympana, broad vomerine odontophores, and in having a relatively broad head. They are readily distinguished in that *E. bufoniformis* has only basal toe webbing, heavy cranial crests, and lacks a tarsal fold. *Eleutherodactylus anomalus* is similar to *E. anatis* and *E. zygodactylus* in having extensive but less toe webbing (cf. fig. 1D, E), but differs in having coarser skin on the dorsal surface, broader vomerine odontophores, a broader head, and in lacking enlarged discs on the fingers.

DESCRIPTION: Boulenger (1898) and Coch-

ran and Goin (1970) described and illustrated one of the syntypes.

COLOR IN LIFE: Dull grayish brown, yellowish brown, or brown above, with indistinct darker blotching. Groin variably mottled brown or black on pale yellow, yellowish tan, or pink. Rear of thigh dark brown or black, with yellow (pale to medium, dull to bright) or tan mottling or spots. Throat slightly to heavily suffused with brown or gray, with white spots or mottling; throat darker, mottled black and white, in three juveniles. Venter dull white or yellowish white to pale yellow, or, occasionally (AMNH 87011), a bright, more intense yellow.

The iris is conspicuously marked in a pattern that seems reasonably constant in *E. anomalus* (see fig. 14).⁶ The pupil lies in the

⁶ The basic pattern of a conspicuous brown butterfly-shaped mark and usually ill-defined lines radiating ventrad from the pupil is very much like that of the sympatric but more widely distributed *Eleutherodactylus bufoniformis*, which is ecologically similar at least to the extent that both it and *E. anomalus* are large streamside frogs. The iris of the sympatric, large streamside *E. zyo-*

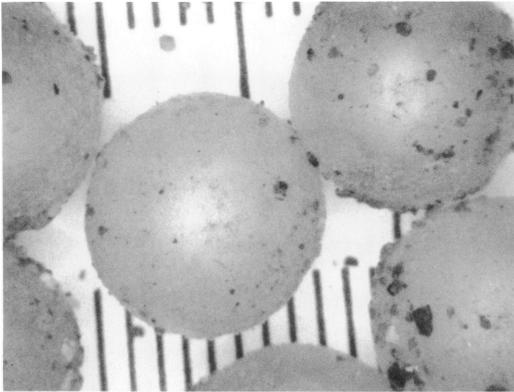
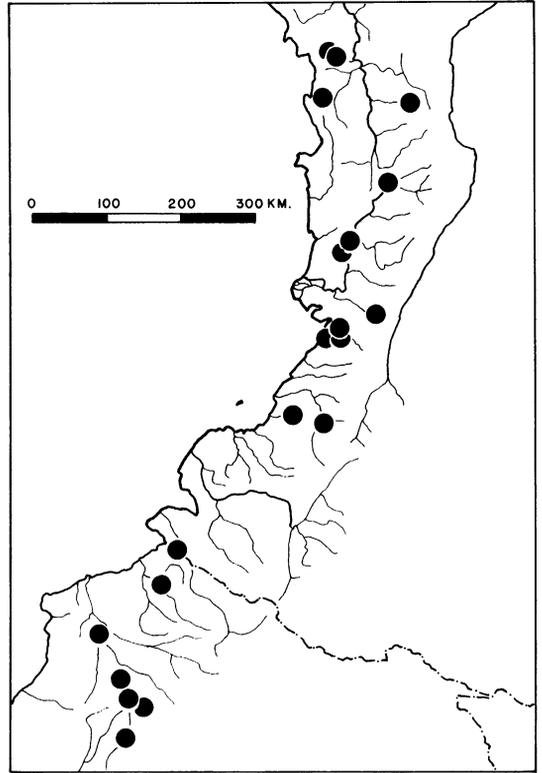


FIG. 15. Eggs of *Eleutherodactylus anomalus* (AMNH 88984) from Quebrada Guanguí, 100 m., Cauca, Colombia. Photographed in preservative; scale divisions in mm.

narrow part of a brown butterfly-shaped mark, and there is a tendency for several paler brown streaks or vague lines to radiate ventrad from the pupil to the bottom of the eye, on a pale gray (usually), tan or yellowish ground. The upper part of the iris is pale bronze, pale golden brown, or copper, with inconspicuous black venation and, in some individuals, with a dark vertical line from the pupil to the top of the eye. Whatever the hue, the upper and lower parts of the iris always seem to be conspicuously lighter than the intervening brown butterfly mark. The eye reflected orange on individuals shined at night with a headlamp.

ECOLOGICAL NOTES: *Eleutherodactylus anomalus* occurs mainly along clearwater, gravelly streams flowing through either well-drained or swampy lowland rain forest. Even at the highest elevation (820 m.), the portions of streams in which we collected these frogs

dactylus is also similar, except that the horizontal brown stripe is not butterfly-shaped (at least in the one specimen on which detailed notes were taken, see description herein). Another large streamside member of the genus is the Central American *E. punctariolus*, which has an iris also similar to the above species, except that the horizontal stripe is less well defined and the ventral lines better defined and tending to be more vertical than radiating. We doubt that such similarities between frogs of similar size and habitat are fortuitous or that iris pattern lacks selective value, but we have no explanations to offer.



MAP 3. Distribution of *Eleutherodactylus anomalus* (northwestern Colombia to central Ecuador).

tended to be relatively slow flowing, although some do become torrential when flooded. The frogs usually are to be found at night while they are sitting on the ground or on rocks beside or in the stream, or sitting in shallow water on gravel, silt, or submerged leaf litter. Escaping individuals dive into pools. They have been found in the same parts of streams as *E. bufoniformis* and *E. zygodactylus* and it seems likely that they also occur with *E. anatipes*. Nothing is known about possible resource partitioning among these species of large streamside *Eleutherodactylus*.

One instance of breeding of *E. anomalus* was observed on February 7, 1973, at Quebrada Guanguí in lowland Cauca, Colombia. After dark, at 9:15 P.M., a male frog was seen in axillary amplexus atop a larger female (now AMNH 88972), which was sitting on the ground in a shallow (~2.5 cm.) depression that was newly formed as evidenced by dark

(moist) diggings around the edge. The female was making an occasional squirming movement with her hindquarters, apparently still in the process of excavation. The spot was marked and re-examined at 11:30 P.M., by which time the male was gone and the female was crouched on a mass of 69 large, non-adherent eggs. After removing the eggs, the nest depression was seen to measure about 7.5 cm. across by 5 cm. deep, in moist, sandy, fine gravel. The nest was on a low gravel bar near its brushy bankside and about 2.5 m. from the edge of a shallow stream. It is not known whether the female would have brooded the clutch or would have buried and deserted it, but in either case it seemed extraordinary that a presumed direct-development species would have laid its terrestrial eggs in a spot so likely to be flooded at the next heavy rain. The area is thought to lack a true dry season and to receive a yearly rainfall probably in excess of 5 m. (Myers, Daly, and Malkin, 1978, pp. 321–322).

Some of the above eggs were preserved 42–44 hours after laying; they were unpigmented and averaged 8.26 mm. (7.9–8.5 mm., $N = 29$) in greatest diameter (fig. 15); the ovum without the jelly envelopes was about 5 mm. in diameter. Although the eggs were unconnected and did not adhere to one another, fine gravel and sand readily clung to their surfaces. The outer coat was translucent and very tough, being comprised of several close layers; its removal showed two eggs to be only in late blastula stage. Thus, early development would seem very slow in this species, unless the developing eggs had in fact died before preservation (several dozen eggs not preserved were kept in a shaded plastic bag, where they had visibly spoiled within several days).

DISTRIBUTION: *Eleutherodactylus anomalus* occurs in rain forest at elevations between 20 and 820 m., from northern Colombia (Serranía de Baudó) south to central Ecuador (map 3).

REMARKS: *Eleutherodactylus anomalus* is a very distinctive species that is readily identified from the original description alone (Boulenger, 1898), which has a fine illustration and which emphasizes the extensive foot webbing. Nonetheless, of the 21 specimens listed under this name by Cochran and Goin



FIG. 16. *Eleutherodactylus caprifer* (AMNH 88967) from Quebrada Guanguí, 100 m., Cauca, Colombia.

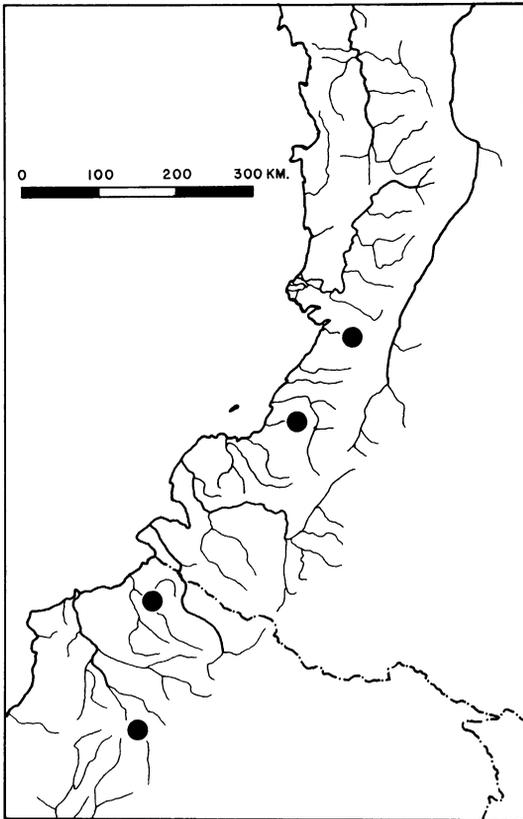
(1970), only five are correctly identified as *E. anomalus* (including one syntype). The other specimens are *E. longirostris*, *E. raniformis*, and *E. zygodactylus*. Cochran and Goin (1970) misidentified a specimen from Serranía de Baudó (ANSP 25675) as *E. bufoniformis*.

Eleutherodactylus caprifer Lynch

Figure 16; Map 4

Eleutherodactylus caprifer Lynch, 1977, p. 282 (holotype, KU 131589, an adult male taken at Las Palmas [(sic) = La Palma], Pichincha Province, Ecuador, on August 8, 1970 by J. D. Lynch).

DIAGNOSIS: A moderate-sized species (adult males 23.4–30.4 mm. SVL, adult females 40.5–43.8 mm. SVL) of the *fitzingeri* group that is unique in the group in having areolate ventral skin; measurements and proportions in tables 1, 2. Skin of dorsum smooth without dorsolateral folds; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid as wide as IOD, lacking pungent tubercles; tympanum prominent, its length one-fourth to one-third of eye length; snout short, E–N < eye length; vomerine odontophores separated on midline by space equal to an odontophore width; males with vocal slits



MAP 4. Locality records for *Eleutherodactylus caprifer* (western Colombia and northwestern Ecuador).

and a large, externally conspicuous, subgular vocal sac; HW 33.1–36.3 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on all fingers round; adult males lacking nuptial pads; toes bearing expanded discs; toes not webbed, bearing keel-like lateral fringes; short, obscure inner tarsal keel on distal half of tarsus; no calcar on heel; dorsum and limbs tan to pale brown, with few to many thin brown chevrons; posterior surfaces of thighs brown, flecked with cream; groin not mottled; two longitudinal brown stripes usually evident on pale throat; venter white; undersides of limbs white.

Eleutherodactylus caprifer differs from all other species of the *fitzingeri* group in having areolate instead of smooth skin on the venter. It differs from all other species of the group in the Chocoan lowlands in that males lack

nuptial pads. Except for the gular markings (distinctive within the group), *E. caprifer* generally resembles *E. achatinus* in pattern (in part because both species are rather variable), in lacking toe webbing, and in possessing an externally conspicuous vocal sac.

DESCRIPTION: Lynch (1977) provided a detailed description of the type series and a photograph of a paratopotype of *E. caprifer*.

COLOR IN LIFE: There seems to be some geographic variation in dorsal hue and pattern and in the colors of the throat and the rear thigh surface. Ecuadorian topotypes varied from pale orangish to (usually) tan with a green to yellow wash; brown markings included numerous dorsal chevrons and oblique lateral bars (Lynch, 1977, fig. 1), as well as limb bars and canthal and dorsolateral lines. The lips were paler than the dorsum, the groin dull brown (sometimes with pea-green flecks), and the rear of the thighs varied from yellowish to dull brown. The throat was fleshy pink in males and dull white in females, with a pair of dull gray longitudinal bars that were most distinct in females. The iris was bright copper, darker below, with a dark brown horizontal stripe.

For comparison with the above, notes and transparencies are available for two male *caprifer* from different localities in Colombia (map 4); these specimens bear more resemblance to each other than to the geographically distant Ecuadorian frogs. The Colombian frogs were bright yellowish green and bright olive green—evidently greener⁷ than those from Ecuador—and the dorsal chevrons were few and inconspicuous, the limb bars faint, and the bars on the flanks essentially absent (fig. 16). These markings and the more conspicuous face mask and dorsolateral lines were black rather than brown; one individual had a slight suffusion of orange along the upper edge of the black dorsolateral line. The rear of the thigh was very pale gray (vs. yellowish to brown in Ecuador), in noticeable contrast to the green bodies and dorsal limb surfaces. Their throats were pale greenish yellow.

⁷ Curiously, this green was photographically elusive, since transparencies (from different lots of Kodachrome II) rendered the two frogs yellowish brown and light brown. Similar results were obtained when photographing a rare green variant of *E. longirostris*.

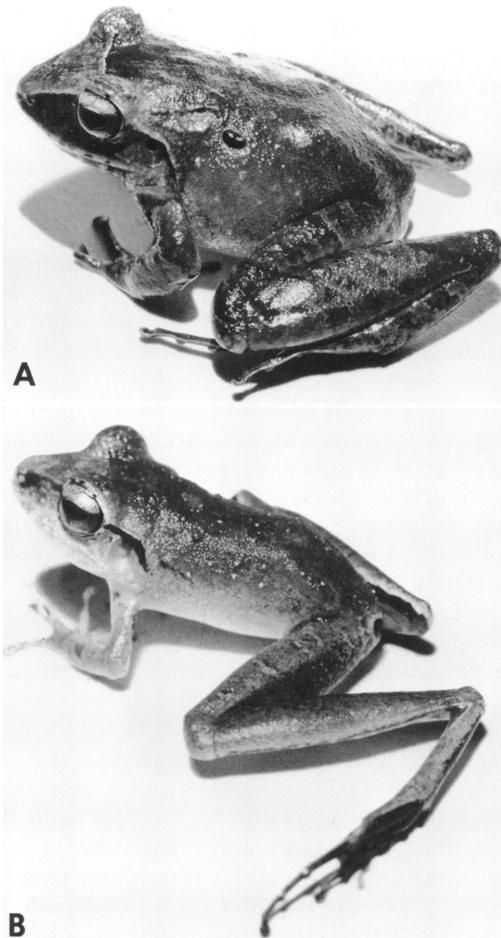


FIG. 17. Panamanian specimens of *Eleutherodactylus crassidigitus*. A. Fortuna Dam Site, 1000 m., upper Río Chiriquí, Chiriquí (AMNH 94980). B. Canal Zone of Panama, below 100 m. (not preserved).

low (vs. pink in Ecuadorian males); the longitudinal gray bars—not noted in life—are vaguely present on AMNH 88966, whereas AMNH 88967 has a faint indication of a median white stripe on a throat with an otherwise uniform dispersion of sparse melanophores. The venters appeared silvery white, owing to the peritoneal color showing through the translucent grayish white skin. The iris was pale gold or golden bronze above and reddish bronze or reddish brown below, with a black horizontal streak through the pupil.

ECOLOGICAL NOTES: All localities are in areas of lowland or lower montane rain forest, but, except for the common features of high humidity and low nighttime perches, microhabitats are varied. The two Colombian specimens were sitting on low (~1 m. aboveground) vegetation at night, one in a hot lowland forest and the other in a ravine in a cooler upland forest. At La Palma, Ecuador (the type locality, 920 m.), all specimens were found on low perches (<0.5 m.) within 1 m. of a stream in the spray-zone of a waterfall, the spray extending some 6 m. downstream from the base of the waterfall. The species remained common in this limited area even after destruction of the original forest: In August 1970, the stream was shaded by forest canopy. By July 1977, the forest had been cleared and the streambank was sheltered only by low vegetation less than 0.5 m. high; but *E. caprifer* seemed at least as abundant as formerly, although the forest-edge *E. achatinus* (q.v.) also was now present. Male *caprifer* were calling on both occasions, the call being a series of 8–10 high pitched piercing chirps.

DISTRIBUTION: *Eleutherodactylus caprifer* has been found at only four localities in southwestern Colombia and northwestern Ecuador, in an elevational range of 20–920 m. (map 4).

REMARKS: The general rarity of *Eleutherodactylus caprifer* contrasted to its local abundance at the type locality is puzzling, particularly since the type population remained dense despite dramatic habitat alteration between 1970 and 1977. We are aware of no particularly close relative of *E. caprifer*, with the possible exception of *E. achatinus*.

Eleutherodactylus crassidigitus Taylor
Figures 5A, 7C, 10, 17, 18B, 19, 20; Map 5

Eleutherodactylus longirostris, not of Boulenger: Dunn, 1931a, p. 386; 1931b, p. 418; 1933, p. 67; Schmidt, 1933, p. 6; Goin, 1959, p. 136; Heatwole and Sexton, 1966, p. 58; Duellman, 1967, p. 157; Myers, 1969, p. 47; Myers and Rand, 1969, p. 2; Savage, 1974, p. 293; 1980, p. 24.

Eleutherodactylus crassidigitus Taylor, 1952, pp. 740–744, fig. 31 (holotype, KU 28369, obtained at Isla Bonita, [1200 m.], eastern slope of Volcán Poás, [Alajuela Prov.], Costa Rica, between July

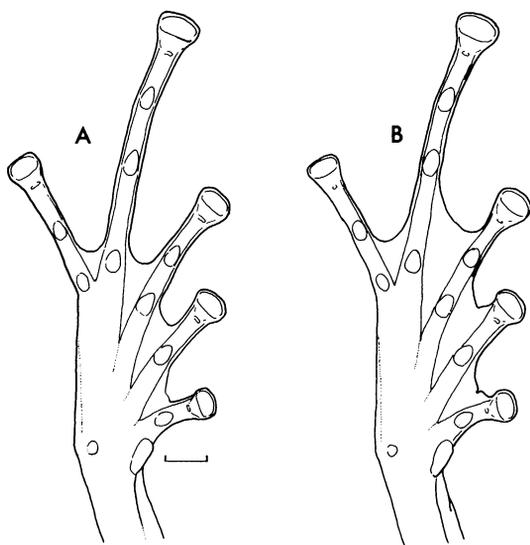


FIG. 18. Nearly maximal webbing in specimens of two previously confused species. A. *Eleutherodactylus longirostris* (USNM 144781, Andagoya, Chocó, Colombia). B. *Eleutherodactylus crassidigitus* (AMNH 88703, Altos de Majé, Panamá). Some specimens of *E. crassidigitus* have about the same degree of webbing as the maximal condition in *E. longirostris*, but the latter never has as much web as shown for *crassidigitus*.

22 and August 3, 1947, by Richard C. Taylor and Edward H. Taylor).

DIAGNOSIS: A moderate-sized species (adult males 20.2–30.2 mm. SVL, adult females 34.3–44.7 mm. SVL) of the *fitzingeri* group; skin of dorsum finely shagreened, with some low warts in scapular region; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid about as wide as IOD, bearing one pungent tubercle; tympanum prominent, its length one-half to two-thirds of eye length in adult males, two-fifths to three-fifths of eye length in females; snout of moderate length, E–N less than eye length in males, greater than eye length in females; vomerine odontophores separated on midline by space less than half the width of an odontophore; males with vocal slits and with subgular vocal sac not usually evident externally; HW 35.5–41.0 percent of SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers I and II round, those on fingers III

and IV truncate; adult males bearing non-spinous nuptial pads on thumbs; toes bearing expanded discs; toes moderately webbed (web encompasses basal subarticular tubercles of all toes and often the distal subarticular tubercle on toe III); modal webbing formula I 2⁻–2 II 1½–3⁻ III 2–3½ IV 4⁻–2½ V; lateral fringes on unwebbed portions of toes; inner tarsal fold on distal two-thirds of tarsus; no calcar on heel; in preservative, dorsum tan to light brown, variably patterned (see Color in Life); posterior surfaces of thighs brown; groin not mottled; venter cream, breast sometimes spotted with brown; throat cream with very slight brown peppering (especially highland populations in Costa Rica and western Panama) to heavily stippled with brown, sometimes defining a narrow to broad median white stripe (Panamanian populations); undersides of limbs cream with some lateral invasion of brown.

Eleutherodactylus crassidigitus is most similar to *E. longirostris* and *E. talamancae* in lacking distinct pale spots on the posterior surfaces of the thighs (occasional unpigmented dots do not form a definite pattern, see fig. 7C). It differs from these two species and also from species having patterned thighs (*E. andi*, *E. fitzingeri*, *E. malkini*, and *E. raniformis*) in having more extensive toe webbing (especially evident between toes II, III, and IV; see fig. 18B). Some Panamanian specimens resemble sympatric *E. fitzingeri* in dorsal patterns and throat coloration, but *fitzingeri* can usually be quickly separated at a glance by the pale spots on the rear of the thigh.

DESCRIPTION: Taylor's (1952) original description and illustrations remain useful. For measurements and proportions, see tables 1 and 2. The toe webbing varies as follows:

MALES

I (1½–2)–(2–2⁺) II (1–2)–(2⁺–3⁺) III (2–3⁻)–(3½–4⁺) IV (3¾–4⁺)–(2⁺–2½) V

FEMALES

I (1⁺–2)–(2⁻–2⁺) II (1–1¾)–(2⁺–3) III (1½–2½)–(3⁺–4) IV (3¾–4⁺)–(2⁺–2½) V

COLOR IN LIFE: Taylor (1952, p. 743) described the Costa Rican types as being “generally lavender to reddish olive brown” above.

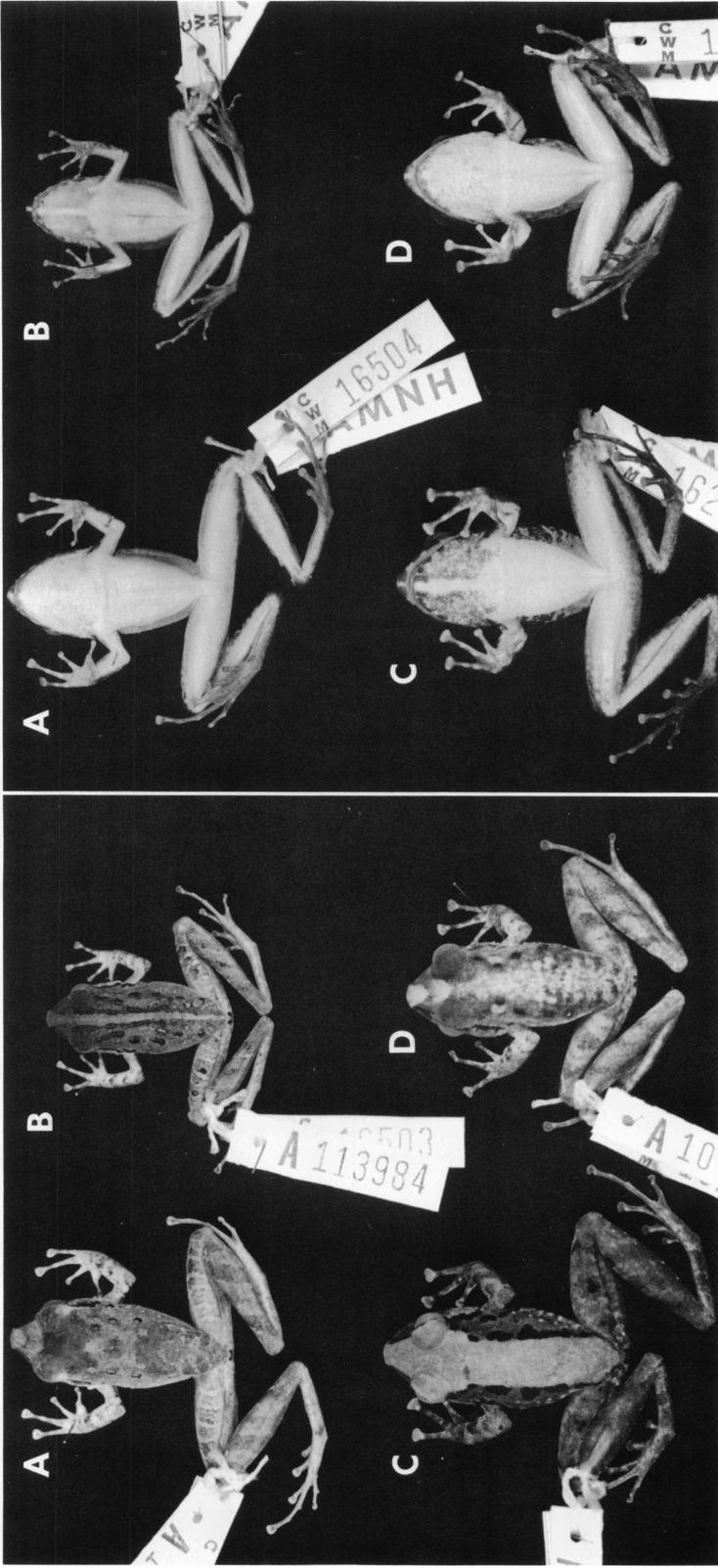


FIG. 19. Color pattern polymorphism in *Eleutherodactylus crassidigitus*. All from lowland northwestern Panama, as follows. A, B. 7.1 km. WSW Chiriquí Grande, 70–100 m., Bocas del Toro (AMNH 113985♂, 113984 juv., respectively). C, D. Ridge above Río Changuanola near Quebrada El Guabo, 170–200 m., Bocas del Toro (AMNH 1073006♂, 1073016♂).

Panamanian specimens are usually some shade, or combination of shades, of brown or gray, with the range of ground colors including gray, grayish brown, light or dark brown, pinkish brown, orange-brown, red-brown, or, rarely, green.⁸ Many Panamanian populations contain the following three pattern morphs. *Type 1* (fig. 19A): A usually uniform ground color with vague dark markings on the back (dorsal hourglass or scapular butterfly or W-shaped mark), atop the snout (irregularly shaped or as an inverted chevron), and between the eyes (an interorbital bar or butterfly mark). These markings are not equally evident on all specimens and are rarely vivid or well defined. The interorbital marking and a few black warts are the only noticeable dorsal markings on many specimens (fig. 17A; also Taylor's 1952 illustration of the Costa Rican holotype). *Type 2* (fig. 19C): The dorsum from the snout to the end of the body is a usually unmarked pale color (e.g., tan, orange-brown, red) sharply set off from the darker, duller sides of the head and body; black warts and short black lines or small spots may be aligned dorsolaterally along the edges of the pale dorsum of some specimens, further emphasizing the bicolouration. *Type 3* (fig. 19B): Similar to type 2 except that the dorsal pale color is restricted to a median pale stripe (rarely a thin line) extending from the tip of the snout to the end of the body. The median stripe most often is pale tan, but it may be some other shade of pale brown, gray, or white, always in sharp contrast to the rest of the body.

There is some intermediacy between the three morphs. Some type 1 specimens have the snout sharply set off in very pale tan, gray, etc., reminiscent of type 2 morphs. Occa-

sional individuals have a pale middorsal area that is narrower than in type 2 but wider than the stripe in type 3, and less sharply defined than in either (e.g., figs. 19D, 20). Type 2 morphs (e.g., AMNH 59559) rarely have a pale, thin vertebral line superimposed on the light dorsum. Some specimens, especially type 1 morphs, are sparsely to heavily dotted with white or pale yellow (e.g., fig. 17B).

The lips vary from uniformly light (without any suggestion of a pale labial line) or dark, to vaguely or conspicuously barred in shades of brown or gray. Pigmentation is highly variable on the throat, which ranges from nearly uniform white, with a faint speckling or light mottling of gray, to light or dark gray or even black (some juveniles), with a faint to vivid median white stripe and, in some specimens, scattered white spots. The venter is overall white, light yellow, or yellowish green, or else white on the chest and yellow or green on the belly. The undersides of the hind limbs are usually pale green or yellow, rarely with some orange suffusion.

The rear of the thigh is uniformly pigmented or nearly so (fig. 17B), and usually appears more colorful by day than by flashlight at night. Only rarely does the rear of the thigh appear pure brown, since there is usually at least a tinge of orange or red and these colors often predominate over the brown. Specimens from central Panama normally have orangish brown thighs, but, in western Panama, specimens in various populations have bright orange, orange-red, or red thighs, in addition to specimens having brown thighs weakly suffused, or flecked, with orange or red. Many individuals have a suffusion of orange or red in the groin and/or on the anterior face of the thigh.

The upper part of the iris may be gray, very pale (almost white) bronze, light bronze, golden bronze, or light brown—above a brown or red-brown horizontal stripe through the pupil—but the lower part of the iris is less variable, being usually pale or light gray, although often darkened by a suffusion of brown or red pigment from the lower edge of the horizontal stripe.

ECOLOGICAL NOTES: *Eleutherodactylus crassidigitus* occurs in regions of humid forest, where it is found in both mature and second-growth forest, and also in forest-edge

⁸ Green was specifically recorded only for two specimens from humid upland forest. A juvenile from central Panama had a suffusion of deep green over the head and shoulders (AMNH 84930, Cerro Campana, 800–900 m.). The second specimen was an adult male from Darién (KU 114644, Altos de Quia, 740–800 m., on the Colombian border). This individual (fig. 20) had the mid-dorsal region tan, with the rest of the body and dorsal limb surfaces being olive green (notes by Myers recorded in field catalogue of Duellman). A rare green variant of *E. longirostris* (q.v.) is also known from the Darién uplands.

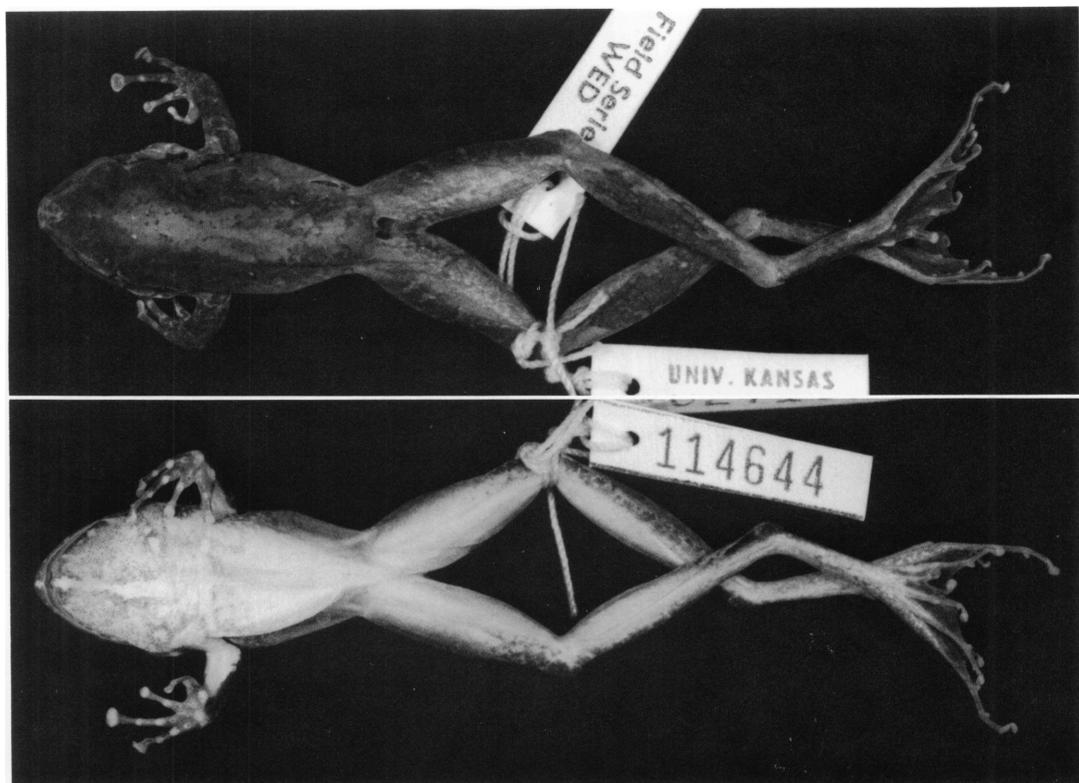


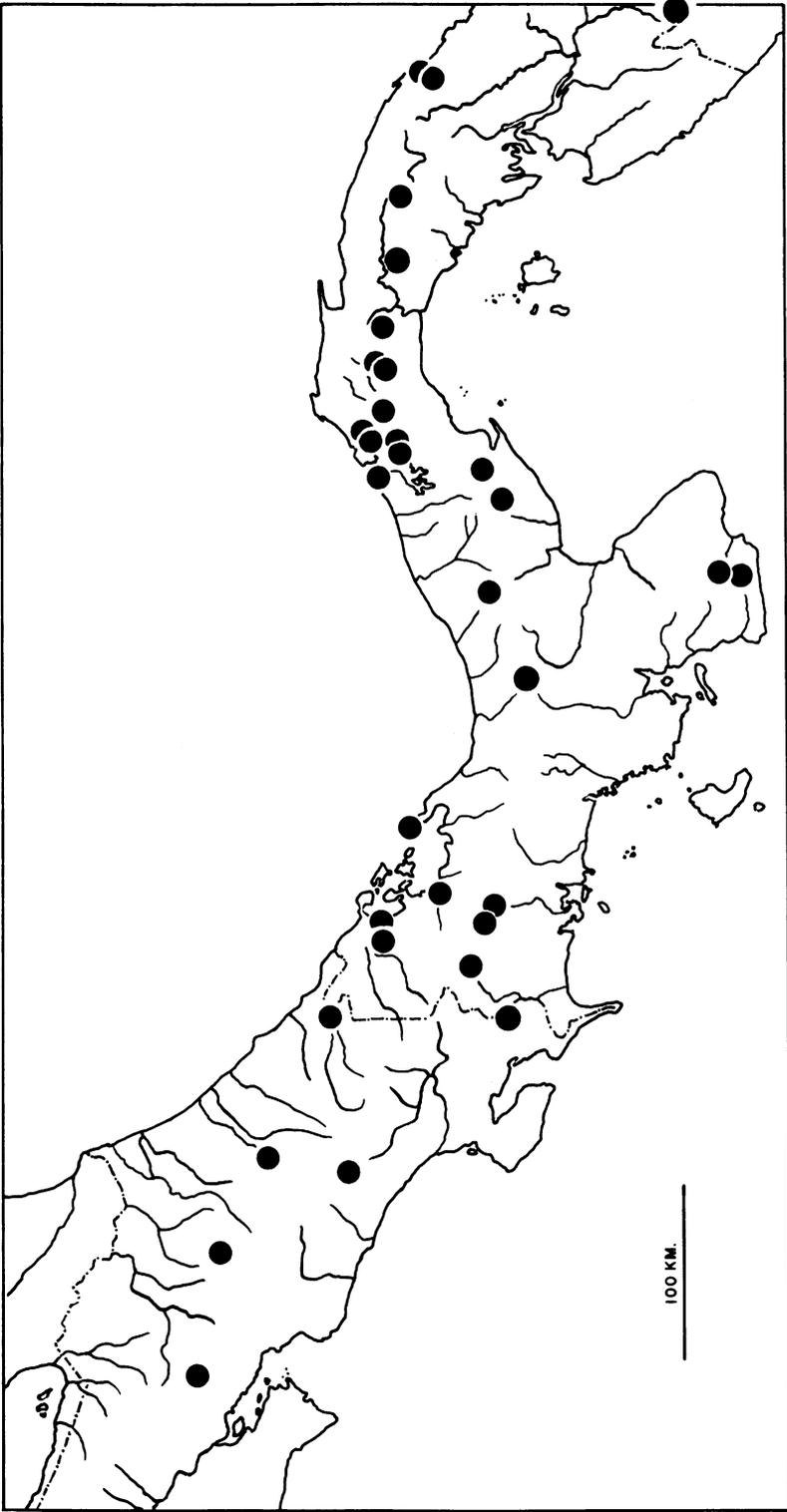
FIG. 20. *Eleutherodactylus crassidigitus* (KU 114644) from Altos de Quia, 740–800 m., Darién, Panama. This specimen extends the range of *E. crassidigitus* to the Colombian borderland, slightly overlapping the northern distribution of *E. longirostris* (maps 5, 7). The dorsal color and pattern, although unusual, fall within observed variation of *E. crassidigitus* (cf., fig. 19D and fn. 8). Note especially the relatively extensive foot webbing and well-defined throat stripe (compare Panamanian *E. longirostris* in fig. 25).

situations, including brushy pasture, coffee plantations, and stream banks. Although the species is found in lowland rain forest and monsoonal rain forest along the north coast of Panama, it generally is more abundant in upland forest, particularly in areas below 1500 m. elevation having at least a minimal dry season.

This frog is found by night on the forest floor, in low vegetation, and even on rocks in and along small streams (but it has no particular aquatic tendencies). Specimens not infrequently were recorded as being active by day on the forest floor, suggesting a higher degree of diurnality than in most other *Eleutherodactylus*. But by day it usually conceals itself on the forest floor; it prefers to hide in leaf litter, even when dry, rather than

in water-containing ground bromeliads, which *crassidigitus* seems to shun. Myers (1969, p. 47) mentioned this species, under the name *E. longirostris*, as being the only amphibian found in a borderline cloud forest at 1250–1270 m. elevation on Cerro Hoya, at the southern tip of the Azuero Peninsula; although bromeliads occurred in profusion on trees and on the ground (*op. cit.*, p. 31) and although a great many were examined, the half-dozen frogs collected were found in leaf litter by day and on low bushes at night. But *crassidigitus* is not averse to exploring new situations and was rather a pest at a 940-m. camp on Cerro Hoya, where the frogs got into boxes of supplies and into the water bucket.

Eleutherodactylus crassidigitus is active in the dry season, but calling behavior is inhibited



MAP 5. Some locality records for *Eleutherodactylus crassidigitus* in Costa Rica and Panama.

ited by long periods of dryness or even by short-term drying winds in otherwise damp forest. Only occasional calls were heard during dry season (March) in the Azuero highlands, but an exceptional rain that lasted from midnight until 4 P.M. brought on a frenzy of calling before dusk and throughout the early part of the night. Males call from twigs or other perches, usually less than 0.5 m. above-ground, although a specimen (fig. 20) from near the Colombian border was several meters up in a tree in dense forest, being found only by tracking its call—a sporadic “aaah.” In western Panama, at least, males produce two kinds of chirp calls (see fig. 10 and associated text under Vocalizations). Taylor (1952, p. 744) mentioned that a Costa Rican specimen (sex not stated) was found under a rock with 26 eggs.

An adult female *crassidigitus* (AMNH 87319) being eaten by a diurnal snake (*Liophis epinephelus*) was discovered because of its high-pitched *Rana*-like distress call; the snake evidently had found the frog concealed in a pile of leaves by a rocky stream. Another specimen of *crassidigitus* had been eaten by the nocturnal vine snake *Imantodes cenchoa*, at a highland locality in the Azuero Peninsula, where the usual lizard food of this snake was either absent or extraordinarily rare (Myers, 1982, p. 26).

DISTRIBUTION: *Eleutherodactylus crassidigitus* occurs from northern Costa Rica south and east through Panama to the Colombian border (map 5), from elevations essentially at sea level (10 m.) on the Atlantic coast to at least 1440 m. in Panama and to a recorded high of 2000 m. in Costa Rica (Taylor, 1952, p. 740). The species is most common at upland sites (see Ecological Notes) and seems absent in the Pacific lowlands of western Panama; a highland population in the southern Azuero Peninsula is isolated from the main part of the range. *E. crassidigitus* appears to follow the low continental divide through eastern Panama and south along the Colombian border, where it slightly overlaps the range of *E. longirostris* (cf., maps 5 and 7).

REMARKS: Except for a mention by Myers (1982, p. 26) in anticipation of the present paper, *Eleutherodactylus crassidigitus* has not

previously been reported from Panama. Starting in the mid-1960s, Myers had used the name in his field catalogue for specimens in western Panama, but he followed Dunn and others in misapplying the name *longirostris* for central and eastern Panamanian populations, not distinguishing these in the field from specimens of bona fide *E. longirostris* that he collected in the Darién highlands. The previous published misuse of the name *longirostris* is discussed under that species; although we have not examined every reported specimen, we suspect all previous reports of *E. longirostris* from Costa Rica and Panama to be based on *E. crassidigitus* and a few misidentified *E. fitzingeri*.

The present restriction of the name *E. longirostris* to a morphologically and geographically definable species (Ecuador to extreme eastern Panama), and the present expanded concept of *E. crassidigitus* for populations of smaller frogs with more webbing (eastern Panama to northern Costa Rica), is an improvement over previous confusion. Nonetheless, the populations assigned to *crassidigitus* are a rather variable lot and we cannot with confidence exclude a possibility that we are using the name for a composite of sibling species. Our preliminary survey of variation is inadequate for addressing the problem, although a few geographic trends are indicated. Development of a vivid median white stripe on an exceptionally dark throat is most common in central and eastern Panama and in the western Atlantic lowlands (fig. 19), although many specimens will have the throats as pale as in specimens from the western highlands. It is our impression that dorsal pattern polymorphism (fig. 19) may also be most common in the Atlantic lowland and central and eastern Panamanian populations. But these same populations tend to be more uniform in coloration on the rear of the thigh, which is usually orangish brown in life as compared with brighter orange or red in some specimens from the western highlands (with occasional individuals in all populations having predominantly duller brown thighs). Most of the variation detected by us has a strong intrapopulation component.

Savage (1980a, p. 24) distinguished two taxa of the *crassidigitus* complex in Costa

Rica, as follows (characters omitted at the ellipses are male nuptial pads and vocal slits, listed as present in each place):

- “Lips weakly barred or uniform; posterior surface of thigh reddish-brown with red more apparent in life . . . males to 28 mm, females to 42 mm *Eleutherodactylus longirostris*
 “Lips strongly barred with dark and light; posterior surface of thigh dark rust brown . . . males to 32 mm, females to 45 mm
 *Eleutherodactylus crassidigitus*”

We have not seen specimens assigned by Savage to “*longirostris*” (from lower elevations in southwestern Costa Rica), but the maximum sizes barely overlap minimal adult size of real *longirostris* from farther south, nor can the purported size differences in the above key be properly interpreted without some idea of sample sizes and measures of dispersion. The different states of the two color characters are found within single Panamanian populations that we assign to *E. crassidigitus* and likewise cannot be interpreted without more data. We suspect that both of Savage’s taxa fit our present definition of *E. crassidigitus*, which needs further attention.

We are especially curious about the status of one western Panamanian highland population here assigned to *Eleutherodactylus crassidigitus*. It is represented by eight specimens (AMNH 94980–94987) from the Fortuna Dam Site, at 1000 m. elevation at the lower end of the upper valley of the Río Chiriquí, Chiriquí Province (Myers and Duellman [1982] describe the physical geography of this unusual highland valley). These frogs come from a decidedly wetter environment than do most of our other Panamanian samples and show a uniformity in several characters. All resemble the common, nearly patternless morph of *crassidigitus*, although the lips of all are quite dark, with a hint of vertical bars in only a few (fig. 17A); thigh color ranged from bright orange to brown. They seem unusual, for a sample of *crassidigitus*, in throat coloration and in reduced foot webbing. The throats are rather densely and almost uniformly peppered with brown flecks (gray in life), without the clearly defined white stripes that would be evident in most Panamanian specimens having similarly dense throat pigmentation. On the basis of foot webbing, the

series cannot be differentiated from geographically distant *E. longirostris*. The modal webbing formula for five adult males (21.7–24.4 mm. SVL) is I 2–2⁺ II 2–3⁺ III 3–4 IV 4–2^{3/4} V, and for one adult female (40.3 mm. SVL) I 2⁻–2⁺ II 1½–3⁻ III 2½–4⁻ IV 4⁺–2½ V. Variation is slight in the series of males and a juvenile, and in one subadult female. In no case does the web reach the distal subarticular tubercle on the lateral side of toe III as is characteristic of adult *crassidigitus*.

In the aforesaid throat coloration and in the vague dorsal pattern, as well as webbing, the frogs from the upper Río Chiriquí valley resemble certain specimens in a small series of *E. longirostris* from an equivalent elevation in western Colombia (AMNH 102074–102078, Serranía de Baudó, 800–1000 m.), as can be seen by comparing figures 17A and 23B. However, the Panamanian specimens are much smaller and none has any indication of the posterior chevron markings that commonly appear in the variation of *longirostris* samples, including the Baudó series. The Río Chiriquí specimens seem most closely related to *E. crassidigitus*, where they are assigned pending further study (additional specimens were collected subsequent to this writing).

It is suggested elsewhere (under *E. longirostris*) that *E. crassidigitus* may be the sister species of *longirostris* + *talamancae*, but the suggestion is based on general resemblance rather than verifiable synapomorphy.

Eleutherodactylus fitzingeri
(O. Schmidt)

Figures 1C, 5B, 6A, B, 7A, 11, 21, 22; Map 6

Hylodes fitzingeri O. Schmidt, 1857, p. 12; also 1858, p. 248 (holotype, Krakow Museum 1012/1343, now lost, obtained by Josef Warszawicz in the mountains of New Grenada [western Panama], “4000” ft. [≈900 m., see fn. 15]; Savage’s [1974] designation of LACM 76859, from Barro Colorado Island, Panama Canal Zone, as neotype is here considered invalid and not binding on other authors [see Remarks]).

Hyla grisea Hallowell, “1860” [1861], p. 485 (holotype formerly in ANSP, now lost, from Nicaragua. Savage’s [1974] invalid designation of LACM 76859 as neotype is here rejected [see Remarks]).

Craugastor pulchrigulus Cope, 1862, p. 357 (holotype, USNM 4354, now lost, obtained at

Truandó, Depto. Chocó, Colombia. Savage's [1974] invalid designation of LACM 76859 as neotype is here rejected [see Remarks].

Leiyla Güntherii Keferstein, 1868a, p. 330 (holotype formerly in Göttingen Museum, now lost, from Costa Rica. Savage's [1974] invalid designation of LACM 76859 as neotype is here rejected [see Remarks]).

Hylodes nubilus Günther, 1901 (1885–1902), p. 237, pl. 69, fig. A (holotype, BMNH 1902.5.13.29 [reregistered as 1947.2.15.80], obtained at Escazu, San José, Costa Rica, 1000 m., by Mr. Underwood).

DIAGNOSIS: A moderate-sized species (adult males 23.5–35.0 mm. SVL, adult females 36.5–52.5 mm. SVL) of the *fitzingeri* group; skin of dorsum usually bearing pungent warts and ridges (frequently obliterated in preservatives); snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid as wide as (or slightly wider than) IOD, bearing pungent (but not conical) warts; tympanum prominent, its length three-fifths to four-fifths of eye length in males, two-fifths to three-fifths in females; snout of moderate length, E–N \cong eye length (usually < eye length in males); vomerine odontophores separated on midline by space equal to one-third to one-half of odontophore width; males with vocal slits and with subgular vocal sac not usually evident externally; HW 34.0–37.5 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers I and II round, those on fingers III and IV truncate; adult males bearing nonspinous nuptial pad on thumb; toes bearing expanded discs; toes moderately webbed (web encompasses basal subarticular tubercles of all toes, but not the more distal tubercles); modal webbing formula I 2⁻–2⁺ II 1^{3/4}–3⁻ III 2^{1/2}–4⁻ IV 4⁻–2^{1/2} V; lateral fringes on unwebbed portions of toes; inner tarsal fold on distal two-thirds of tarsus; no calcar on heel; in preservative, dorsum tan to gray or brown, sometimes with broad middorsal yellow stripe, with darker brown to black markings (see Color in Life); posterior surfaces of thighs brown with usually conspicuous small pale spots (some usually as large as thumb pad in adults, smaller and poorly defined in some juveniles); groin mottled or uniform; pale venter immaculate or with dark flecking or



FIG. 21. *Eleutherodactylus fitzingeri* (AMNH 87051) from Quebrada Vicordó, about 5 km. above Noanamá on middle Río San Juan, 80–110 m., Chocó, Colombia.

weak mottling; throat sparsely to heavily flecked with brown except that absence of melanophores along midline of throat creates a narrow to broad white stripe⁹; undersides of limbs white, rarely mottled with gray or brown.

Eleutherodactylus fitzingeri has essentially the same amount of toe webbing (fig. 1C) as the somewhat similar-appearing *E. andi*, *E. longirostris*, *E. malkini*, and *E. raniformis*, and it might also be confused with sympatric *E. crassidigitus*, which has more webbing, and possibly with *E. talamancae*, which has less. *E. fitzingeri* differs from all the preceding species in being usually more rugose, with more warts and ridges on the skin of the dorsum and upper eyelid (see figs. 21, 22). The presence of pale spots on the rear of the thighs

⁹ Although shared with some other species (especially many populations of *E. crassidigitus*), a median white gular stripe is an important diagnostic character in *E. fitzingeri*. It is very evident on individuals with dark throats, but those having pale throats may require close inspection in order not to overlook a median area devoid of melanophores. An occasional individual has a vague stripe owing to an irregular invasion of dark pigment, or even one that is aberrantly zigzagged (e.g., UMMZ 137753, Barro Colorado Island).

immediately distinguishes *fitzingeri* from *crassidigitus*, *longirostris*, and *talamancae*, which are uniform brown on the rear of the thigh. *Eleutherodactylus fitzingeri* is most easily separated from the larger *raniformis* by having a usually conspicuous white gular stripe (fig. 6A, B) and in having more discrete and usually larger pale spots on the rear of the thigh (fig. 7A); in life, the pale thigh markings are tan in *raniformis* but normally a brighter greenish yellow (or yellowish green) in sympatric *fitzingeri*.

At its upper elevational limits in the northern part of its range, *E. fitzingeri* might be confused with *E. andi*,¹⁰ which shares similar webbing and a white gular stripe, but which has large, well-spaced bright yellow spots or vertical stripes on the rear of the thigh, a usually red-suffused, bright yellow belly, larger body size (adult males 45–55 mm. SVL, females 65–80 mm. SVL), and larger, emarginate (dorsally indented) digital discs (width of discs on fingers III and IV \geq length of inner metatarsal tubercle). The geographically remote *E. malkini* (upper Amazonia) is readily separated from *fitzingeri* by lack of a gular stripe, by rear thigh surfaces being pale with dark marbling, and by a flaplike inner tarsal fold.

DESCRIPTIONS: The old descriptions and illustrations of *Eleutherodactylus fitzingeri* are mainly of historical interest (see references in abbreviated synonymy herein and in the more complete one in Savage, 1974, p. 296). Taylor (1952, pp. 735–739) provided a detailed description and good illustration under the misapplied name *ranoides*, and he also (pp. 739–740) gave an English translation of the German part of Schmidt's second (1858) des-

cription of the type specimen of *fitzingeri*.¹¹ Savage (1974) summarized pertinent characteristics of *fitzingeri* and provided photographs of several preserved specimens and comparisons with *E. andi*, *E. fleischmanni*, *E. rugulosus*, and *E. crassidigitus* (as *E. longirostris*).

COLOR IN LIFE: *Eleutherodactylus fitzingeri* comes in various ground colors, including grayish brown, tan, light orangish brown, and olive. Some individuals have a contrasting broad middorsal stripe (never a thin line) of gray, tan, or yellow (figs. 5B, 22), but more often there are a few small blackish spots and a vague, complex dorsal pattern that is somewhat darker than the ground color; this pattern often consists of interorbital and scapular butterfly or W-shaped markings, with or without similar markings lower on the back and atop the snout. Often, these various markings and the ground color are in contrasting shades of brown, and there may be additional dorsal suffusions of red-brown or green, or a few warts that are vivid orange, but individuals also may be rather dark and drab with markings of low contrast. The lips have usually noticeable bars of gray or brown alternating with whitish interspaces.

The throat varies from very pale gray to dark gray or grayish brown—nearly always with an evident white stripe down the middle (see fn. 9 and fig. 6A, B). The chest is usually white, rarely pale gray or pale grayish brown. The belly may either be white like the chest or else some shade of pale to bright greenish yellow or yellow; variation in belly color may have a sexual component, with females tending to be white and males yellowish, but this is not confirmed. The undersides of the hind

¹⁰ Other highland species in Costa Rica and western Panama which might be confused with *E. fitzingeri* include *E. cuaquero*, *E. rayo* and one or two apparently undescribed species. These, like *E. andi* above, differ from *fitzingeri* in their exceptionally large, emarginate discs on fingers III and IV, as well as in characters of skin texture and coloration. In the same region, *fitzingeri* conceivably might be confused with young individuals of certain riparian species (see Savage, 1975) that attain larger adult size and more robust habitus, and which have shorter snouts and rounded (vs. truncate) discs on fingers III and IV.

¹¹ Omitted in translation is the brief Latin diagnosis of *Hylodes fitzingeri*, which comprised the entire text of Schmidt's original description (1857, p. 12) of the species, and which was included verbatim in the second, more detailed description (1858, p. 248 [p. 12 in reprint]). The latter includes a poorly executed drawing (pl. 1, fig. 10) of the right hind foot in plantar view, showing the well-developed "osse primo cuneiformi" (inner metatarsal tubercle) stressed in the diagnosis, and basal webbing which extends from one proximal subarticular tubercle to another (slightly above the tubercles on the medial sides of the fourth and fifth toes).

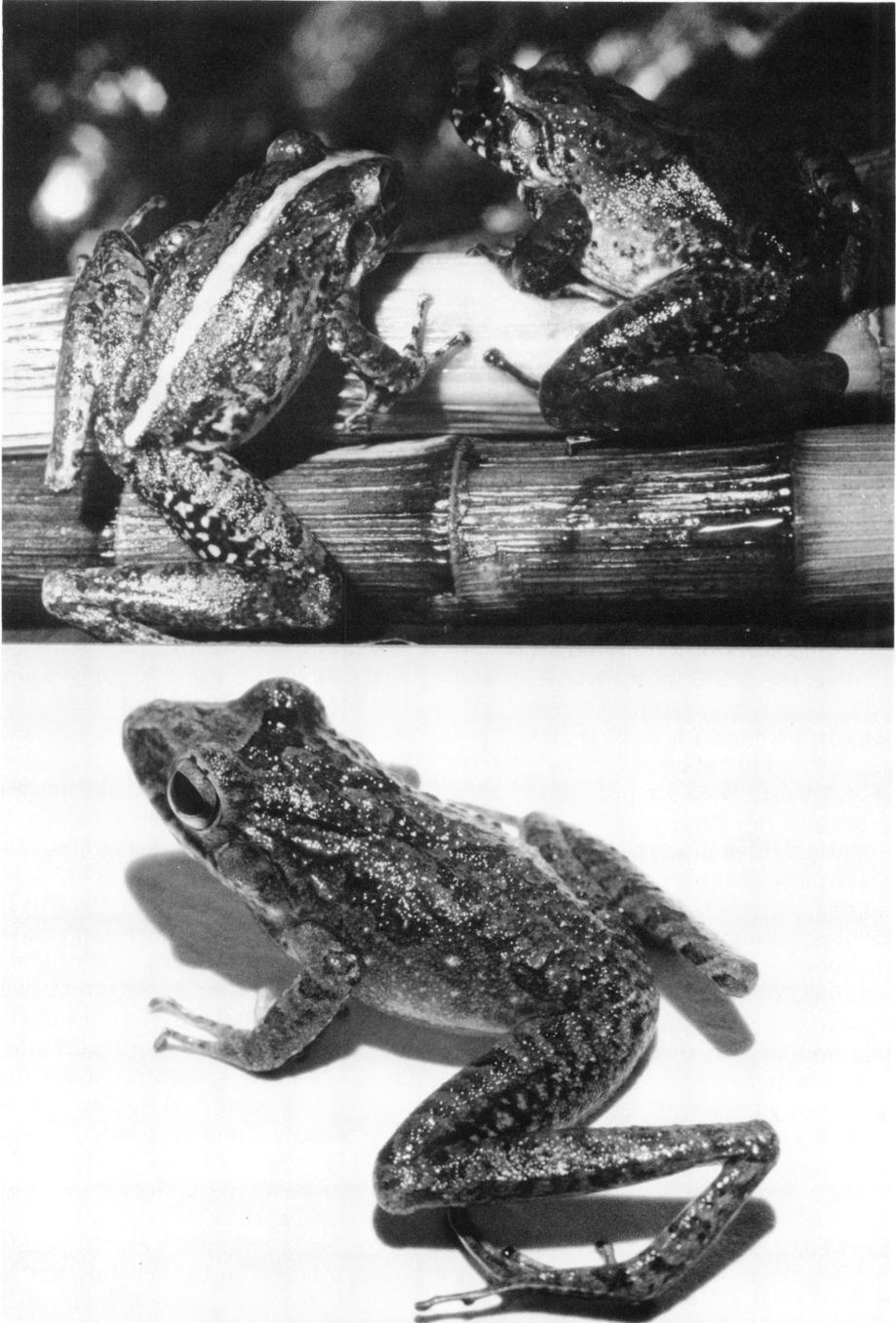


FIG. 22. Panamanian specimens of *Eleutherodactylus fitzingeri* (not to scale). *Top*: Two adults (probably females) from El Valle de Antón, Coclé (from a transparency by Kenneth T. Nemuras). *Bottom*: Greatly enlarged view of a small male 23.5 mm. SVL (adult, vocal slits present) from Río Changuinola near Quebrada El Guabo, 50–200 m., Bocas del Toro (AMNH 107309). The pale thigh spots tend to be less well demarcated in juveniles and some small adults as can be seen in this individual.

limbs are the same yellowish hue as the belly in some individuals, but usually they are a more definite (but pale) green. None has been noted to have white limbs, but a yellow-bellied specimen (AMNH 107307) from the Atlantic lowlands of northwestern Panama had the undersides of its hind limbs pale gray (green in several others from same locality); and a specimen from the Atlantic lowlands of Costa Rica (AMNH 81466) had them mottled with pale bluish gray on pale greenish yellow.

The rear of the thigh varies from brown to blackish brown, with pale spots which are irregularly shaped but mostly well spaced and usually well demarcated (figs. 7A, 22), at least in adults.¹² These pale thigh spots characteristically are a rather vivid greenish yellow (or yellowish green); less often, the pale thigh spots were perceived as yellowish tan, pale tan, or pale gray. Part of this variation is real.¹³ In specimens from central and eastern Panama, which account for about 80 percent of the total (of about 100 specimens described in life), and also in several from western Colombia, the spots nearly always were yellowish green, whereas specimens from western Panama and Costa Rica seemed more likely to have tan or gray spots (in 7 of 17 specimens). The greenish hue of the rear-thigh spots is a usually reliable character for helping to separate *fitzingeri* from *raniformis* in the area of sympatry (eastern Panama and western Colombia).

The iris of *Eleutherodactylus fitzingeri* is usually pale bronze or golden bronze above the pupil and pale gray or bronzy gray below the pupil, which is set in a reddish brown (usually) or brown horizontal stripe that separates the two areas. Occasionally, the pale areas of the iris appear uniformly tan or gray,

but the lower part of the iris seems never to become uniformly dark (as in *E. raniformis*).

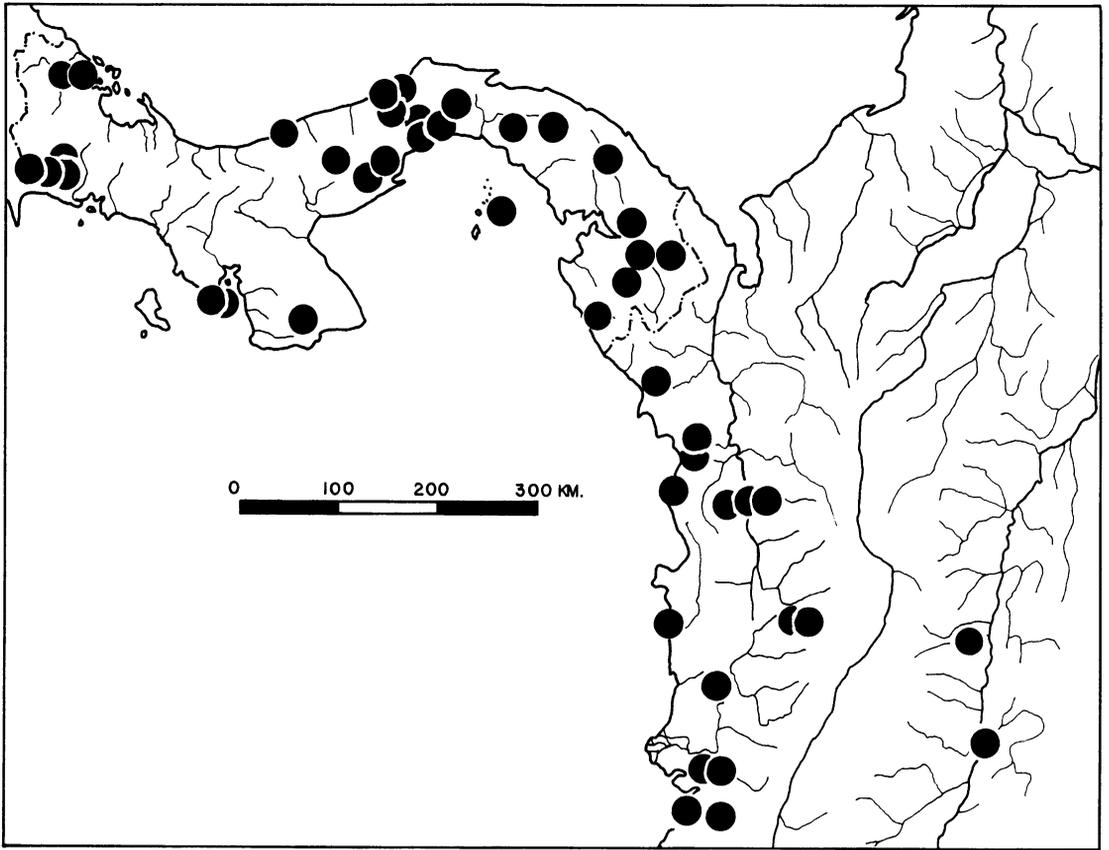
ECOLOGICAL NOTES: *Eleutherodactylus fitzingeri* inhabits a variety of humid forests, from the wettest rain forest in western Colombia to seasonally dry gallery forest on the Pacific side of central Panama. It may be locally abundant in lower montane forest above 600 m., as in the highlands northeast of Panama City, although the majority of museum specimens are from the hot lowlands. In some areas one gathers the impression that *fitzingeri* attains its highest densities in disturbed or edge situations, such as brushy clearings, but certainly it may be common in mature forest as well. Unfortunately, published census data from forest plots in the Río Silugandí area of Panama Province must be disregarded, since the investigators (Heatwole and Sexton, 1966, p. 53) did not differentiate *fitzingeri* from sympatric *raniformis* (compare UMMZ material ["Río Silugandí at Pan-Am Hwy"] in Specimens Examined).

By day this frog is usually found on the forest floor, sometimes crouched in the open but usually concealed in leaf litter. One individual was seen to be alertly looking out from under a fallen leaf during a period of daytime rain, and it seems likely that some feeding might occur in the leaf litter by day (see also calling activity below). It also can be found sitting amongst the leaf litter after dark, or on gravel bars or other exposed sites, but at night it is likely to climb onto logs or into low vegetation in the forest, or even onto rocks in small streams. Individuals pursued by day have been seen to leap into a stream and hide on the bottom. Although *fitzingeri* is found frequently along forest streams, it is not "usually found near water" (Dunn, 1931b, p. 411) except perhaps in some places in the dry season or by collectors who so confine their own activities.

Males call mainly from elevated positions on low herbs, in bushes, low tree limbs etc., with calls being usually most frequent at dusk and then becoming sporadic. A heavy daytime rain is likely to cause intensified calling activity the same evening. Occasional calls heard on wet, dark days probably are made from concealment in leaf litter. The call is a variable series of harsh chirps that may be perceived to have a laughing-like quality (see

¹² There seems to be an ontogenetic component in observed variability in thigh pattern. Occasional individuals, mostly juveniles, have relatively small, poorly defined spots or speckling. In life, the rear thigh surfaces even appeared nearly uniform brown in one juvenile, although unpigmented flecking was evident under magnification (AMNH 107308, 21.5 mm. SVL).

¹³ Some of the recorded variation almost certainly owes itself to varying light quality under which color notes were made, particularly in forest camps. One note states that the rear-thigh spots were "yellowish green, but almost appearing light tan in some light."



MAP 6. Distribution of *Eleutherodactylus fitzingeri* in the eastern part of its range (Panama and Colombia).

audiospectrograms in fig. 11 and associated text under Vocalizations).

As noted under Vocalizations, collectors usually find that the call of *Eleutherodactylus fitzingeri* is tediously difficult to trace, which presumably may help reduce its vulnerability to sound-responsive predators generally. One sympatric predator known to hunt by sound is the fringe-lipped bat, *Trachops cirrhosus* (see Tuttle and Ryan, 1981). Charles O. Handley, Jr., Smithsonian Institution, recently found that *Trachops* preys naturally on *Eleutherodactylus fitzingeri*—thus confirming the applicability of Tuttle's striking photograph (frontispiece) showing a "trained" *Trachops* that had been directed to a specimen of *fitzingeri*. Handley (personal commun.) netted, on Barro Colorado Island, a

specimen of *Trachops cirrhosus* that was carrying a male *E. fitzingeri*.

Eleutherodactylus fitzingeri tends its eggs as do some other species of the genus. Dunn (1931b, p. 411) recounted the experience of Loomis and Shannon who found a specimen "on June 6 sitting on 44 eggs under leaves on a hillside." These "were left until June 12, when both frog and eggs were collected." Dunn stated that the attendant frog was a male, but, if the measurement ("51 mm.") given is that of snout-to-vent length, the frog would certainly have been a female.

DISTRIBUTION: *Eleutherodactylus fitzingeri* occurs in humid lowland and lower montane forest (0–1200 m.) from eastern Nicaragua south and east throughout both Atlantic and Pacific versants of Costa Rica and Panama,

and into northwestern Colombia. In Colombia, *E. fitzingeri* occurs in the inter-Andean valleys and in the Chocoan lowlands as far south as the Bay of Buenaventura (map 6; see Savage [1974, p. 297] for map of distribution in Costa Rica).

REMARKS: *Hylodes fitzingeri* O. Schmidt (1857, 1858) is one of the earliest names now assigned to a valid species of *Eleutherodactylus*. Accordingly, its first descriptions (see fn. 11), although doubtless considered adequate for the times, were so brief as to be of little or no subsequent use. Boulenger (1882) failed for some reason even to include the name in his *Catalogue of Batrachia Salientia*,¹⁴ and it is listed as a *nomen dubium* in Neiden's catalogue (1923, p. 467). Authors as recent as Taylor (1952, p. 739) and Cochran and Goin (1970, p. 386) have evidently considered *fitzingeri* too poorly described to justify positive identification of the name. Indeed, except for indicating the approximate degree of toe webbing (see fn. 11), Schmidt's descriptions do not mention the characters of greatest diagnostic value. However, as discussed by Savage (1974), the holotype was examined (before its loss) by Dunn (1931a, p. 387), who applied the name to many museum specimens of a common lower Central American frog. Dunn unfortunately did not discuss the holotype specifically, although one might assume from another context (*op. cit.*, p. 386) that it probably had important "*fitzingeri* characters" such as "the throat mark, the wartiness, [and] the spotting on the hind side of the thigh." Dunn's unpublished manuscript notes are in the possession of Savage (1974, p. 291), who indicated that the

notes are consistent with Dunn's identifications. Savage (*op. cit.*) argued that Dunn distinguished *E. fitzingeri* without confusing it with similarly webbed species or with some nearly webless species for which it might be mistaken. Therefore, in order to establish stability based on Dunn's usage, Savage (1974, p. 296) designated a neotype to replace the lost holotype of *fitzingeri*.

Contrary to Savage's assertions, however, Dunn did confuse *fitzingeri* with *E. raniformis*, although Dunn had examined the types of that name also. It was Dunn who identified the large mixed series of Panamanian *raniformis* and *fitzingeri* that was reported under the latter name by Breder (1946, pp. 404–405), as shown by Breder's acknowledgment (p. 381) and by bottle notes and correspondence at the American Museum. In the case of specimens from west of the range of *raniformis*, however, we agree that Dunn seemed consistently to apply the name *fitzingeri* to a single species, and Savage's neotype locality (Barro Colorado Island) in central Panama is fortunately a bit outside the known range of *raniformis* (compare maps 6 and 8). Unfortunately, however, the locality designation creates another problem in that it contravenes one of the qualifying conditions which must be met if a neotype is to be considered "validly designated" under generally accepted rules of nomenclature. Article 75c(5) (Internatl. Comm. Zool. Nomenclature, 1964) requires "evidence that the neotype came as nearly as practicable from the original type-locality."

After admitting that "it seems almost certain that the holotype was from western Panama," Savage (1974, p. 297) gave several commonsense albeit nomenclaturally irrelevant reasons for designating a specimen collected by Dressler and Savage in central Panama. Savage (*loc. cit.*) contradicted his own findings in stating that, "The type locality for *fitzingeri* is sufficiently vague (mountains of New Grenada) and the altitude (915 m) is, as I (1970) have shown, erroneously high . . ." In his own 1970 paper just cited, Savage (on p. 277) claimed with some justification that the itinerary of Josef Warszewicz (who collected the holotype) "may be traced with some accuracy" and presented a map showing the general route traveled by War-

¹⁴ Boulenger claimed in the preface (p. iii) to have included "descriptions of, or references to, all the species introduced into the literature," including those "known from imperfect descriptions only." According to Boulenger (*loc. cit.*), an earlier edition of the *Catalogue* (Günther, 1858) had not been so thorough and had excluded the latter group of names. But Boulenger's treatment of the frog names published by Oskar Schmidt belies his claim for completeness. Whereas such species as *Bufo simus* and *Dendrobates lugubris* are included on the authority of Schmidt's 1858 paper, others such as *Dendrobates pumilio* (from the same page as *D. lugubris*), *D. speciosus*, and *Hylodes fitzingeri* are missing in Boulenger's edition of the *Catalogue*—although included in Günther's first edition.

szewicz across western Panama. Furthermore, the "915 m." elevation is Savage's (1970, p. 278) own corrected elevation for the type locality of *fitzingeri*,¹⁵ and it is well within the 0–1100 m. elevational range given by Savage himself (1974, p. 299). Although *fitzingeri* does not seem to be particularly abundant in western Panama, there were museum specimens so identified from elevations of 1–1200 m., at localities not far from Warszewicz's route on both the Atlantic and Pacific versants.

Inasmuch as the original description is poor, and because Dunn did not see reason to publish a redescription of the now-lost holotype (nor did Savage mention the existence of a description in Dunn's manuscript notes), there might always be some doubt that the name has been correctly applied. Nonetheless, like Savage, we are content to follow Dunn's authority in using the name *fitzingeri* (at least for the present time, and excluding the aforementioned confusion with *raniformis*). We do not, however, see that this is a case where "exceptional circumstances" make a neotype "essential for solving a complex zoological problem" (another requirement of art. 75, *vide supra*), much less one that is purposely in violation of the type locality rule. We are obliged to judge the designation as being invalid and not binding on later workers.¹⁶

The invalid neotype of *Hylodes fitzingeri* also was designated by Savage (1974, p. 298) as the common neotype of *Craugastor pul-*

chrigulus Cope (from Colombia), *Hyla grisea* Hallowell (Nicaragua), and *Leiyla Güntherii* Keferstein (Costa Rica). Savage's presentation that all are synonyms of *Eleutherodactylus fitzingeri* seems correct in light of current knowledge, but the imperious use of a common neotype to prevent application of the names to currently unrecognized species or subspecies *must* be rejected by any worker trying to adhere to the provisions and spirit of the *International Code*, of which Article 75 is among the most clearly written and easily understood sections. The aforesaid designations are not admitted under 75a, they are excluded under 75b, and they fail to qualify under 75c(5).

Noble (1924) misapplied the name *E. longirostris* to Panamanian specimens of *E. fitzingeri*. Although Dunn (1931a, 1931b [in key]) later indicated the differences between *Eleutherodactylus fitzingeri* and *E. "longirostris"* (*crassidigitus*), Cochran and Goin (1970) failed to grasp the distinction and included specimens of *fitzingeri* under the name *longirostris*. Cochran and Goin also included specimens of *fitzingeri* under the name *E. raniformis*, whereas authors reporting *fitzingeri* from eastern Panama have included specimens of *raniformis* (Breder, 1946; Heatwole and Sexton, 1966). All these species are locally common frogs that must be ecologically significant as prey, predators, and niche competitors.

Eleutherodactylus longirostris
(Boulenger)

Figures 6E, 7D, 18A, 23–25, 26C; Map 7

Hylodes longirostris Boulenger, 1898, p. 120, pl. 15, fig. 1 (syntypes, BMNH 98.4.28.101–98.4.28.105 [reregistered as 1947.2.15.56–1947.2.15.60], collected at Cachabé [=Cachabí, see fn. 5], Prov. Esmeraldas, Ecuador, by Mr. W. F. H. Rosenberg).

DIAGNOSIS: A moderate-sized species (adult males 27.3–39.2 mm. SVL, adult females 43.1–59.6 mm. SVL) of the *fitzingeri* group; skin of dorsum smooth or finely shagreened, with occasional low warts and thin, low ridges outlining dark marks in scapular region; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid as wide as IOD, smooth or bearing flat, nonpungent warts;

¹⁵ Corrected from 4000 feet (nineteenth-century Polish feet equaling 9 inches each) to 3000 ft. = 915 m. *vide* Savage (*op. cit.*).

¹⁶ Savage (1974, p. 298) expressed fear of "nomenclatural mischief" if future taxonomists were not severely restrained in their choices for the application of old names, whereas we are more concerned lest today's notion of stability becomes tomorrow's paradox. In the present case, for example, suppose that a nonmischievous biologist were to discover the existence of sibling species, with the montane frogs from near the type locality of *fitzingeri* being a different species than lowland frogs at the "neotype" locality. Would true *fitzingeri* then have to be the species to be given a new name? The intent of the "International Code" is that a neotype should be designated *only as needed* to solve a particular zoological problem. It is *not* a mechanism by which a subsequent user of a name may ensure the stability of his own concept just in case a problem *might* be discovered.

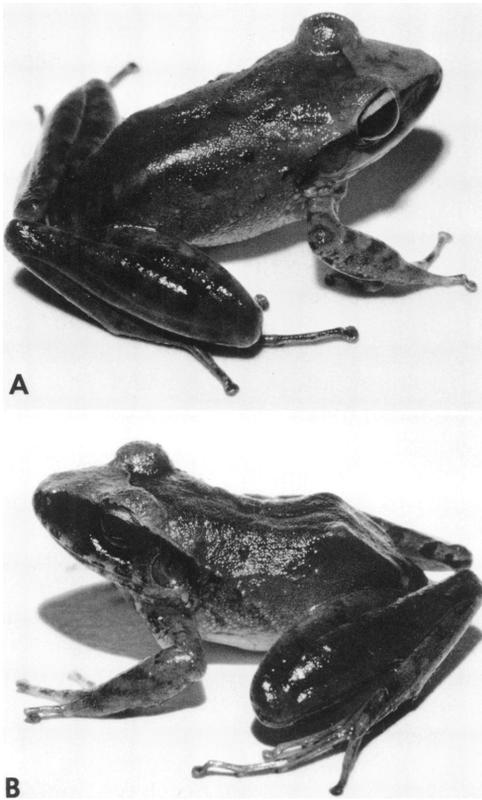


FIG. 23. *Eleutherodactylus longirostris* from western Colombia. A. Quebrada Vicordó, about 5 km. above Noanamá on middle Río San Juan, 80–110 m., Chocó (AMNH 87064). B. North slope Alto del Buey, 800–1000 m., Serranía de Baudó, Chocó (AMNH 102074; see also fig. 24D).

tympanum prominent, its length one-half to three-fourths of eye length in males, two-fifths to three-fifths of eye length in females; snout of moderate length, E–N \geq eye length; vomerine odontophores separated on midline by space equal to one-third to two-thirds of odontophore width; males with vocal slits and with subgular vocal sac not usually evident externally; HW 32.7–41.2 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers I and II round, those on fingers III and IV truncate; adult males bearing nonspinous nuptial pads on thumb; toes bearing expanded discs; toes moderately webbed (web encompasses basal subarticular tubercles of all toes, but

not the more distal tubercles); modal webbing formula I 2⁻–2 II 2⁻–3 III 2½–4⁻ IV 4–2½ V; lateral fringes on unwebbed portions of toes; inner tarsal fold on distal two-thirds of tarsus; no calcar on heel; in preservative, dorsum reddish tan to dark brown, usually with darker brown hourglass-shaped mark (only rarely with a broad yellow middorsal raphe); occasional specimens with one to several closely spaced dark chevrons on rear of body behind the hourglass mark; posterior surfaces of thighs brown; groin tan or brown, not mottled; venter cream or white; throat usually cream, with dark spots and/or stripes extending onto upper chest (chest markings sometimes absent); throat sometimes pigmented uniformly brown or with a faint, median white stripe; undersides of limbs white, with some lateral invasion of brown or tan.

Eleutherodactylus longirostris has about the same amount of toe webbing as sympatric *E. fitzingeri* and *E. raniformis*, as well as allopatric *E. andi* and *E. malkini*, but is readily distinguished from these species by coloration of the posterior surfaces of the thighs—virtually uniform brown in *longirostris*, but with pale spots, speckling, or marbling in the others. *Eleutherodactylus longirostris* is most easily confused with *E. crassidigitus* and *E. talamancae*, two Central American species whose ranges approach that of *E. longirostris* and which also have the posterior thigh surfaces uniformly brown.

Eleutherodactylus longirostris is similar in general appearance to *E. crassidigitus*, which, however, is a smaller species (table 1) with more toe webbing (fig. 18). In *longirostris*, the web on the lateral side of toe III fails to reach the distal subarticular tubercle, often ending closer to the proximal tubercle, whereas in adult *crassidigitus* the web usually reaches and often includes the distal subarticular tubercle. *Eleutherodactylus longirostris* often has distinctive dark throat and chest markings (figs. 6E, 24), which are not present in *crassidigitus*; a middorsal light stripe is very rare in *longirostris* but occurs as a variant in many populations of *crassidigitus*.

Eleutherodactylus longirostris is similar to some adult specimens of *E. talamancae*, which, however, undergoes a distinctive ontogenetic change in color pattern. In juvenile and adult *longirostris* and some adult *tala-*

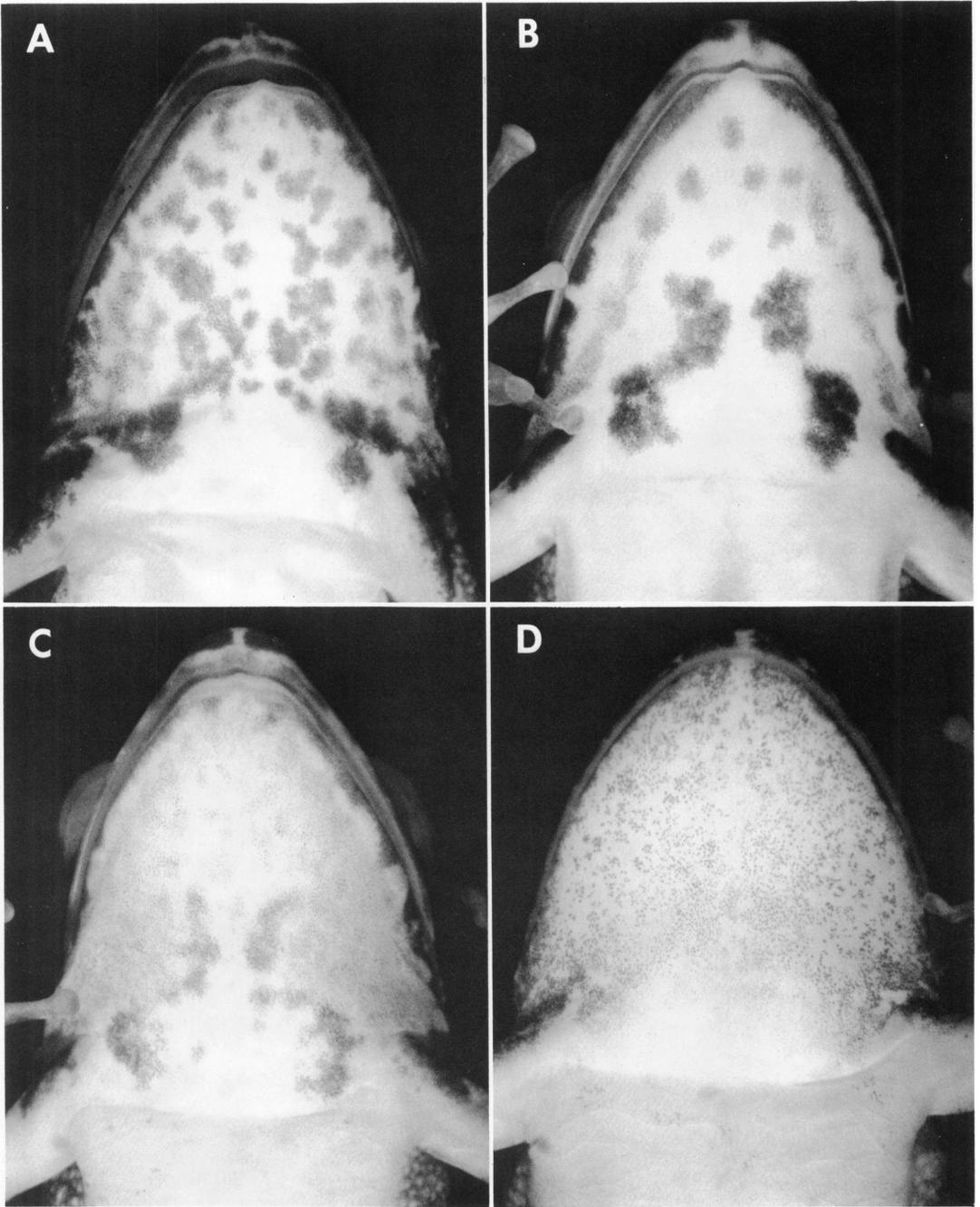


FIG. 24. Intra- and interpopulational variation in throat pigmentation of *Eleutherodactylus longirostris*. A–C. Specimens from Quebrada Guanguí, 100 m., Cauca, Colombia (AMNH 88369, 88963, 88964, respectively; see fig. 6E for another specimen). D. North slope Alto del Buey, 800–1000 m., Serranía de Baudó, Chocó, Colombia (AMNH 102074; see also fig. 23B).

mancae, the basic pattern on the upper lip is one of alternating dark and lighter bars

(sometimes obscured by a dark suffusion), whereas juvenile *talamancae* have a con-

spicuous white labial stripe. Juvenile *talamancae* also have a white ventrolateral line and/or one or two oblique whitish lines (often vague) on the flank, and, in some populations, there is a conspicuous white line from the groin to above the eye (causing such juveniles to resemble some species of *Colostethus*). Some indication of the white labial and lateral lines is retained in some adult *talamancae*, especially in central Panama. *Eleutherodactylus talamancae* has less toe webbing than *longirostris*, but, pending an analysis of variation of this character in *talamancae*, we hesitate to recommend it for identifying single specimens. *Eleutherodactylus longirostris* apparently is distinguishable from *talamancae* by the presence of a distinct inner tarsal fold, which is absent or poorly developed in *talamancae*. Ontogenetic series should be collected when possible, otherwise some specimens of *talamancae* are helpfully allocated by geography, since the two species are allopatric so far as known (see also Remarks and map 7).

DESCRIPTIONS: Boulenger's (1898) original description and illustration of one of the Ecuadorian types remain useful. Cochran and Goin (1970, p. 384, pl. 47D-F) illustrated and described a Colombian specimen in some detail, but, unfortunately, their discussion and list of specimens confuse at least five other species with *longirostris*.

COLOR IN LIFE: *Eleutherodactylus longirostris* is usually some shade of light to dark brown, with darker brown or blackish brown markings, including a dark hourglass mark (faint to conspicuous) and, in some specimens, one to several closely spaced dark chevrons on the rear of the body. A specimen from the Serranía de Pirre in eastern Panama (KU 114635) was unusual in having a pale tan vertebral stripe (a common variant in some other species but rare in *longirostris*). One of several specimens from the Cordillera de Juradó in southeastern Panama (KU 114631) was unusual in that the top of the head and body was covered by a heavy suffusion of dark green pigment, with this color extending somewhat less heavily over the upper surfaces of the hind limbs; sides of the body were grayish brown. (The green color of this individual was photographically elu-

sive, as already noted under *E. caprifer*; see fn. 7.)

The lips are barred in dark and lighter brown or tan. The throat color varies from basically white or gray to pale green, sometimes with a uniform overlay of light to dark brown speckling, but often with irregular gray or brown spots or mottling; a median pale stripe on the throat is usually absent or only very faintly indicated. Commonly there is a pair of especially dark brown spots or short lines on the base of the throat, and a similar but more widely separated pair of spots on the chest (figs. 6E, 24). The venter varies from white to pale yellow or bright greenish yellow. The undersides of the hind limbs may be uniformly pale green or greenish yellow, but, from Panama to Ecuador, specimens more commonly have a suffusion of orange under the legs.

The rear of the thigh occasionally is pure brown in life, but normally there is a weak to strong suffusion of orange or orangish red on the rear of the thigh—this color being conspicuous by day albeit not obvious by flashlight at night.

The iris of *Eleutherodactylus longirostris* is pale bronze, pale bronzy or pinkish tan, or pale gold, with a narrow to broad brown or reddish brown horizontal stripe or butterfly-shaped mark through the pupil. Probably as a result of ontogenetic change, the lower part of the iris may be darkened by a suffusion of brown, reddish brown, or black, which tends to obscure at least the lower edge of the aforesaid stripe.

ECOLOGICAL NOTES: *Eleutherodactylus longirostris* is usually found on the ground or in low vegetation at night, or concealed in leaf litter by day, but little else is known except that it inhabits a variety of forest types. At the northern end of the range, in extreme eastern Panama (map 7), it has been found only in lowland hill forest (evergreen seasonal forest) and adjacent cloud forest in an elevational range of 320–1100 m. Although a few Colombian specimens have been found in swamp forest (210 m. near Playa de Oro, upper Río San Juan, Chocó) and in second-growth riverside vegetation (e.g., 100 m. at Quebrada Guanguí, Cauca), it seems most common in relatively well-drained rain forest

along the Andean foothills and in the isolated Serranía de Baudó. *Eleutherodactylus longirostris* is principally a frog of the deep forest in Panama and Colombia, but in somewhat drier forests in Ecuador it was found mainly along streams. The presumably relictual populations in the inter-Andean Río Magdalena drainage (map 7) are probably confined to relatively dry gallery forest.

DISTRIBUTION: *Eleutherodactylus longirostris* occurs contiguously from the Darién highlands of extreme eastern Panama, south throughout western Colombia to southern Guayas Province, Ecuador—in humid forest below 1200 m. elevation. In addition, there is a disjunct inter-Andean population (or populations) well to the east, in the middle and upper drainage of the Río Magdalena (map 7). We are unaware of specimens from the intervening valley of the Río Cauca.

REMARKS: Noble (1924) used the name *Eleutherodactylus longirostris* for Panamanian specimens of *E. fitzingeri*. As noted by Savage (1974, p. 293), Cochran and Goin (1970, p. 387) included Nicaraguan, Costa Rican, and Panamanian specimens of *E. fitzingeri* among specimens reported as *E. "longirostris."* Only eight of the 214 specimens they reported from Colombia are assignable to *E. fitzingeri*, although specimens of *E. achatinus*, *E. raniformis*, *E. w-nigrum*, and a species of the *unistrigatus* group also are misidentified in their list of specimens. Of the specimens reported as *E. longirostris*, 58 percent are correctly identified and 20 percent are *E. w-nigrum*. Cochran and Goin's (*op. cit.*, pp. 385–386) discussion of variation reflects the confusion of at least six species. Boulenger (1913) misapplied the name *Hylodes palmatus* to Chocó specimens of *E. longirostris*.

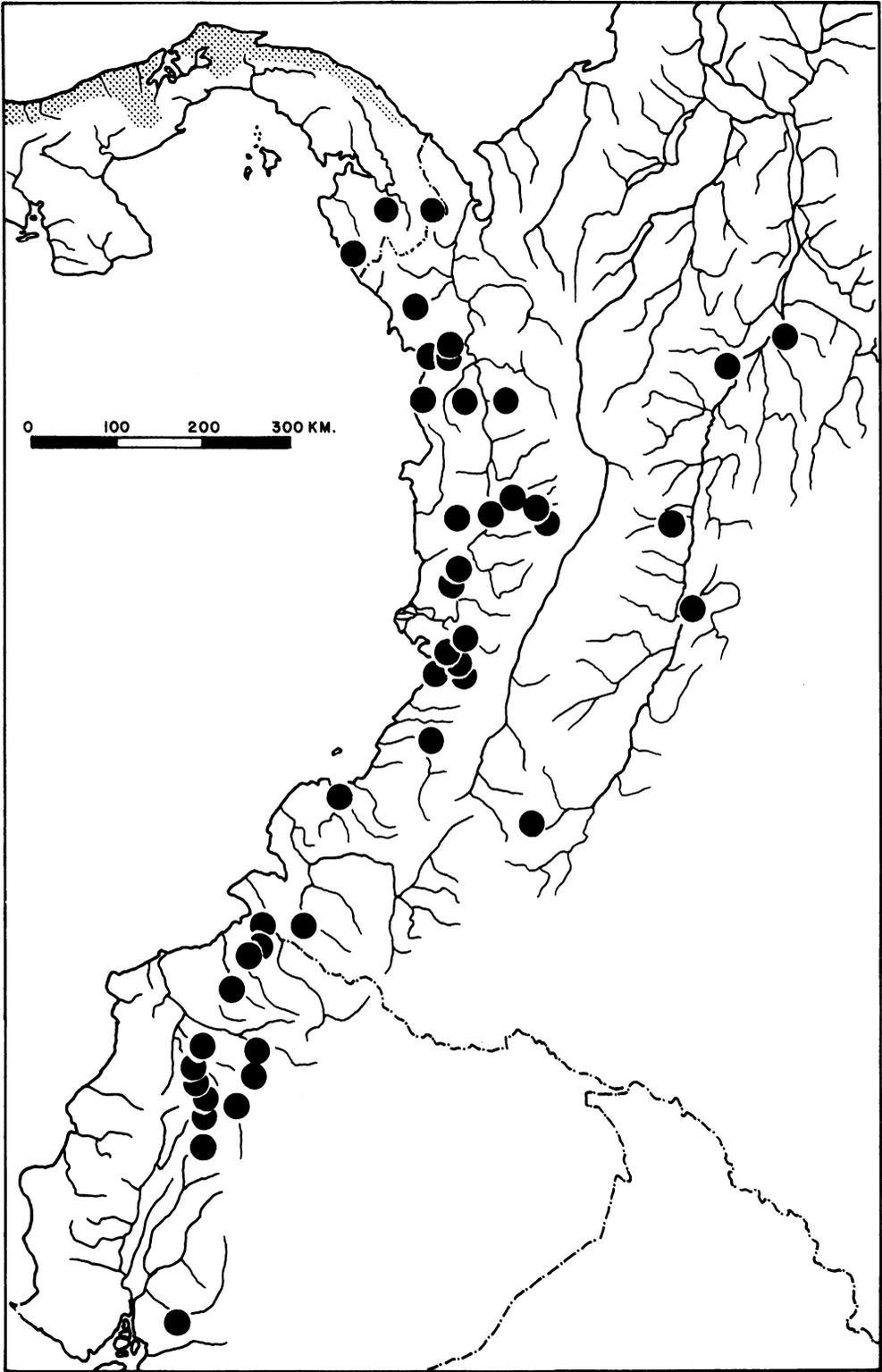
In addition to misidentifications of *Eleutherodactylus fitzingeri* (see above), *Eleutherodactylus longirostris* also has been erroneously reported from Costa Rica by Dunn (1931a) and Savage (1980), and wrongly mentioned or recorded from Panama by Duellman (1967), Dunn (1931a, 1931b, 1933), Goin (1959), Heatwole and Sexton (1966), Myers (1969), Myers and Rand (1969), Savage (1974, 1975), Schmidt (1933), and Toft (1981). *Eleutherodactylus longiros-*

tris barely gets into Panama, and the only Panamanian specimens known to us were collected by the junior author in the years 1966–1967 and 1975; these specimens (e.g., fig. 25) have not been previously reported and provide the first bona fide records for the country. The authors just cited have used the name *longirostris* for specimens of *E. crassidigitus*, which was described from Costa Rica 30 years ago (Taylor, 1952).

Eleutherodactylus crassidigitus has a much broader range than previously realized, but, despite our account in this paper, its variation remains inadequately studied. It has been confused with *longirostris* because of a general resemblance in habitus and color, including the uniformly brown (usually orangish or reddish in life) posterior surfaces of the thighs. As already stated, *crassidigitus* is smaller and has more extensively webbed toes than *longirostris*. The ranges of the two species seem to overlap slightly, although sympatry has not been documented (compare maps 5 and 7).

Notwithstanding the close resemblance and previous confusion between *E. longirostris* and *E. crassidigitus*, we suggest that the sister species of *longirostris* is more likely another Central American frog, namely *E. talamancae* Dunn (1931a). Occasional adult *talamancae* from western Panama are very similar to *longirostris* in color pattern, but, even though its variation remains to be assessed in detail, *E. talamancae* seems to be a distinct species. It undergoes an ontogenetic color change quite different from *longirostris* (see Diagnosis), and many adult *talamancae* from the eastern part of its range (approaching that of *longirostris*, see map 7) are readily identified because of a tendency to retain aspects of the juvenile pattern.

Two features of color pattern that occur in the variational repertory of both *E. longirostris* and *E. talamancae* seem especially pertinent to an assessment of relationship: (1) A few western Panamanian specimens tentatively assigned to *talamancae* have, on the throat and chest, two pairs of dark markings that conform in appearance and position to those possessed by some individuals in most if not all populations of *longirostris* (figs. 6E, 24); (2) Some individuals of each species have



MAP 7. Distribution of *Eleutherodactylus longirostris* (eastern Panama to southern Ecuador). Shaded pattern in Panama indicates approximate distribution of a related species, *Eleutherodactylus talamancae*, at the eastern end of its range.

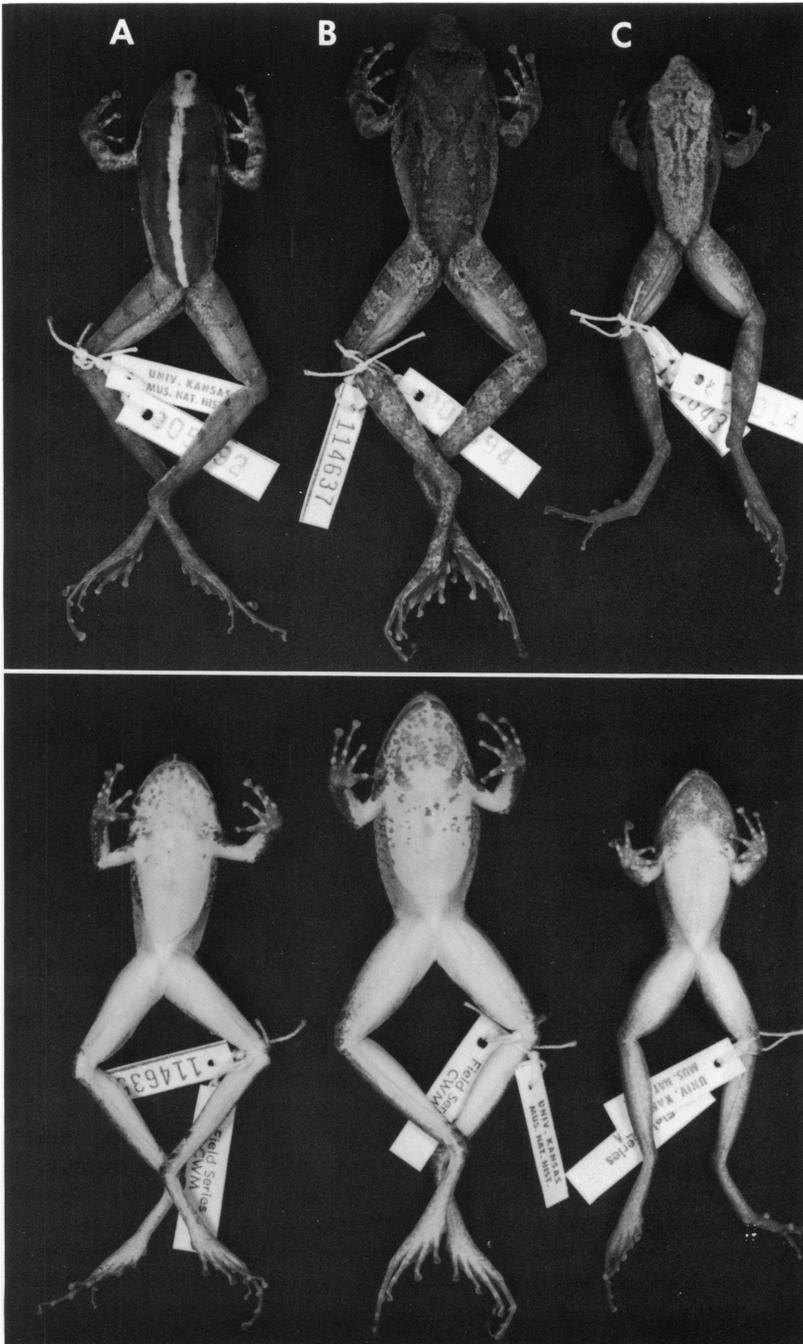


FIG. 25. Variation in *Eleutherodactylus longirostris* at the northern end of its range in Darién Province, eastern Panama. A, B. Extreme north end Serranía de Pirre 500 m. (KU 114635, 114637, respectively). C. North ridge Cerro Cituro, 1100 m., atop northern end Serranía de Pirre (KU 114643).

Dorsal color pattern of middle specimen (B) is essentially normal throughout the range of *E. longirostris*, whereas A and C represent color morphs that appear to be absent in most populations.

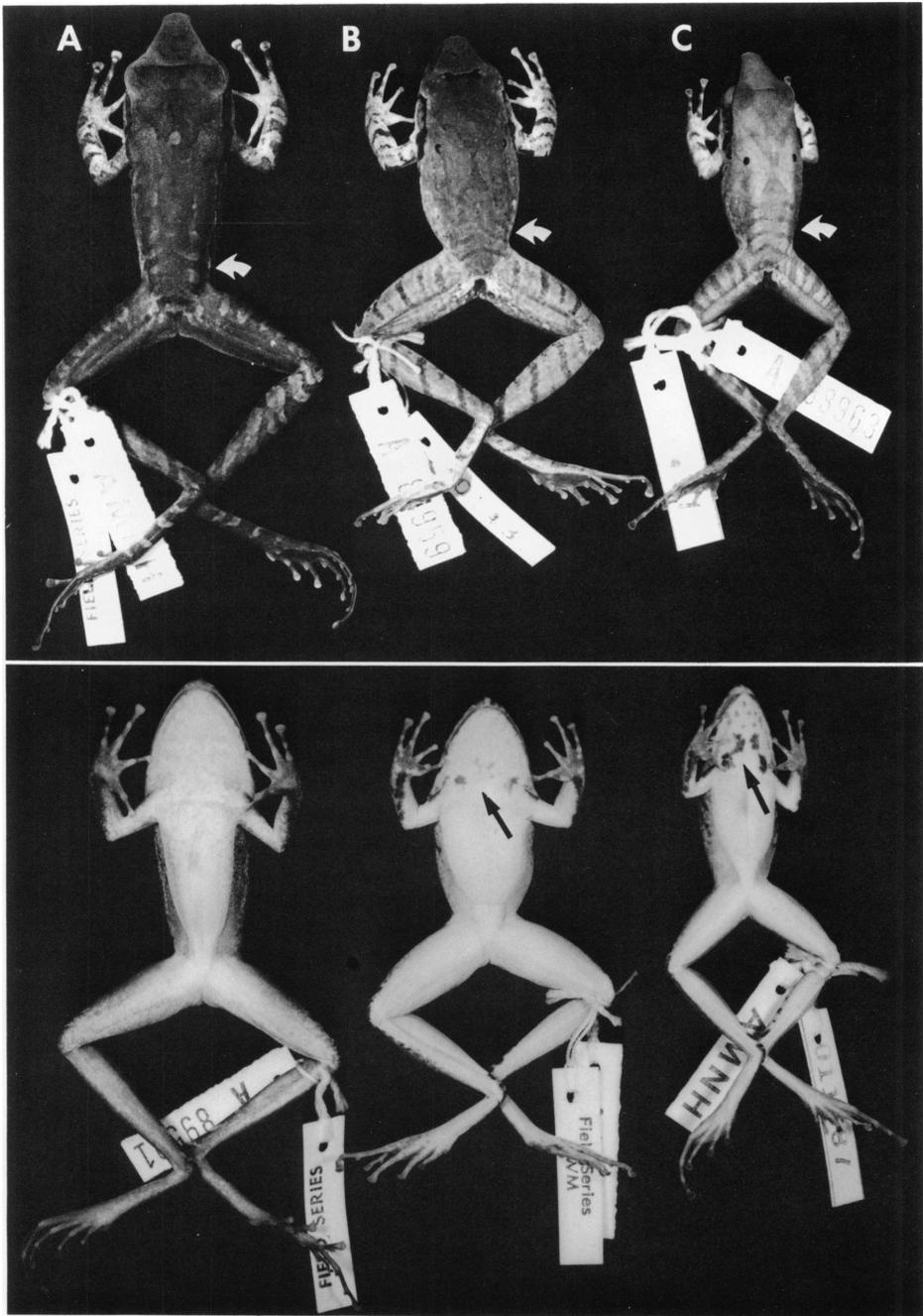


FIG. 26. Pattern similarities (arrows) between certain specimens of *Eleutherodactylus talamancae* (A, B) and *Eleutherodactylus longirostris* (C). A. *E. talamancae* (AMNH 89501, El Llano–Cartí Road, 290 m., Panamá Prov., central Panamá). B. *E. talamancae*? (AMNH 84959, near Almirante [=type locality of *E. talamancae* Dunn], 30–40 m., Bocas del Toro, western Panamá). C. *E. longirostris* (AMNH 88963, Quebrada Guanguí, 100 m., Cauca, Colombia).

closely spaced dark chevrons (fig. 26) on the rear of the body. Pending closer study of *E. talamancae*, but assuming that it is correctly diagnosed, we suggest that these markings are synapomorphies that show a sister-group relationship between the two species. With its greater degree of webbing, *E. crassidigitus* may in turn stand as the sister species of *longirostris* + *talamancae*.

Eleutherodactylus raniformis
(Boulenger)

Figures 4, 6C, D, 7B, 27–29; Map 8

Hylodes raniformis Boulenger, 1896, p. 19 (syn-types, BMNH 95.11.16.48–95.11.16.51 [re-registered as 1947.2.16.16–1947.2.16.19], collected at Buenaventura, Depto. Valle del Cauca, Colombia, and BMNH 95.11.16.52–95.11.16.53 [re-registered as 1947.2.15.83–1947.2.15.84], collected at Cali, Depto. Valle del Cauca, Colombia, by W. F. H. Rosenberg). Lectotype by present designation BMNH 1947.2.16.16, adult ♀ 68 mm. SVL (see fig. 29).

DIAGNOSIS: A large species (adult males 27.2–43.2 mm. SVL [smaller on the Pearl Islands of Panama], and adult females [except those from Pearl Islands] 52.0–74.0 mm. SVL) of the *fitzingeri* group; skin of dorsum smooth with occasional low warts and short, low ridges; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid wider than IOD, bearing nonpungent tubercles; tympanum prominent, its length one-half to three-fourths of eye length in males, two-fifths to three-fifths in females; snout of moderate length, E–N \cong eye length; vomerine odontophores separated on midline by space equal to one-third to one-half of odontophore width; males with vocal slits and with subgular vocal sac usually not evident externally; HW 34.7–39.0 percent SVL; finger discs moderately expanded, discs on fingers III and IV narrower than length of inner metatarsal tubercle; discs on fingers I and II round, those on fingers III and IV truncate; adult males bearing nonspinous nuptial pads on thumb; toes bearing expanded discs; toes moderately webbed (web encompasses basal subarticular tubercles of all toes but not the more distal tubercles); modal webbing formula I 2⁻–2⁺ II 2⁻–3 III 2^{2/3}–4⁻ IV 4–2⁺ V; lateral fringes

on unwebbed portions of toes; inner tarsal fold on distal two-thirds of tarsus; no calcar on heel; in preservative, dorsum tan to dark brown, usually with dark brown to black markings (see Color in Life), occasionally with a broad middorsal pale stripe; posterior surfaces of thighs brown with many small cream flecks or larger, poorly defined and crowded spots; groin mottled; pale venter immaculate or with some dark flecking; throat white to cream, finely to heavily peppered with brown, with melanophores normally present across entire throat¹⁷; undersides of limbs white, sometimes with weak mottling of dull gray.

Eleutherodactylus raniformis is most likely to be confused with sympatric *E. fitzingeri* and *E. longirostris*, somewhat smaller species that have virtually the same degree of toe webbing as *raniformis*. *E. raniformis* is most easily separated from *fitzingeri* by the absence of a median white gular stripe (cf., fig. 6A–D; see also fns. 9 and 17 regarding variation in this character), and by pale markings on the rear of the thigh that are denser, less well demarcated, and often smaller than those in adult and many juvenile *fitzingeri* (cf., fig. 7A, B). The color of the posterior thigh spots in life is diagnostic—they are tan in *raniformis* but usually a brighter greenish yellow in sympatric populations of *fitzingeri*. *E. raniformis* attains a larger size (table 1), and it usually has smoother skin on the upper eyelid and back, fainter labial stripes, and a more uniformly colored dorsum than *fitzingeri*; the lower part of the iris tends to be dark in adult *raniformis*, pale in immature *raniformis* and in all *fitzingeri*.

Eleutherodactylus raniformis is distinguished readily from the smaller *longirostris* by the pale markings on the rear of the thigh

¹⁷ Occasional specimens of *E. raniformis* have reduced pigmentation on the midline of the throat, but only rarely does this give the appearance of a very faint, ill-defined gular stripe (e.g., AMNH 40803, 40810, 88513). This unusual condition approaches the abnormally faint and disrupted gular stripes in occasional *E. fitzingeri* (see fn. 9).

An even rarer condition in *raniformis* is the presence of a well-defined median gular line (thinner than the stripe in *fitzingeri*), as in AMNH 98420 and USNM 120366 from Isla de San José in the Pearl Islands.

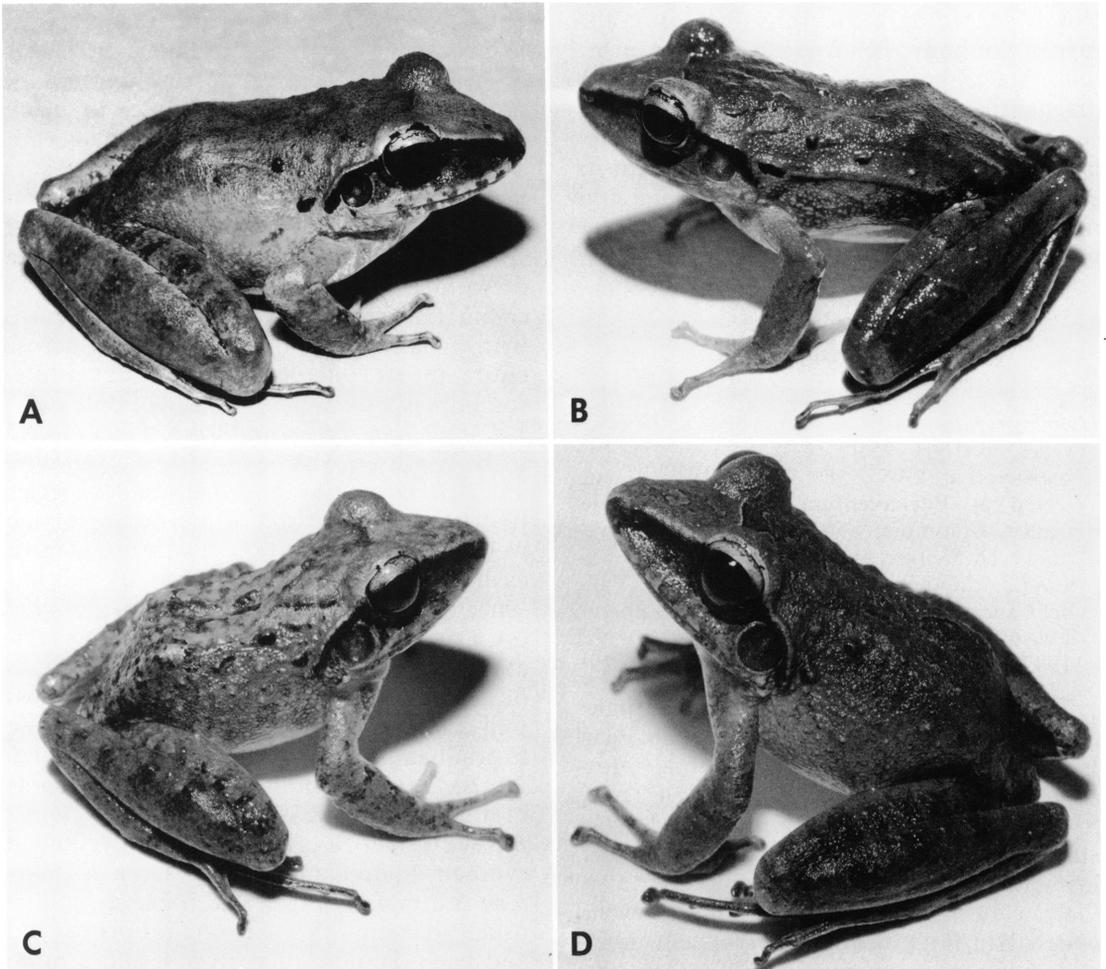


FIG. 27. *Eleutherodactylus raniformis* from a variety of habitats (not to scale). A. Camp Sasardí, 12 m., San Blas, Atlantic coast of Panama (KU 114559). B. Isla de San José, Pearl Islands in Gulf of Panama, Pacific Ocean (AMNH 98420). C. 13 km. W Dagua, 850–1200 m. in Río Anchicayá drainage, Valle del Cauca, Colombia (AMNH 88508). D. Quebrada Vicordó, about 5 km. above Noanamá on middle Río San Juan, 80–110 m., Chocó, Colombia (AMNH 87101).

(uniformly pigmented in *longirostris*). The northernmost populations of *raniformis* are sympatric with the smaller *E. crassidigitus*, which differs in having the rear of the thigh uniformly pigmented as in *longirostris*, and in having more webbing than either *raniformis* or *longirostris*.

DESCRIPTION: Cochran and Goin's (1970, pp. 382–383) description and illustrations of a single Colombian specimen are adequate, but their discussion of variation and list of specimens should be disregarded (being based on at least seven species, see Remarks).

COLOR IN LIFE: The ground color of body and limbs varies from brown to orange-brown among individual *Eleutherodactylus raniformis* collected in the same place at the same time. Usually there are a few small dorsolateral and post-tympanic black spots, and often some dorsal markings of a darker brown than the ground color. When present, the usually vague dorsal pattern normally includes an interocular bar and a W-shaped scapular mark, which are sometimes interconnected to form a butterfly figure. Occasional individuals have a conspicuous middorsal stripe

(fig. 28) of a hue paler than the general ground color, such stripes usually being tan or orangish tan according to notes taken (in daylight) at times of preservation. At least the middorsal stripe, when present, is capable of metachromatism, having been observed in one Panamanian population (Sasardí, San Blas) to change from reddish orange at night to light tan by day.

The throat is white, varying from nearly immaculate to lightly suffused with gray. Any melanophores present are usually rather evenly distributed across the throat, but in some populations there is clumping of pigment, giving a dusky mottled appearance to the throats of many individuals. The white of the throat may extend onto the chest, but otherwise the venter is a usually pale yellow. The undersides of the hind limbs are pale green or pale yellow.

The pale flecks or small spots on the rear of the thighs are characteristically "tan" or "pale brown," based on field notes for about 90 specimens from over a dozen localities in eastern Panama and northwestern Colombia. Only a single Panamanian specimen—preserved in poor light—was described as having "yellowish" spots. The pale markings are set in a dark ground color which seems subject to interpopulational variation: The ground color of the posterior thigh surface was noted as *black* in a population sample from the Caribbean coast of Panama (Sasardí), but *brown* or *dark brown* in samples from throughout the Pacific drainage of eastern Panama and in a specimen from the Pearl Islands. Frogs from the lower slopes (~230–900 m.) of the western Andes had *grayish brown* thighs (at Tabor, Chocó, and Anchicayá drainage, Valle).

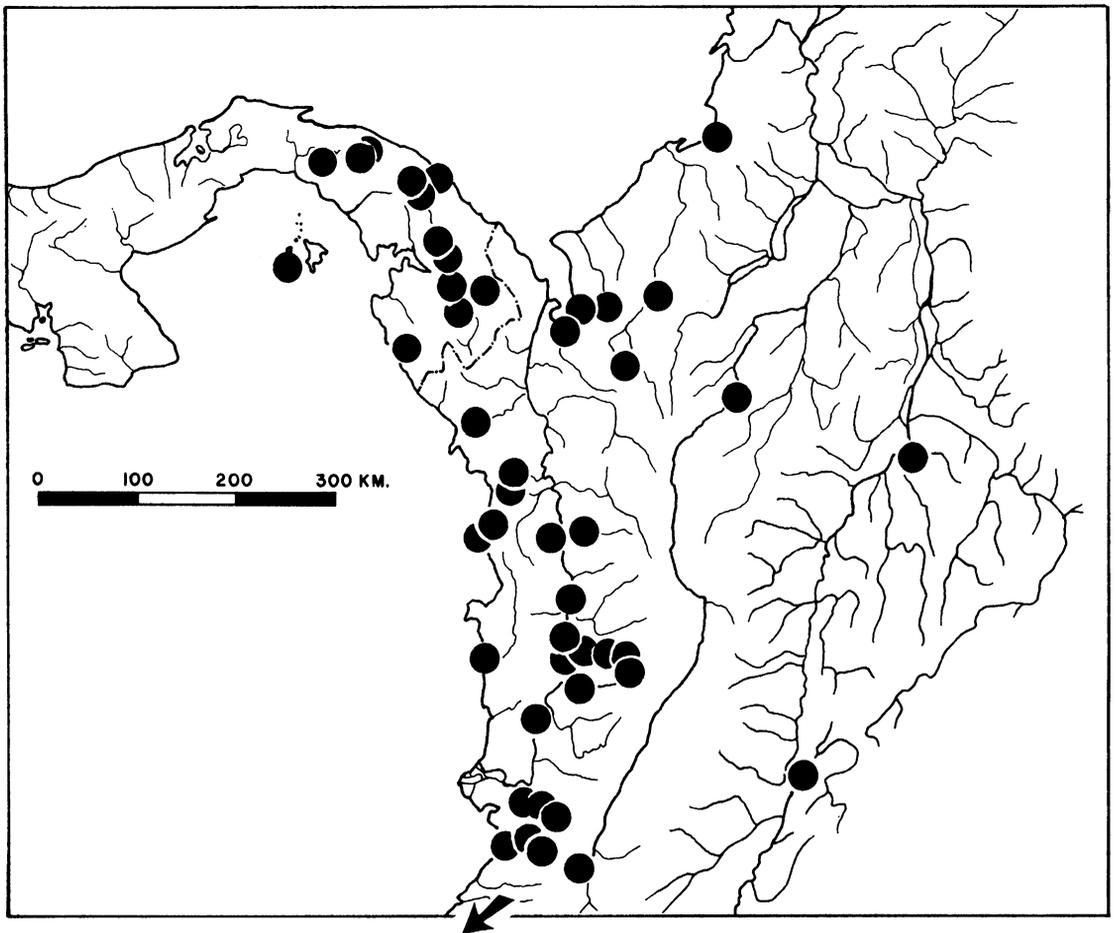
The iris of *Eleutherodactylus raniformis* is usually pale gold or golden bronze (rarely pale tan or gray) above the pupil and some shade of gray or brown below the pupil, which is often set in a brown or red-brown horizontal stripe. The upper edge of said stripe seems always sharply defined against the clear, pale upper part of the iris, whereas the lower edge often blends into the usually darker color of the lower part of the iris—or the lower half of the eye may be uniformly dark without trace of a horizontal stripe. There might be some interpopulational variation in aspects



FIG. 28. *Eleutherodactylus raniformis* with median pale stripe, on bush at night at Camp Sasardí, 12 m., San Blas, Panama (February 1967). Striped morphs are relatively uncommon in this species (compare normal patterns in fig. 27).

of iris color (e.g., whether the stripe is brown or reddish), but a sufficiently large sample was examined from one population (Altos de Majé, Panama) to show that much variation is due to ontogenetic change: Individuals of all sizes in this population had the upper part of the iris clear, pale gold. Small specimens had a *light* brown horizontal stripe, the bottom edge of which was sharply defined against a light bronze or bronzy gray color. With increasing body size, a suffusion of brown pigmentation increasingly darkened the lower part of the eye, invading and obscuring the bottom of the horizontal stripe. This trend resulted, in the largest frogs, in a sharply bicolored eye, uniformly dark brown from the bottom of the iris to slightly above the pupil, and pale gold above that.

ECOLOGICAL NOTES: *Eleutherodactylus raniformis* occurs within mature forest as well as in forest-edge situations along streams and new clearings. It seems to attain higher densities in lowland evergreen seasonal forests



MAP 8. Distribution of *Eleutherodactylus raniformis* (eastern Panama and northwestern Colombia). Arrow indicates recently obtained records off map, lower Río Micay drainage, Depto. del Cauca (cited in Appendix).

(*Am* climate) than elsewhere; it is particularly common in parts of the odd cuipo forest (*Cavanillesia platanifolia* association [Myers, 1969, p. 7]) of lowland eastern Panama. By day, individuals are found on the forest floor concealed in leaf litter, from which they take long, low leaps when disturbed. They make little or no attempt to conceal themselves at night, when they are found openly sitting on the ground or climbing onto living or dead vegetation to heights of at least 2.5 m. above-ground. Males and juveniles seemingly are the most motivated climbers, with the larger-bodied females tending to stay on the ground. A male was found calling from a branch 2 m. up in a sapling; see figure 11C and asso-

ciated text under Vocalizations. C. M. Breder described the call (on field tag attached to AMNH 40741♂) as "ha,ha,ha,ha," a description that he (1946, pp. 416, 425) erroneously attributed to *Smilisca phaeota* some two decades after his fieldwork. Breder's published claims (pp. 404, 425) that he did not hear *E. raniformis* ("*fitzingeri*") were evidently a lapsus. He also tagged an adult female *raniformis* (AMNH 40621) with a note that "this frog called," presumably pertaining to a distress call.

DISTRIBUTION: *Eleutherodactylus raniformis* occurs south from east-central Panama to the Río San Juan de Micay in western Colombia, in the forested lowlands north and

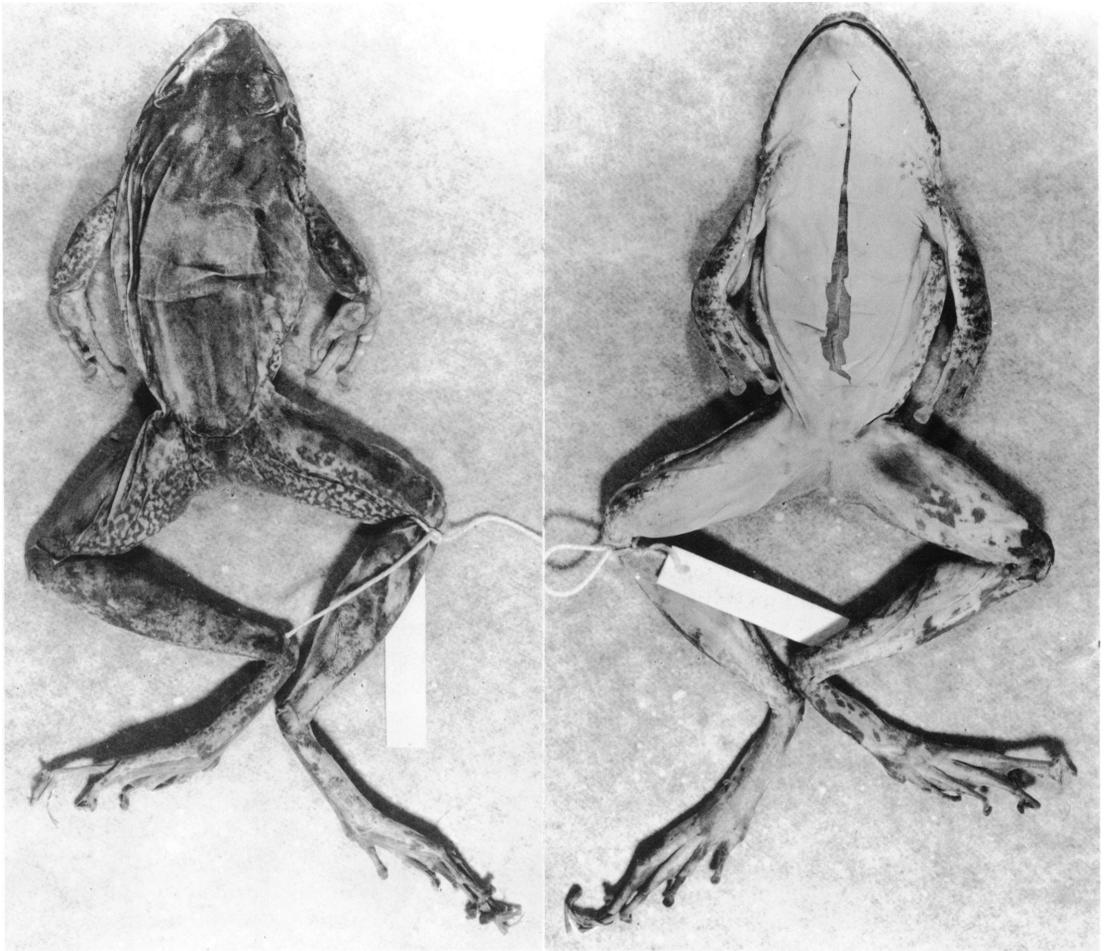


FIG. 29. Lectotype (by present designation) of *Hylodes raniformis* Boulenger, 1896. This specimen (BMNH 1947.2.16.16), from Buenaventura, Colombia, is the largest of the syntypes; it is an adult female 68 mm. from snout to vent (70 mm. in original description). Relatively large size, moderate webbing, lack of a distinctive throat pattern, and especially the rear-thigh pattern (cf., figs. 4, 7B) are among the important diagnostic features of *Eleutherodactylus raniformis* (Boulenger).

west of the Andes, and as possibly isolated populations in the inter-Andean valleys of the Río Cauca and Río Magdalena (map 8). The species is most commonly found in lowland forest but also has been collected as high as 1400 m. elevation in lower montane forest. It occurs also in the Pearl Islands (Isla de San José) in the Gulf of Panama.

REMARKS: Soon after its description to the present, *Eleutherodactylus raniformis* has been confused with other species. Judging from identifications of old specimens in the British Museum, Boulenger had no greater

success in distinguishing the species (named by him) from its relatives than have more recent authors. The type specimens came from Cali and Buenaventura, Colombia; because of the probable existence of sibling species in *Eleutherodactylus*, a single type locality for this wide-ranging species seems desirable. The specimen that we designate as lectotype (fig. 29) is from Buenaventura, thus associating the name *raniformis* most explicitly with the populations on the Pacific side of the Cordillera Occidental.

Confusion involving Colombian material

was mainly limited to incorrect identification of specimens in various museums, until Cochran and Goin (1970) published their account of the frogs of Colombia. We have examined 113 of the 126 specimens reported as *E. raniformis* in that publication (*op. cit.*, p. 384). Although most (78%) are correctly determined, we consider the 113 specimens to represent seven species (*E. achatinus*, *E. anomalus*, *E. fitzingeri*, *E. longirostris*, *E. raniformis*, *E. taeniatus*, and *E. zygodactylus*). Cochran and Goin (*op. cit.*) reported other specimens of *E. raniformis* under the names *E. anomalus*, *E. conspiciatus*, and *E. longirostris*.

From eastern Panama, Breder (1946) and Heatwole and Sexton (1966) have reported *Eleutherodactylus fitzingeri* on the basis of mixed samples of *fitzingeri* and *raniformis*. These two species occur sympatrically at many sites in eastern Panama (but apparently not in all places, nor in the Pearl Islands), although one or the other (usually *fitzingeri*) tends to be relatively rare at a given locality. The junior author collected throughout the region, but, although recognizing the differences in size and color between central Panamanian *fitzingeri* and most Darién-San Blas "*fitzingeri*" (following Breder), he was for several years uncertain whether the differences denoted the existence of separate species or reflected geographic variation within *fitzingeri*. This question was resolved to his satisfaction in 1972, when adequate series of both species were obtained at Altos de Majé (now an island in man-made Bayano Lake). The senior author independently arrived at the same conclusion during a survey of most available museum specimens and was able to fix the name *raniformis* by examining the syntypes in the British Museum. Thus, we hope that the long period of confusion between *raniformis* and *fitzingeri* is now at an end, even though occasional specimens are likely to remain difficult to identify. Misidentification is probably most likely to occur in the case of occasional specimens of *fitzingeri*, particularly juveniles, that have unusually pale throats and/or small thigh spots, especially if such specimens turn up in larger samples of *raniformis*. Close examination of the details of throat and thigh pigmentation,

and comparison of adult sizes, should discriminate most of the difficult specimens.

Cochran and Goin's (1970, p. 383) discussion of variation in *Eleutherodactylus raniformis* is explicable on the basis of their confusing several species, as indicated above. There is some geographic variation of body size in *raniformis* (table 1), with the sample from the Pearl Islands consisting of smaller frogs than those in any sample from the mainland. *E. raniformis* exhibits slight sexual variation in degree of foot webbing, but there is no apparent geographic variation in this character.

The series of species having moderate webbing (figs. 1C, 18) includes *Eleutherodactylus andi*, *E. fitzingeri*, and *E. longirostris*, in addition to *E. raniformis*. All are probably closely related and are distinguished primarily on the basis of coloration. Geographic separation of the four is incomplete: *E. andi* is an upland species (560–1360 m.) of the cordilleras Central and Talamanca in Costa Rica and extreme western Panama; it is sympatric with *fitzingeri* over the lower half of its elevational range. Part of the geographic range of *fitzingeri*—in eastern Panama and western Colombia—coincides with that of *raniformis* and both have nearly the same southern limit (maps 6 and 8). *Eleutherodactylus longirostris* occurs by itself in western Ecuador and southern Colombia, but the northern part of its range coincides with that of *E. raniformis* in northwestern Colombia and adjacent Panama (maps 7, 8). The probable sister species of *E. longirostris* is *E. talamancae*, which has less webbing than the others and whose range in eastern Panama overlaps that of *E. raniformis*. Although the relationships of these various species are not known precisely, there seems to have been considerable dispersal in northwestern Colombia and adjacent eastern Panama, as evidenced by the sympatry of related species in that region. If the sister species of *E. raniformis* is *E. fitzingeri*, as might be suspected from general resemblance, the wider-ranging *fitzingeri* may have almost completely penetrated the range of *raniformis*. Competitive exclusion seems a possibility in places where only one or the other species is known to occur, such as *raniformis* at Sasardí, San Blas, and the separate

island records in the southern Pearl Islands; but *raniformis* seems usually to occur in sympatry with *fitzingeri*. Possible ecological interactions can be studied now that these common frogs have been shown to be separate entities that are identifiable in the field.

***Eleutherodactylus zygodactylus*,**

new species

Figure 30; Map 2

HOLOTYPE: KU 168518, an adult female taken at the Río Anchicayá, 8 km. W D nubio, 300 m., Department of Valle del Cauca, Colombia, on June 13, 1975 by William E. Duellman (field no. WED 50234).

PARATYPES: All from Colombia, as follows: ICN 4944, KU 168519–168551, from the type locality; FMNH 54356, 54602, "Pueblo Rico, Santa Cecilia, 800 m.," Dept. "Caldas" [Risaralda];¹⁸ LACM 73158–73159, north slope Alto del Buey, 300–420 m., Dept. Chocó; USNM 151291, Mutis, Dept. Chocó; AMNH 87099, Tabor, upper Río San Juan, 230 m., Dept. Chocó; KU 168517, 13 km. SE Llano Bajo, 375 m., Dept. Valle del Cauca. (See Appendix for nonparatypic specimens examined after this account was written.)

ETYMOLOGY: The specific epithet, a noun

¹⁸ Field Museum specimens bearing the imprecise data "Pueblo Rico [=Pueblorrico], Santa Cecilia, 800 m." probably were obtained by Emberá Chocó Indians for Kjell von Sneider in the forested mountains about 400 m. elevation above Santa Cecilia (380 m.) on the upper Río San Juan, or above La Unión (~400 m.), a river junction about 4 km. SSE Santa Cecilia. Formerly in Caldas, the location is in the present-day Department of Risaralda. The Field Museum specimens were obtained in November 1945. Wassén (1957) gave a brief account of a later trip led by von Sneider in May 1955.

The old horse trail used by von Sneider approached La Unión–Santa Cecilia through a dry, rain-shadow valley that extends northwestward from Pueblorrico (~1500 m.). Although the airline distance between Pueblorrico and Santa Cecilia is only 15 km., the habitat changes greatly from open, relatively semiarid land to rainforest, in an elevational drop of about 1100 m. Today, the trip can be made by car over a gravel road that until recently ended at Santa Cecilia (this road is now being extended westward; some older maps optimistically showed a completed road along the Río San Juan from Santa Cecilia to Playa de Oro and Tadó).

in apposition, is derived from the Greek *zygos* (yoke) + *daktylos* (toe), in allusion to the fully webbed (yoked or joined together, not free) toes.

DIAGNOSIS: A large species (adult males 39.6–54.1 mm. SVL, adult females 76.5–83.8 mm. SVL) of the *fitzingeri* group. Skin of dorsum smooth with some nonpungent warts on lower back and flanks; dorsolateral folds absent; snout subacuminate in dorsal view; canthus rostralis sharp; upper eyelid much wider than IOD, lacking pungent tubercles; tympanum prominent, small, its length one-third to two-fifths of eye length; snout short, E–N < eye length; vomerine odontophores separated on midline by space equal to half the width of an odontophore; males with very short vocal slits and shallow subgular vocal sac not conspicuous externally; HW 37.1–40.3 percent SVL; finger discs moderately expanded, discs on fingers III–IV narrower than length of inner metatarsal tubercle; discs on fingers I–II round, those on fingers III and IV truncate; adult males bearing nonspinous nuptial pad on thumb; toes bearing expanded discs; toes very extensively webbed, webbing reaching discs of all toes except IV, modal webbing formula I 1–1 II 1–1 III 1–2 IV 2–1 V; prominent lateral fringes on unwebbed portions of toes and along outer margins of toes I and V; inner tarsal fold along distal two-thirds of tarsus; no calcar on heel; dorsum dark brown with indefinite darker mottling; posterior surfaces of thighs dark brown with dull cream flecks; groin brown; throat uniformly stippled with brown; venter cream; undersides of limbs cream, suffused with brown along lateral margins.

Within the *fitzingeri* group, only *E. anatypes* has comparable webbing of the toes. *Eleutherodactylus zygodactylus* differs from *E. anatypes* in having an inner tarsal fold, sharp canthi rostrali, smooth skin on the dorsum, a longer snout (especially males), and pale markings on the posterior surfaces of the thighs. The two species cluster with *E. anomalus* on the bases of large body size, small tympana, and narrow IODs. *Eleutherodactylus anomalus* is readily distinguished in having a broad head, less toe webbing (three phalanges of toe IV free of web), pungent ridges and warts on the dorsum, a dark throat



FIG. 30. *Eleutherodactylus zygodactylus*, new species (KU 168529, a paratopotype). From a color transparency by William E. Duellman.

with pale spots, large pale areas on the posterior surfaces of the thighs, and in lacking expanded discs on the fingers.

DESCRIPTION: Head as wide as to slightly narrower than body; head as wide as long. Snout weakly subacuminate in dorsal view, rounded to nearly truncate in lateral profile; snout short, E-N less than eye length (except in some juvenile females); nostrils weakly protuberant, directed dorsolaterally; canthus rostralis sharp, concave anteriorly, convex posteriorly; loreal region concave, sloping abruptly to lips; lips not flared. IOD very narrow; no palpable cranial crests. Supratympanic fold prominent, concealing upper edge of tympanum. Tympanum small, round in males, higher than long in females; tympanum separated from eye by distance equal to 1.5–2.0 times tympanum length. Postriotal tubercles conical, 2 to 4 on each side of head. No other enlarged tubercles on head.

Choanae moderate-sized, not concealed by palatal shelf of maxillary arch. Vomerine odontophores somewhat larger than a choana, median and posterior to choanae; odonto-

phores triangular in outline, elevated, each bearing 8–10 teeth in a nearly transverse row along posterior border; tooth row extending more posteriad at midline than at outer edge. Tongue slightly wider than long, oval, its posterior border shallowly notched, posterior one-fourth not adherent to floor of mouth. Males with very short vocal slits near corner of mouth; subgular vocal sac shallow and not externally conspicuous.

Skin of top and sides of head, upper surfaces of limbs, and anterior part of dorsum smooth; that on lower back and flanks bearing flattened warts; some warts on the flanks may coalesce, forming short ridges in some specimens. Skin of throat, venter, and undersides of limbs smooth. Low folds extend laterally from above the vent onto the posterior surfaces of the thighs. Anal opening not extended in sheath. Discoidal folds not apparent.

Forearm lacking ulnar tubercles. Palmar tubercle bifid, larger than oval thenar tubercle. Some low supernumerary tubercles present (at bases of fingers I, II, IV). Subarticular

tubercles not conical, basal tubercles longer than wide, more distal tubercles (if present) round. Fingers bearing lateral keels. Fingers bearing subdigital pads on discs; pads longer than wide. Discs of inner two fingers only slightly wider than digit below disc, those on outer two fingers twice as wide as digit below disc; discs rounded apically. First finger longer than second. Thumb of male swollen at base, bearing nonspinous, glandular nuptial pad.

No tubercles on knee, heel, or tarsus; inner edge of tarsus bearing low fold along its distal two-thirds. Inner metatarsal tubercle elongate, its length 3–4 times its width, not compressed. Outer metatarsal tubercle round or elongate (length twice width), low, one-eighth to one-sixth size of inner. No supernumerary plantar tubercles. Subarticular tubercles longer than wide, subconical; the most distal tubercle on toes III and IV least elongate. Toes fully webbed except on toe IV (similar to fig. 1E), bearing strong lateral fringes along unwebbed portion of IV and along outer edges of toes I and V; no fringe along outer edge of sole. Toe discs slightly smaller than those of outer fingers.

Dark brown above with indefinite darker flecking, mottling, and interorbital bar. Supratympanic stripe and three or four labial bars evident. Limbs indistinctly barred. Posterior surfaces of thighs dark brown with dull cream flecks. Venter and undersides of limbs dirty cream, invaded laterally by brown. Throat uniformly stippled with brown.

MEASUREMENTS OF HOLOTYPE (IN MM.): SVL 76.5; shank 45.5; HW 30.1; upper eyelid width 8.0; IOD 5.0; tympanum length 3.2; eye length 9.4; E–N 9.3. The female holotype is spent.

COLOR IN LIFE: Dorsum varying from black to dull olive green, with dark brown to dull reddish brown markings. Posterior surfaces of thighs black with yellow or (in AMNH 87099) gray flecks. Throat heavily suffused with gray, usually with median white streak; in others the throat is white with gray mottling. Venter bright yellow in larger individuals and creamy white in smaller ones. Undersides of thighs and shanks pale yellow or greenish yellow. Iris recorded as dull olive-gray to dull grayish brown in KU topotypes. The iris of a specimen of *E. zygodactylus*

(AMNH 87099) from the upper Río San Juan was compared directly with that of a specimen of *E. anomalus* (AMNH 87005) from the same stream: In the former, the upper part of the iris was brownish gray above a brown horizontal stripe (with parallel edges) extending through the pupil, and the part of the iris below the stripe was pale brown with some vague darker brown lines radiating downward from the pupil. The iris of the specimen of *anomalus* was identical except that its horizontal brown stripe was distinctly butterfly-shaped (fig. 14) and the bottom part of the iris was pale gray rather than brown.

VARIATION: Sizes and body ratios are summarized in tables 1 and 2.

ECOLOGICAL NOTES: William E. Duellman and his associates obtained 38 specimens immediately below a waterfall on a stream draining into the Río Anchicayá near a hydroelectric generating station (Central Hidroeléctrica de Anchicayá). All were collected on rocks beside and in the stream at night. Larger individuals were found primarily in the spray-zone of the waterfall. Some of the smaller individuals were found farther downstream; others were found on the lee side of boulders in the windy spray zone of the waterfall. The collectors did not note any mating activity, but three of the five adult females are gravid and two are recently spent. The adult males also seem reproductively active, with swollen testes and enlarged thumbs.

A specimen of *E. zygodactylus* (AMNH 87099), from the upper Río San Juan drainage, was found at night in the same short section of rocky stream as a specimen of *E. anomalus* (AMNH 87005), thus documenting microsympatry between these two extensively webbed stream species. But the abundance of *E. zygodactylus* in the spray-zone of a waterfall (at the type locality), together with its seemingly spotty distribution (map 2), suggests that it might have somewhat more specialized habitat preferences than the more commonly encountered *E. anomalus*. Like *E. anomalus* (see fn. 6), *E. zygodactylus* probably also occurs microsympatrically at some localities with the large streamside *E. bufoniformis*.

DISTRIBUTION: *Eleutherodactylus zygodactylus* occurs in the Pacific lowlands of north-

western Colombia, in a known elevational range of about 230–800 m. (map 2).

REMARKS: Three paratypes of *E. zygodactylus* were misidentified by Cochran and Goin

(1970) as *E. anomalus* (FMNH 54356, 54602, USNM 151291), and one of these (USNM 151291) was also listed (p. 384) under the name *E. raniformis*.

DISCUSSION

As a working basis, we have assumed that the *Eleutherodactylus fitzingeri* group *sensu* Lynch is a natural (i.e., monophyletic) group. Although this view is certainly subject to modification, published criticism has not provided comparative data that would be useful for a rearrangement of the 61 nominal species currently placed in the group (see discussion under The *fitzingeri* Species Group). In any case, the assumption of monophyly is not critical to our primary objective, which was to characterize species limits and distributions of an ecologically important series of frogs which have been much confused in the literature. Among problems remaining is the possibility that undefined sibling species may be included under the names *E. achatinus* and *E. crassidigitus*.

As we noted at the beginning, South American species of the *fitzingeri* group are unusually numerous in the Chocoan region. Species densities range from one in southwestern Ecuador and on various islands, to six and seven in the Río San Juan drainage and adjacent Buenaventura area of northwestern Colombia (map 9). Densities would remain high even if the three large streamside species (*E. anatipes*, *E. anomalus*, *E. zygodactylus*) were excluded from the group, since only one to three *fitzingeri*-group species normally occur at localities in other parts of the continent. Although there are no known major differences in times of activity of the Chocoan species (all seem to be broadly nocturnal although some may be more crepuscular than others), the frogs do appear to be ecologically separated by size (implying different food resources) and microhabitats.

The size spectra (using means only) for males range from 25.8 mm. SVL (*E. caprifer*) to 48.4 mm. (*E. zygodactylus*), and for females from 38.0 mm. (isthmian *E. crassidigitus*) to 85.4 mm. (*E. anomalus*). The size ratios (larger/smaller) of sympatric species for all areas range from 1.00 to 1.77 (\bar{x} = 1.14

for 17 male and 1.21 for 17 female comparisons). The largest values obtain for the comparison of *E. anomalus* and *E. longirostris* in northwestern Ecuador (males 1.47, females 1.77). The 34 size ratios in figure 31 show considerably more scatter than Duellman's (1978, p. 309) computations for the *Eleutherodactylus* of an Amazonian lowland fauna, although the ratios are within the range of values recorded for *Eleutherodactylus* in southern Andean Ecuador (Lynch, 1979c, table 3). Duellman's ratio plots of succeeding larger species form a virtually linear series between the values 1.0 and 1.2 (excluding one misplaced symbol at <1.0); these narrowly defined values are for a relatively narrow ecological assemblage of small- to moderate-sized arboreal species (nocturnal bush habitat). The greater spread in the present data (1.0–1.8, fig. 31) seemingly is more related to habitat differences than to character displacement; this conclusion is consistent with the habitat-correlated size ratios of Amazonian slope *Eleutherodactylus* (Lynch and Duellman, 1980, table 8). None of these size plots, however, has been tested for departures from randomness (see Simberloff and Boecklen, 1981).

The habitat segregation of the Chocoan species of the *fitzingeri* group is not readily quantified, although some differences are obvious. The synopsis of microhabitats (fig. 32) suggests ecologic microsymbatry of no more than four species. The three species with extensively webbed feet (*E. anatipes*, *E. anomalus*, *E. zygodactylus*) are apparently exclusively associated with streams in heavily forested areas of high rainfall. *Eleutherodactylus anomalus* is the most widely distributed and perhaps the most ecologically tolerant of these three species, occurring microsymbatrically with *E. zygodactylus* and possibly also with *E. anatipes*. The last two frogs, which are well-separated geographically, may prefer more specialized conditions (e.g., smaller streams, waterfall spray areas) than *E. anom-*



MAP 9. Species density of Chocoan frogs of the *fitzingeri* group of *Eleutherodactylus* in Panama, western Colombia and Ecuador. Arrows indicate insular records of single species.

Two species (*E. crassidigitus*, *E. fitzingeri*) extend west through the Isthmus of Panama and northward into Costa Rica or Nicaragua. The shaded areas in Panama indicate the additional presence of strictly Central American species of the *fitzingeri* group. The range of *E. gaigeae*—a peculiar dendrobatid mimic—is not included in the numbers, although it ranges from Costa Rica well into Colombia (Lynch, ms; Myers and Daly, 1983).

alus, but very little is known of these two newly described species.

Little also is known of the recently described *Eleutherodactylus caprifer*, which has

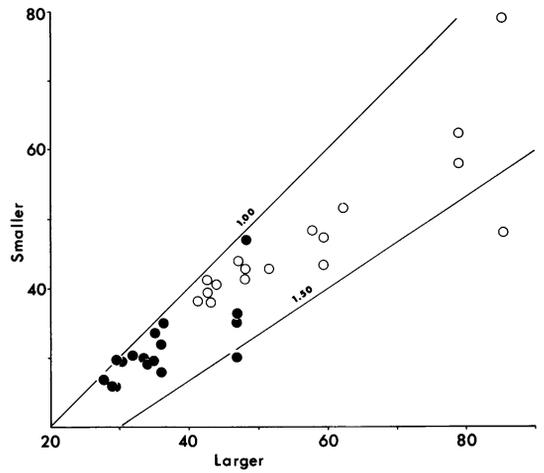


FIG. 31. Ratios of body lengths of succeeding larger sympatric species of *fitzingeri*-group *Eleutherodactylus*. Considering all possible competing pairs (males and females computed separately) in the geographic array of Chocoan species (map 9), there are 17 pairings each of males (●) and of females (○). Ratios of 1.00 and 1.50 are denoted by lines; axes are in mm.

been taken at several wet forest localities but which has been found abundantly only in the spray zone of a waterfall. All specimens were found on low perches by night, a common situation also for the following species.

Eleutherodactylus longirostris is almost restricted to very wet rain forests, although a few presumably relictual populations (inter-Andean Magdalena Valley) may be holding on in drier gallery forest. In the largest part of its range *longirostris* is mainly a frog of the deep forest. *Eleutherodactylus crassidigitus*, *E. fitzingeri*, and *E. raniformis* range from humid seasonal forests into very wet rain forest, although *crassidigitus* seemingly has not penetrated the exceptionally wet region of northwestern Colombia. The last three species have broad ecological tolerance, being found along forested streams and in forest edge situations and also in upland primary forest well away from streams. But *E. fitzingeri* and *E. raniformis* are usually most abundant in the hot lowlands, whereas *E. crassidigitus* tends to be more common in the cooler uplands.

Eleutherodactylus achatinus is distinctive in its seeming preference for pastures and other disturbed areas, where it attains higher

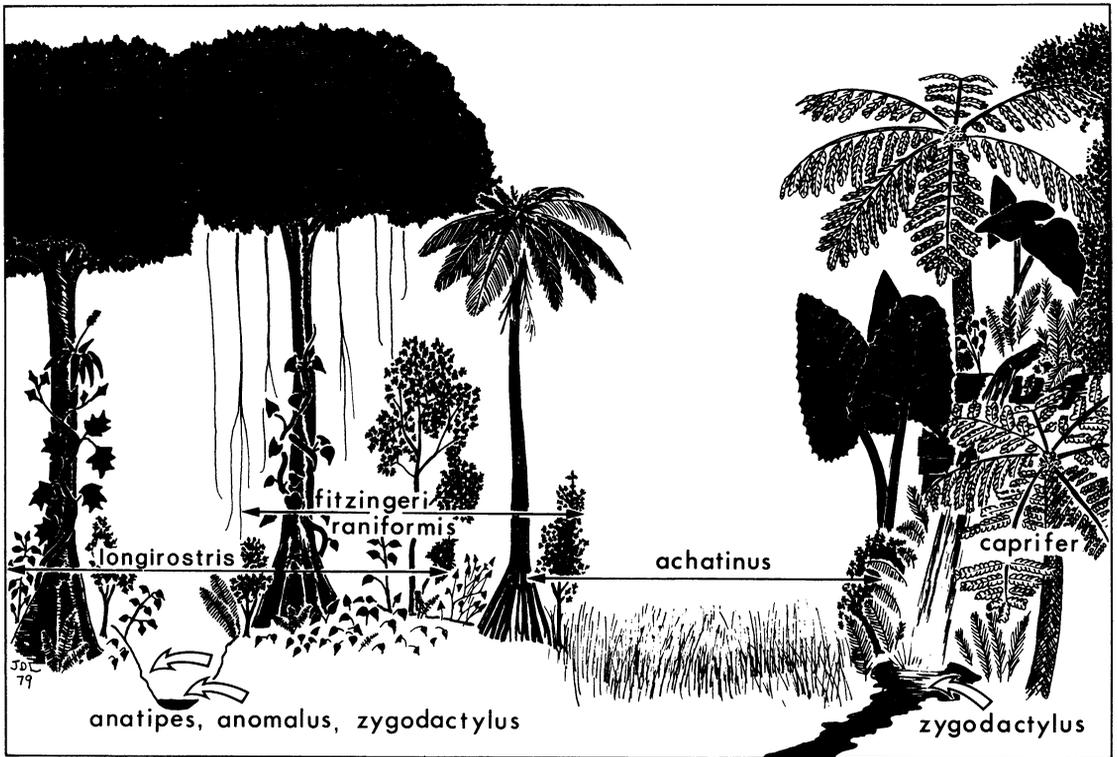


FIG. 32. Nocturnal microhabitats of eight species of Chocoan *Eleutherodactylus* of the *fitzingeri* group.

densities than in adjacent forest. It is more of a forest-edge species than any of the other frogs mentioned above.

All the forest and forest-edge species occur mainly in the ground litter by day, but by night they commonly climb and become members of the bush habitat. However, the largest females of at least *E. raniformis* tend to remain terrestrial by night as well as day. Egg laying probably is terrestrial (vs. arboreal) in all cases although only recorded for *crassidigitus* (under a rock) and *fitzingeri* (leaf litter); eggs of the streamside *E. anomalus* were laid in a shallow depression formed by the female on a gravel bar. At least *crassidigitus* and *fitzingeri* seem to stay with the eggs, although the sex of the nurse frog is unknown.

Judging from an observation on male-combat behavior in *E. achatinus*, and on intraspecific response vocalizations in *E. achatinus* and *E. fitzingeri*, these frogs must be

territorial to some degree. Vocalization thus probably serves a territorial as well as mate-attracting function. The calls of several species have not been identified, and the absence of a vocal sac in *E. anomalus* raises the possibility of that species being voiceless.

Eleutherodactylus achatinus, *E. crassidigitus*, and *E. fitzingeri* may call most frequently at dusk, with calling activity tapering off later, although there is much variation depending at least in part on the recency of rainfall. The nighttime calls especially of *E. crassidigitus*, *E. fitzingeri*, and *E. raniformis* tend to be sporadic and difficult to locate, and the call especially of *E. crassidigitus* is quite variable. We suggest that a propensity for a flurry of calling at dusk, call variability, and infrequency of nighttime calls are predator-avoidance mechanisms. Investigators in Panama have recently shown what has long been suspected, namely that a variety of predators do hunt calling frogs by sound. Such

predators include a giant toad (Jaeger, 1976), philander opossums (Tuttle, Taft, and Ryan, 1981), and bats (Tuttle and Ryan, 1981). Most documentation of predation has involved a pond chorusing frog (*Physalaemus pustulosus*), but bats also respond to the calls of perching frogs such as *Centrolenella* (Tuttle and Ryan, 1981) and might be particularly

significant nocturnal predators of perching *Eleutherodactylus*, as suggested by Tuttle's striking photograph (frontispiece). Indeed, while this paper was in press, we received confirmation from C. O. Handley, Jr., that the bat *Trachops* is a natural predator of *Eleutherodactylus fitzingeri* (q.v., species account).

APPENDIX: MUSEUM ABBREVIATIONS AND SPECIMENS EXAMINED

Catalogue numbers of museum specimens are preceded by the following abbreviations. We are grateful to the curators of these institutions for facilitating access to the specimens listed.

AMNH, American Museum of Natural History, New York
 ANSP, Academy of Natural Sciences of Philadelphia
 BMNH, British Museum (Natural History), London
 CAS, California Academy of Sciences, San Francisco
 CAS-SU, Stanford University collection, now housed at the California Academy of Sciences, San Francisco
 FMNH, Field Museum of Natural History, Chicago
 ICN, Instituto Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá
 INDERENA, Instituto Nacional de los Recursos Naturales Renovables y del Ambiente, Bogotá
 KU, Museum of Natural History, University of Kansas, Lawrence
 LACM, Natural History Museum of Los Angeles County, Los Angeles
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge
 MLS, Museo del Instituto de La Salle, Bogotá
 MZS, Museo Zoologico della Specola, Firenze, Italy
 RMNH, Rijksmuseum van Natuurlijke Historie, Leiden
 UIMNH, University of Illinois Museum of Natural History, Urbana
 UMMZ, University of Michigan Museum of Zoology, Ann Arbor
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
 UVMP, Universidad del Valle, Museo Parasitología, Cali
 WCAB, Werner C. A. Bokermann collection, São Paulo

Eleutherodactylus achatinus

COLOMBIA: Antioquia: Alto de Churrimo, nr. San Rafael (LACM 47112); Andes (town), 1350–1400 m. (LACM 73094); 10 km. W Andes, 1840 m. (LACM 73116–73125); 10 km. W Andes, 2030–2130 m. (LACM 73126–73133); 10 km. W Andes, 2100–2330 m. (LACM 73109–73115); La Rochela, vic. Andes, 1400–1450 m. (LACM 73108); La Rochela, vic. Villacesar (nr. Andes), 1800–1900 m. (LACM 73095–73107); Medellín (AMNH 39089); Río Arquía, Belén (LACM 46938–46939); Río Arquía, 5 km. W Finca Chibiquí (LACM 47191); Río Arquía, Finca Los Llanos (LACM 45998, 46926); Río Arquía, Puerto Palacios (LACM 45966); Sabaneta (MLS 460); San José de Andes (10 km. from Andes toward Río Cauca), 1860–1970 m. (LACM 73134–73152); Santa Rita (LACM 47113–47115, 47118). **Caldas:** Alto de las Cruces (MLS 188); Filadelfia (MLS 148); La Paletina (MLS 154); Montañita, E of Salamina (KU 150707, MLS 48 [2]); Pereira (FMNH 82015, MLS 164); Salamina (MLS 321). **Cauca:** Gorgona Island, prison camp (USNM 145137); La Costa, El Tambo (KU 144977–144983); Quebrada Guanquí, 0.5 km. above Río Patia, upper Saija drainage, 100–200 m. (AMNH 86372); Río San Joaquim (FMNH 54354). **Chocó:** Andagoya (BMNH 1916.4.25.26, FMNH 81839–81840); Camino de Yupe [trail from nr. Río Yupe (tributary upper Río Orogadó) towards upper Río Domingodó, Atrato drainage], 420–625 m. (LACM 73045, 73054, 73241–73242); Camino de Yupe, 560–624 m. (LACM 73041); Quebrada Bochoramá nr. lowest Cholo tambo (LACM 46935–46937); Quebrada Vicordó, about 5 km. above Noanamá, 80–110 m. (AMNH 87021–87025); upper Río Orogadó (LACM 46928); Serranía de Baudó, ridges paralleling Río Yupe (LACM 46927, 46929–46934); Sierra de los Saltos, on Río Truandó (LACM 50522, 50547, 50582). **"Cundinamarca":** "east base of Cordillera of Bogota and extreme limits of llanos" (ANSP 24392–24393). **Nariño:** 5.5 km. SE Divisa, 1040 m. (KU 167891–167894). **Junín:** no specific locality (LACM 50570); La Guayacana (FMNH

61818); vic. La Guayacana (LACM 50519); Río Mateje (USNM 147330, 147332, 147340, 147361, 147372–147373, 147375–147376). **Risaralda:** Pueblorrico, La Selva (FMNH 54320, 54352–54353, 54500, 54507); “Pueblorrico, Santa Cecilia” [see fn. 18] (FMNH 54350–54351); north of Santa Cecilia (LACM 50516); Río San Juan, opposite Santa Cecilia (LACM 50517). **Tolima:** no specific locality (UMMZ 132889–132890). **Valle del Cauca:** 3 km. E Cali (USNM 148797); Camp Cartón de Colombia, lower Río Calima (USNM 149734–149735); 13 km. W Dagua, Anchicayá drainage, 850–1200 m. (AMNH 88506–88507); Granja Bajo Calima (UVMP 243, 285–286); Río Anchicayá, 300 m. (KU 167888–167890); Río Calima, 1230 m. (KU 167887); bajo [Río] Calima, 15 km. NE Buenaventura (RMNH 18221); Río Raposa biological station (LACM 50546, 50568–50569, USNM 151389–151394).

ECUADOR: **Bolívar:** Balzapamba, 800 m. (KU 130387–130452). **Cañar:** Chimbo (BMNH 98.3.1.31–98.3.1.32); at Cotopaxi border about 7 km. SSW El Corazón, 800 m. (AMNH 104960). **Carchi:** Maldonado, 1410 m. (KU 117597–117611); 2 km. NE Río Blanco, 930 m. (USNM 204640–204642). **Chimborazo:** Pagma Forest in Chanchan River basin (ANSP 18244 [holotype of *Hylodes pagmae*]); Río Pescado, 1600 feet (AMNH 17546–17547, 17550, 17634–17635). **Cotopaxi:** 3 km. E Macuchi, 1500 m. (USNM 204636–204637); 18.6 km. W Pilaló, 930 m. (KU 141751); 20.3 km. W Pilaló, 930 m. (KU 141769); Sigchos (USNM 204638–204639). **El Oro:** 7 km. SE Buenavista, about 100 feet (USNM 204643–204649); Gualtaco (USNM 204651–204657); 7 km. ESE Machala, 10 m. (USNM 204650); 10 km. SE Machala, 20 m. (AMNH 91552–91557); 3 km. E Pasaje, 30 m. (AMNH 89738–89742); 18 km. W Piñas, 780 m. (KU 165088–165092); 4.4 km. NW Piñas, 1100 m. (KU 141770–141771). **Esmeraldas:** Bulum (UMMZ 58907); Cachabí [see fn. 5 in text] (BMNH 98.4.28.106, reregistered as 1947.2.15.69 [holotype of *Hylodes achatinus*]); 1 km. SW Cachabí, 20 m. (USNM 204628–204629); Pambelar (BMNH 1901.6.27.13); 2–4 km. W Placer, 360–390 m. (USNM 204626–204627); 3 km. W Placer, 380 m. (USNM 204624–204625); 10.5 km. from Quinde, 130 m. (KU 141747); region of Río Caoni, Sector de Lagartera (UIMNH 53425, 53428–53430); Río San Miguel, about 1 km. up from Río Cayapas (MCZ 92931–92932, 92940, 92947–92949); Salidero [probably = Salinero *vide* Paynter and Traylor, 1977, p. 106], 350 feet (BMNH 1901.8.3.13); San Javier, 350 feet [a Rosenberg locality, not located; see Paynter and Traylor, *op cit.*, p. 109] (AMNH 10708); San Javier [de Cachabí?] (UIMNH 55720); San Miguel (MCZ 92942–92946); 31 km. NNW Santo Domingo de

los Colorados, 1000 feet (USNM 204616, 204622–204623); 38 km. NW Santo Domingo de los Colorados, 1000 feet (USNM 204609–204615, 204617–204621). **Guayas:** Bucay, 900 feet (AMNH 16250, 16987–16988); 20 km. W Guayas, 300 feet (USNM 204660); Naranjal, sea level (AMNH 17631–17632); nr. jct. Río Chimbo and Río del Oro, 2000 feet (CAS-SU 9434); Río Frio (UMMZ 123899). **Imbabura:** Lita, Río Mira (KU 132605–132609, USNM 204658); Paramba (BMNH 98.3.1.30). **Los Ríos:** Quevedo (USNM 204630); 1 km. N Quevedo, 300 feet (USNM 204631–204635); 4 km. N Quevedo, 140 m. (KU 130365–130386, 135326–135338); 3 km. E Quevedo, road to El Corazón (MCZ 89913–89915). **Manabí:** 50 km. WSW El Carmen, 400 m. (MCZ 92014–92018); 2 km. W Desvio, 250 m. (USNM 204659); 23 km. N Manglarato, road to Puerto Lopez, 120 m. (MCZ 92038–92047); 25 km. N Manglarato, 60 m. (MCZ 92019–92020). **Pichincha:** 1 km. N Buena Fe (MCZ 89905–89912, 93320–93419); 10 km. E Chiriboga, 7000 feet (USNM 204548); 25.8 km. W Chiriboga, 1720 m. (KU 141748); Dos Ríos, 10 km. NE La Palma, 1270 m. (KU 135491–135493); 4 km. NE Dos Ríos, 1140 m. (KU 156093–156111); 3 km. W Dos Ríos, 1050 m. (KU 141765–141767); Guatea [probably Gualea], 2900 feet (BMNH 1920.2.9.8–1920.2.9.9); Estación Biológica Río Palenque, 220 m. (AMNH 89730–89732, KU 146049–146055, 147557–147560, 152572, 165082–165087, MCZ 88427–88430, 89901–89904, 89918, 89920–89926, 89928–89947, 92114, 93456–93462, 93464, 93468–93472, 93474–93475, 94800–94806); Hacienda Cerro Chivo, 46 km. N Quevedo (MCZ 91987–92013); 5 km. E La Palma, 900 m. (KU 165112–165119); 12.6 km. E La Palma on Chiriboga road (MCZ 92847); 13.5 km. E La Palma on Chiriboga road, Río Faisanes, 1380 m. (MCZ 94470, 94917–94918); 14.4 km. E La Palma on Chiriboga road, 1380 m. (MCZ 91986); 16 km. E La Palma on Chiriboga road, 1500 m. (MCZ 89117); 22 km. E La Palma on Chiriboga road, 1770 m. (MCZ 89916); Llambo, Camino de Gualea, 0°01'N, 78°40'W (USNM 204606–204608); Miligali ([also spelled Millegale]) MCZ 3009, USNM 204599–204600; Mindo, 4000 feet (UMMZ 55518); about 18 km. N Mindo, 1500 m. (USNM 204584); 3.5 km. NE Mindo, 1540 m. (KU 165120–165127); 1 km. E Mindo, 1400 m. (USNM 204573–204583); Nanegalito (USNM 204585–204587); 9 km. by road N Nanegal Chico (UMMZ 132918 [4]); 5 km. NW Nanegal Chico (USNM 204588–204590); 10 km. NW Nanegal Chico (USNM 204591–204593); 1.5 km. SW Nanegal Chico (USNM 204594–204595); Pachijal (USNM 204601); below Pacto (USNM 204602); Pacto, road to Guailabamba (USNM 204603);

Puerto de Ila (USNM 204604); 8 km. ESE Puerto Quito, 530 m. (KU 165128); Río Baba, 4 km. E, 10 km. S Santo Domingo de los Colorados, 400 m. (KU 141752–141764, 146056–146059); Río Toachi, 8 km. E Alluriquin, 800 m. (KU 141768, USNM 204596–204598); San Miguel de los Colorados (USNM 204605); Santo Domingo de los Colorados (including localities east of town at Hotel Zaracay), 500–660 m. (KU 109060, 117778–117779, 119465–119472 [119472 cleared and stained skeleton], 141749–141750, USNM 204549–204553, 204566–204568); 6 km. E Santo Domingo de los Colorados, km. 121 (USNM 204569–204572); 16 km. E Santo Domingo de los Colorados (MCZ 93318–93319); about 35 km. E Santo Domingo de los Colorados, Hacienda Lelia (CAS-SU 10607–10609, 10614); 8 km. SE Santo Domingo de los Colorados (UMMZ 132916 [4]); 0.5 km. S Santo Domingo de los Colorados, 670 m. (USNM 204554); 5 km. W Santo Domingo de los Colorados (USNM 204555); 6 miles W Santo Domingo de los Colorados (CAS 85180); 9 km. W Santo Domingo de los Colorados, road to Chone, Hacienda Espinosa (CAS 94853–94854, CAS-SU 10481–10492, 10495); 18 km. NW Santo Domingo de los Colorados (USNM 204556–204565); Tandapi, 1460–1500 m. (KU 111278–111344 [111306–111308 are cleared and stained skeletons], 120256–120260, 135463–135468, 135470, 135483–135484, 135487–135488, MCZ 75152–75174); 2.1 km. E Tandapi, 1500 m. (MCZ 92839); [Hotel] Tinalandia, 16 km. E Santo Domingo de los Colorados, 800 m. (MCZ 88420, 88426, 89883–89900).

PANAMA: **Darién:** Cana, 500 m. (KU 113785); Cerro Quia [=Altos de Quia, nr. Colombian border at about 77°30'W], 740–800 m. (KU 113766–113773); northeast slope Cerro Sapo, La Jarcia (ridge), 540–560 m. (KU 113775–113776); summit Cerro Sapo, 1080 m. (KU 113774); Chalichiman's Creek (AMNH 40523 [holotype of *E. brederi*]); Laguna, 820 m. (KU 76185–76202); near junction of Río Estil with Río Paca (Cana trail), 400 m. (KU 113778); Río Jaqué, 1.5 km. above Río Imamadó, 50 m. (KU 113779–113783); ridge between Río Jaqué and Río Imamadó, 800–900 m. (KU 113784); north end Serranía de Pirre, 320 m. (KU 113777); Tacarcuna, 550 m. (KU 77670, cleared and stained skeleton). **San Blas:** Camp Summit, 300–400 m. (KU 113786).

Eleutherodactylus anatipes

ECUADOR: **Carchi:** Maldonado, 1410 m. (KU 177625, 177626 [holotype]). **Esmeraldas:** 2 km. S junction Río Lita and Río Mira, 520 m. (USNM 233092–233093).

Eleutherodactylus anomalus

COLOMBIA: **Antioquia:** Río Arquía, Finca Chibiquí (LACM 46851); Río Arquía, 5 km. W Finca Chibiquí (LACM 46704); Río Arquía, Finca Los Llanos (LACM 46852–46856). **Cauca:** Quebrada Guanguí, 0.5 km. above Río Patia (upper Saija drainage), 100–200 m. (AMNH 86377–86391, 88972–88975, 88984 [eggs]); Río Micay, Municipio López, vereda de San Antonio (ICN 6401); Río Michenque, El Tambo, 800 m. (KU 144984–144986). **Chocó:** Alto del Buey, north slope, 300–420 m. (LACM 73266–73270); Camino de Yupe [trail from nr. Río Yupe (tributary upper Río Opogodó) towards upper Río Domingó, Atrato drainage], 420 m. (LACM 73250–73263), 420–625 m. (LACM 73264–73265); La Pepé, Quebrada Manuela (ICN 4949, 4951); near Playa de Oro, Río San Juan (USNM 147210–147211); 2 km. above Playa de Oro, upper Río San Juan, 210 m. (AMNH 87010–87014); Quebrada Docordó, about 10 km. above junction with Río San Juan, 100 m. (AMNH 87008–87009); Quebrada Vicordó, about 5 km. above Noanamá, 80–110 m. (AMNH 87006, 87007 [3 juv.]); Quesada River, Atrato River (AMNH 13603); divide between Río Atrato and Río San Juan, near Tadó (LACM 46881); trail between headwaters of Río Napipí and Río Opogadó (LACM 46880); upper Río Napipí below mouth of Río Merendó (LACM 46857–46862); upper Río Opogadó above mouth of Río Merendó (LACM 46863–46879); Serranía de Baudó (ANSP 25675); Tabor, upper Río San Juan, 230 m. (AMNH 87005). **Nariño:** Río Mataje (USNM 147320, 147594–147595). **Valle del Cauca:** Anchicayá, 87 km. W Cali, 500–600 m. (KU 151965); carretera Buenaventura–Cali, km. 18, Quebrada La Borea (ICN 5174, 5176, 5207); about 13 km. W Dagua, Río Anchicayá drainage, 820 m. (AMNH 88969–88971); Quebrada La Guinea, 2 km. E Cisneros, 400 m. (KU 143856–143858); Río Anchicayá, 300 m. (KU 167895–167899; USNM 144809, UVMP 1721); Río Calima (USNM 145771); Río Raposa biological station (LACM 50565–50566, USNM 151453); 5 km. SSE Sabaletas (UMMZ 132815).

ECUADOR: **Esmeraldas:** Cachabí [see fn. 5 in text] (BMNH 98.4.28.98–98.4.28.100, reregistered as 1947.2.16.8–1947.2.16.10 [syntypes]); Río Cupa (CAS-SU 11455, USNM 204714); 38 km. NW Santo Domingo de los Colorados, 1000 feet (USNM 204719–204720). **Pichincha:** Estación Biológica Río Palenque, 220 m. (KU 152575, 165129–165132, MCZ 93420–93422); Río Toachi (USNM 204718); 2 km. E Santo Domingo de los Colorados, 620 m. (KU uncatalogued); 6 km. E Santo Domingo de los Colorados (USNM 204715–204716); about 35 km. E Santo Domingo de los

Colorados, road to Quito, Hacienda Lelia (CAS-SU 10606); 8 km. SE Santo Domingo de los Colorados (UMMZ 127891 [4 individuals]); 0.5 km. S Santo Domingo de los Colorados, 670 m. (USNM 204717); 9 km. W Santo Domingo de los Colorados, road to Chone (CAS-SU 10467-10480).

Eleutherodactylus caprifer

COLOMBIA: **Cauca:** Quebrada Guanguí, 0.5 km. above Río Patia (upper Saija drainage), 100–200 m. (AMNH 88967). **Valle del Cauca:** about 13 km. W Dagua, Río Anchicayá drainage, 820 m. (AMNH 88966).

ECUADOR: **Esmeraldas:** Cachabí ([see fn. 5] BMNH 98.3.1.29). **Pichincha:** La Palma ("Las Palmas"), 920 m. (KU 131589 [holotype], KU 131590–131602, J. D. Lynch 9337–9356); 1.1 km. E La Palma (MCZ 95630–95635).

Eleutherodactylus crassidigitus

COSTA RICA: **Heredia:** Isla Bonita, east slope of Volcán Poas, 1200 m. (KU 28369, holotype). **Limón:** Suretka (MCZ 9788–9789). **Puntarenas:** 2 km. SSW Cañas Gordas, 1170 m. (AMNH 79854–79855); Monteverde, 1400 m. (KU 157739, 157743). **San José:** Cerro de la Muerte, 16 km. N San Isidro (MCZ 29066–29068).

PANAMA: **Bocas del Toro:** Almirante (KU 79969); about 13 km. W Almirante, 270–360 m. (KU 114674–114675); 7.1 km. WSW Chiriquí Grande, 70–100 m. (AMNH 113984–113985); hill above Miramar, 180–200 m. (KU 114673); Peninsula Valiente, Bluefields, 10 m. (KU 114672); Río Changuinola nr. Quebrada El Guabo, 170–200 m. (AMNH 107300–107301). **Canal Zone of Panama:** Barro Colorado Island (KU 76337, MCZ 24222, UMMZ 101793, 129688); Camp Chagres, 120 m. (KU 76344); about 5 km. NW Gamboa (KU 116990); La Loma MCZ (9843–9846); Río Chenillo (MCZ 10013); pipeline road at Río Frijolita, 90 m. (KU 172328–172334). **Chiriquí:** Boquete, 1160 m. (AMNH 69675–69677, UMMZ 69485–69488, 69489 [3], 69490, 69491 [3], 69492); south slope Cerro Santa Catalina, 8 km. NW El Volcán, 1400 m. (KU 76382–76383, 76385–76386); El Volcán (AMNH 69674); 8–9 km. NW El Volcán, 1170–1200 m. (KU 114090–114092); Finca Ojo de Agua, southeast slope Cerro La Pelota, 1440 m. (KU 114097–114108); Finca Palosanto, 6–7 km. WNW El Volcán, 1230–1280 m. (KU 76352–76363, 76381, 76384, 77671 [cleared and stained]), 114086–114089); Finca Santa Clara, 1200 m. (KU 114676–114680); Las Lagunas, 6 km. W El Volcán, 1200 m. (KU 76380); Quebrada Chevo, south slope Cerro La Pelota, 1440 m. (KU 114093–114096); upper Río Chiriquí, Fortuna

Dam site, 1000 m. (AMNH 94980–94987); Río Chiriquí Viejo, 5 km. WNW El Volcán, 1230 m. (KU 76364–76379). **Coclé:** continental divide north of El Copé (80°36'W), 600–800 m. (AMNH 98391–98401); El Valle de Antón (AMNH 59555–59557 [2000 feet], 59558–59560, 69681–69684, 91939–91946); El Valle [de Antón], 560 m. (KU 76387–76396, 116809); El Valle, Río Antón, 650 m. (AMNH 87314–87317). **Colón:** Achiote, 40 m. (KU 76347–76349, 76351); ridgetop trail SW of Cerro Bruja, 240–370 m. (KU 114664–114670); 3.5 km. SE Puerto Pilon, 260 m. (KU 114671); 8 km. E Puerto Pilon, 400 m. (AMNH 84940); Río Boquerón, about 2.5 km. N Peluca Hydrographic Station, 150 m. (AMNH 89493–89494); Río Guanche, 15 m. (KU 172326–172327). **Darién:** Cerro Quia [=Altos de Quia, nr. Colombian border at 77°30'W], 600–780 m. (KU 114644–114645). **Los Santos:** north slopes Cerro Cambutal, 480 m. (KU 114601); Cerro Hoya, 1260 m. (KU 114623–114628); east slopes Cerro Hoya, 940 m. (KU 114602–114622). **Panamá:** Altos de Majé [now an island in Bayano Lake] (AMNH 88701–88703); Altos de Pacora, 750 m. (KU 80356); below community of Altos de Pacora, 740 m. (KU 114663); nr. community of Altos de Pacora (E of Cerro Jefe), 750–800 m. (KU 114657); 4.8 km. N Altos de Pacora (road to Mandinga), 740 m. (KU 114658–114662); Candelaria and Peluca [hydrographic] stations [N of Madden Lake] (AMNH 53740, 53742–53743); Cerro Azul, 457 m. (USNM 54180–54181); Cerro Azul region (AMNH 108300); Cerro Azul region, Río Piedra (AMNH 108301); Cerro Campana (AMNH 69678–69680, MCZ 82059–82066), 740 m. (KU 172310–172311, UMMZ 131089); south slope Cerro Campana, 740 m. (KU 76338), 800–850 m. (KU 76339–76342), 800–900 m. (AMNH 84930–84939), 850–950 m. (KU 114656); 8 km. NNW Chepo, Gaspar Savanna, 120–360 m. (KU 125018); Finca La Sumbadora, 570 m. (KU 80352, 80354); El Llano-Cartí road, km. 9, 200 m. (KU 172312–172316), km. 10, 200 m. (KU 172317–172319), km. 11.7, 250 m. (KU 172320), km. 12.5, 250 m. (KU 172321–172322), km. 14.6, 370 m. (AMNH 89490–89492), km. 18, 275 m. (KU 172323–172325). **San Blas:** Camp Sasardi, 12 m. (KU 114646); Camp Summit, 300–400 m. (KU 114647–114655). **Veraguas:** 5–6 miles by rd. NW Santa Fe (AMNH 108346–108347).

Eleutherodactylus fitzingeri

COLOMBIA: **Antioquia:** Río Arquía, Belén (LACM 46691–46696, 46715, 46719–46720); Río Arquía, Finca Chibiquí (LACM 47177); Río Arquía, 5 km. W Finca Chibiquí (LACM 46705–46707); Río Arquía, between Finca Chibiquí and

Finca Los Llanos (LACM 46708); Río Arquía, Finca Los Llanos (LACM 46697–46703, 46709–46714); Río Arquía, nr. Puerto Palacios (LACM 46685–46690); Río Atrato, Arquía (LACM 46683–46684). **Chocó:** Alto del Buey, 420–1070 m., Serranía de Baudó (LACM 73038); Camino de Yupe [trail from nr. Río Yupe (tributary upper Río Opopadó) towards upper Río Domingodó, Atrato drainage], 420 m. (LACM 73076–73077); Istmina, Quebrada Cubis (ICN 4952); Pizarro (FMNH 44073); 2 km. above Playa de Oro, 210 m. (AMNH 87056–87060, 87104); Quebrada Vicordó, about 5 km. above Noanamá, 80–110 m. (AMNH 87051–87055); nr. upper Río Buey (LACM 50552); Río Napipi, below mouth of Río Merendó (LACM 46716); upper Río Opopadó, below mouth Río Merendó (LACM 46717); trail between upper Río Opopadó and upper Río Napipi (LACM 46718); upper Río del Valle, 50 m. (LACM 73078); Sierra de los Saltos, Río Nercua (LACM 50553–50554). **Cundinamarca:** Municipio de Nilo, corregimiento de Pueblo Nuevo, en Río Paquey, La Puerquera (ICN 1253). **Risaralda:** “Pueblorrico, Santa Cecilia” [see fn. 18] (FMNH 54588). **Tolima:** Mariquita (LACM 47153). **Valle del Cauca:** Granja Bajo Calima (UVMP 354); Río Anchicayá, 300 m. (KU 168058–168079); lower Río Calima, 15 km. NE Buenaventura (RMNH 18215, 18218, 18220); Río Calima nr. Córdoba (USNM 145769); Río Raposa biological station (USNM 151402–151403, 151411–151412, 151430, 151434, 151442).

PANAMA: **Bocas del Toro:** vicinity Almirante, 10–300 m. (KU 107124); Fish Creek, 1–2 m. (KU 114581); Río Changuinola nr. Quebrada El Guabo, 50–150 m., 16 km. W Almirante (AMNH 107307–107310). **Canal Zone of Panama:** (AMNH 55367); Ancon (UMMZ 98365); Balboa (UMMZ 98363 [10], 98364 [26], 98366–98367); Barro Colorado Island (AMNH 20892, 40447, 50762, 52022, 55371, 59550, 60525–60526, 62324, 62327–62328, 62330–62335, 69663–69664, 69667–69670, KU 76243–76249, 107125; UMMZ 61616–61617, 62646, 63610 [3], 63611 [4], 63612, 63613 [13], 63614 [13], 63615 [7], 63616 [2], 63617 [2], 63618–63619, 75996, 101792 [2], 135391, 137751–137753, 137755–137756, 137758 [2], 137760, 137764–137765, 137769); Chico (UMMZ 75995 [2]); 3.2 km. W Cocali (KU 67917–67922); Fort Clayton (KU 107126); Gamboa (KU 107124); 5 km. NW Gamboa, 90 m. (KU 107136, 116988–116989); 11 km. NW Gamboa, 160 m. (KU 108565); 13 km. NW Gamboa, Río Agua Salud, 60 m. (KU 107135); Gatún (MCZ 35647); 3.2 km. W Locona (KU 67923–67925); Madden Dam (KU 67926); Madden Forest Preserve, 60–140 m. (AMNH 84927–84928, KU 107127); Madden Forest Preserve, 160 m. (KU 107130–107134, 108566); Madden Forest Preserve, George Green

Park, 90 m. (KU 107129); Summit Experimental Gardens, 160 m. (KU 107123). **Chiriquí:** 4 km. WNW Concepción, 230 m. (KU 114576); 13 km. WNW David, Río Platanal, 110 m. (KU 107117); Finca Santa Clara, 1200 m. (KU 114583); 13 km. NE Gualaca, road to Valle Hornito, 570 m. (KU 114578); 5.8 km. ESE Paso Canoas, Río Jacu, 80 m. (KU 107114–107116); Progreso (UMMZ 76084–76086, 101791); 7.5 km. N Puerto Armuelles, 10 m. (KU 114577). **Coclé:** El Valle de Antón, 610 m. (AMNH 55369–55370, 116804); El Valle, Río Antón, 650 m. (AMNH 87313). **Colón:** 4 km. SE Puerto Pilón, 190–240 m. (KU 114570–114572); Río Boquerón, 2.5 km. N Peluca Hydrological Station, 150 m. (AMNH 89484); ridgetop trail SW Cerro Bruja, 240–370 m. (KU 107122). **Darién:** Camp Creek [nr. Yavisa on Río Chucunaque] (AMNH 40770, 40774–40775, 40781–40782, 41695–41696); Camp Creek, Camp Townsend (AMNH 40990, 40994–40995, 41067, 41152–41153, 41157); Cana, 1800–2000 ft. (USNM 50178); south base Cerro Tacarcuna, Río Pucuro, 640 m. (AMNH 104504–104507); Dry Creek, nr. Avelinos, Río Chico (AMNH 41183, 41185); Rancho Abagadó (UMMZ 137855); Río Chico, 0.5 miles above Avelinos (AMNH 40958, 40961, 40963); along banks of Río Chucunaque (UMMZ 137708); Río Chucunaque, mouth Río Canglón [=Canclones] (AMNH 40610–40611); Río Chucunaque, nr. mouth Río Icuantí (AMNH 41693); Río Chucunaque, mouth Río Metetí (AMNH 40710, 40728); Río Chucunaque, about 5 miles above Tupisa (AMNH 40856); Río Jaqué, 1.5 km. above Río Imamadó, 50 m. (KU 114495, 114498); Río Subcutí, Chalichiman’s Creek (AMNH 40522, 40885–40886, 41058); north end Serranía de Pirre, 320 m. (KU 114574–114575); Tacarcuna [abandoned Cuna village site on Río Tacarcuna, upper Pucuro drainage], 550 m. (KU 76263, 76271, 76273); Three Falls Creek [nr. Yavisa on Río Chucunaque] (AMNH 41682, 41689–41690, 41700, 41705, 41707, 41011). **Los Santos:** north slope Cerro Cambutal, 480 m. (KU 114582). **Panamá:** Altos de Majé [now an island in Bayano Lake] (AMNH 88706–88719); nr. settlement of Altos de Pacora, 700–800 m., E of Cerro Jefe (KU 107137–107153); 4.8 km. N Altos de Pacora, road to Mandinga, 740 m. (KU 107154); Arraijan (USNM 53717); 14.4 km. SSW Bejuco, 40 m. (KU 107155–107156); 0.5 km. SW Campana, Río Campana nr. junction with Río Cipira, 150 m. (AMNH 87312); Cerro Campana (AMNH 69672); Cerro Jefe, 880 m. (KU 107158–107159); Chilibrillo caves, nr. Chilibre (AMNH 55366, 55368, KU 107160–107162); Finca La Sumbadora, 570 m. (KU 80345–80350); halfway between burned area near Flora de Laguna and Río Silugandí (UMMZ 137735); Gorgas Laboratory [camp] on

Río Bayano [probably Altos de Majé, *q.v.*] (UMMZ 135355); 9 km. NNE Pacora, 20 m. (AMNH 107157); Río Mamoní (USNM 53990); Río Chibrillo caves S of Alejuela (USNM 50229); Río Silugandí at Pan-Am. hwy., 9°13'N, 78°48'W (UMMZ 137642, 137644, 137647–137648, 137651 [4], 137654–137655, 137658, 137664, 137668 [2], 137683, 137686, 137688–137689, 137691–137692, 137698–137699, 137702, 137704, 137710–137715, 137718–137720, 137725–137727, 137729, 137733, 137737, 137740); Río Tapio, Tapio (AMNH 40860–40872, 40874–40876; UMMZ 60270, 62504 [12]). **Pearl Islands, Bay of Panama:** San Miguel Island [Isla del Rey] (MCZ 8540). **Veraguas:** Isla de Cébaco Platanal (KU 107121); Isla Gobernadora (KU 107118–107120); mouth Río Concepción, 1 m. (KU 114579–114580).

Eleutherodactylus longirostris

COLOMBIA: **Antioquia:** Alto de Churrimo, nr. San Rafael (LACM 47184); Puerto Berrio (FMNH 30809); Río Arquía, Belén (LACM 45982–45994, 46043, 46103, 47170–47171, 122367); Río Arquía, Finca Chibiquí (LACM 46044–46066); Río Arquía, 5 km. W Finca Chibiquí (LACM 46067–46083); Río Arquía, Finca Los Llanos (LACM 45996–45997, 45999–46042, 46084–47102); Río Arquía, Puerto Palacios (LACM 45967–45980, 45995). **Cauca:** Quebrada Guanguí, 0.5 km. above Río Patia, 100–200 m., upper Saija drainage (AMNH 86360–86371, 86373–86376, 88959–88965). **Chocó:** no specific locality (AMNH 3983); Alto del Buey (see Serranía de Baudó); Andagoya (FMNH 81846–81847, MLS 189, USNM 144781–144788, 144800, 145788); Camino de Yupe [trail from nr. Río Yupe (tributary upper Río Opogadó) towards upper Río Domingodó, Atrato drainage], 420–700 m. (LACM 73015–73016, 73039–73040, 73042–73044, 73046–73053, 73055–73061); Caño Sando, tributary of Río Pepé, lower Río Baudó (USNM 144789); Condoto, Peña Lisa, 91 m. (BMNH 1913.11.12.98, 1913.11.12.100, 1914.5.21.82); Condoto, Río Condoto, Río San Juan, 46 m. (BMNH 1910.7.11.57); Istmina, upper Río San Juan (FMNH 15645); Playa de Oro, nr. town, 160 m. (LACM 46258); 2 km. above Playa de Oro, upper Río San Juan, 210 m. (AMNH 87062–87063); Quebrada Bochoramá, nr. lower Cholo tambo (LACM 46247); Quebrada Bochoramá, Loma de Encarnación (LACM 46248–46251, 46253–46257); trail between Quebrada Bochoramá and Río Tadocito (LACM 46252); Quebrada Dorcordó about 10 km. above junction with Río San Juan, 100 m. (AMNH 87072–87075); nr. Quebrada Santa Ana, tributary of Río Opogadó (USNM 125265); Quebrada Vicordó about 5 km.

above Noanamá, 80–110 m. (AMNH 87064–87071); divide between Río Atrato and Río San Juan drainages, nr. Tadó (LACM 46259–46261); upper Río Buey, nr. first Cholo tambo (LACM 50476); upper Río Buey, above tambo (LACM 50477); trail between Río Merendó and Cerro Los Hermanos (LACM 46149–46159); upper Río Napipí, below mouth of Río Merendó (LACM 46104–46148, 46160–46202, 46223, 47178, 47180); upper Río Opogadó, above Río Merendó (LACM 46203–46222); trail between upper Río Opogadó and upper Río Napipí (LACM 46228–46246); Río Quesada, Río Atrato (AMNH 13599–13601); Río San Juan, 10–15 km. W Playa de Oro (USNM 147213–147214); Río Truandó, below Sierra de los Saltos (LACM 50541); Serranía de Baudó (ANSP 25674); Serranía de Baudó, north slope Alto del Buey, 800–1000 m. (AMNH 102074–102078), 300–1070 m. (LACM 73018–73037, 73062–73067, 73069, 73071–73075); Serranía de Baudó, ridges paralleling Río Yupe (LACM 46224–46227); Serranía de Darién (ANSP 25676). **Cundinamarca:** Finca El Cuchero, nr. Tocaima (USNM 144802). **Huila:** nr. Moscopán (USNM 146422–146423). **Nariño:** Espriella (MLS 42); Imbilí, Río Mira (USNM 147451–147456); La Guayacana (ANSP 25678); Río Mateje (USNM 147321–147329, 147331, 147333–147339, 147341–147360, 147362–147371, 147374, 147377–147387, 147389–147390); Río Satinga (USNM 147482). **Risaralda:** “Pueblorrico, Santa Cecilia” [see fn. 18 in text] (FMNH 54384, 54589, 54604–54605); Pueblorrico, La Selva (FMNH 54508); Santa Cecilia, north trail (LACM 50478–50479). **Santander:** El Centro (MLS 112, USNM 150471–150480). **Tolima:** 6 km. NE Mariquita, 480 m. (AMNH 84860–84861); shore of Río Guali, 1–2 km. above Mariquita, 530 m. (AMNH 84858–84859). **Valle del Cauca:** Anchicayá (LACM 50470–50471, 50480, 50561); Anchicayá, shore of Río Anchicayá (LACM 50481); Buenaventura (USNM 150481); Camp Cantón de Colombia, lower Río Calima (USNM 149728–149733); 9 km. SE Llano Bajo, 200 m. (KU 168138); Río Anchicayá, 300 m. (KU 168137); lower Río Calima, 15 km. NE Buenaventura (RMNH 18216–18217, 18219); Río Raposa biological station (LACM 50482–50496, USNM 151407–151410, 151413–151415, 151420–151421, 151423–151429, 151431–151433, 151435–151438, 151444, 151449, 151457).

ECUADOR: erroneous locality data [Sarayacu, Pastaza Prov.] (BMNH 80.12.5.229, 80.12.5.249). “northwest Ecuador” (CAS 66296). **Esmeraldas:** Bulum, 18 m. (AMNH 10698–10700, MCZ 7600, UMMZ 83826 [5]); Cachabí [see fn. 5 in text] (BMNH 98.4.28.101–98.4.28.105 [reregistered as 1947.2.15.56–1947.2.15.60], syntypes of *Hylodes*

longirostris); Hacienda Equinox, 38 km. NW Santo Domingo de los Colorados, 305 m. (USNM-JAP 1794-1795); Pambelar (BMNH 1901.6.27.14-1901.6.27.15); nr. Río Balsalito, Cachabí (USNM-GOV 9349); Río Bogotá (USNM-GOV 6412, 6414); region of Río Caoni, sector de Lagartera (UIMNH 53393, 53424); Río Durango, 107 m. (AMNH 10706, MCZ 3891-3892, UMMZ 51272); Río San Miguel, 1 km. upstream from Río Cayapas (MCZ 92929, 92934, 92963-92971); Salidero [probably = Salinero *vide* Paynter and Traylor, 1977, p. 106], 107 m. (AMNH 10702, 10704, UMMZ 51265); San Javier, 350 feet [W. Rosenberg specimens, locality not located; see Paynter and Traylor, 1977, p. 109] (AMNH 10707, 10709-10710, MCZ 7599); San Javier [de Cachabí?] (UIMNH 55721); 1-1.5 km. SW San Javier de Cachabí, 20 m. (USNM-JAP 2884, 2887, 2963, 2985-2987, 3037-3038); San Miguel (MCZ 85756, 85789, 92952-92960). **Guayas:** Río Chimbo, Naranjito (USNM-GOV 7026). **Pichincha:** Estación Biológico Río Palenque, 220-300 m. (AMNH 89728-89729, KU 147561-147566, 152573, 165474-165495, 166277-166278 [cleared and stained skeletons], MCZ 88431-88433, 89919, 89927, 90055-90107, 91217-91219, 93476-93511, 94838-94841, 94888, 95501-95503); Hacienda Lelia, about 35 km. E Santo Domingo de los Colorados, road to Quito (CAS-SU 10611); 3.5 km. NE Mindo, 1540 m. (KU 165504); Pacto road to Río Guailabamba (USNM-GOV 7850); Puerto de Ila (USNM-GOV 7848); 8 km. ESE Puerto Quito, 530 m. (KU 165496-165503); Río Baba, 5-10 km. SSW Santo Domingo de los Colorados, 500 m. (AMNH 89727); lower Río Toachi (USNM-GOV 8569); Santo Domingo de los Colorados (USNM-GOV 7853); 2 km. E, 1 km. S Santo Domingo de los Colorados, 600 m. (KU-JDL 9009, 10247-10249); 18 km. W Santo Domingo de los Colorados (USNM-JAP 4178).

PANAMA: **Darién:** north ridge Cerro Cituro, Serranía de Pirre, 900-1000 m. (KU 114639-114642); south ridge Cerro Cituro, Serranía de Pirre, 1100 m. (KU 114643); south base Cerro Tacarcuna, Río Pucuro, 640 m. (AMNH 104509); ridge between Río Jaqué and Río Imamadó, 730-800 m. (KU 114629-114631); north end Serranía de Pirre, 320 m. (KU 114634), 500 m. (KU 114632-114633, 114635-114638).

Eleutherodactylus raniformis

COLOMBIA: **Antioquia:** Chigordó (USNM 151892, 153913); Río Arquía, Belén (LACM 46626-46631, 46636-46638); Río Arquía, Finca Chibiquí (LACM 46634-46635); Río Arquía, Finca Los Llanos (LACM 46632-46633); Río Arquía, Puerto Palacios (LACM 46624-46625); Uraba, Río

Currulao (FMNH 63879-63880); Valdivia, 1400 m. (KU 132640); Valdivia, Quebrada Valdivia (FMNH 61813). **Bolívar:** Alto de Quimari (FMNH 61813). **Caldas:** see under Risaralda for localities in Caldas at time of collecting. **Cauca:** Río Micay, Municipio López, vereda de San Antonio (ICN 6402); San Juan de Micay (ICN 4932). **Chocó:** north slope Alto del Buey, Serranía de Baudó, 300-420 m. (LACM 73068, 73070), 420-1070 m. (LACM 73227); Andagoya (BMNH 1915.10.21.66-1915.10.21.67, USNM 124235-124236, 144791-144799, 150449-150457); Boca de la Raspadura (AMNH 13685-13686); Camino de Yupe [trail from nr. Río Yupe (tributary upper Río Orogadó) towards upper Río Domingodó, Atrato drainage], 350-400 m. (LACM 73162), 420-625 m. (LACM 73017); Condoto (UMMZ 121419-121420); Condoto, Peña Lisa, 100 m. (BMNH 1913.11.12.97, 1913.11.13.99); El Valle (USNM 151290); Isthmina, upper Río San Juan (FMNH 15644); Municipio de Acandí, correg. Sapzurro, 30 m. (ICN 1589); Novita, Río Tamaná, Río San Juan (MCZ 15422); Las Animas Creek (AMNH 13605-13606); Pizarro (FMNH 44103-44108); vicinity Playa de Oro (LACM 46677); Quebrada Bochoramá (LACM 47183), Loma de Encarnación (LACM 46679); Quebrada Docordó (MZS 10668); Quebrada Vicordó, about 5 km. above Noanamá, 80-110 m. (AMNH 87101-87102); Quibdo (AMNH 13687); Río Atrato, Quibdo (LACM 46613-46623, 47169); shore of Río Buey, nr. mouth Río Auró (LACM 50473-50475); upper Río Napipí (LACM 47181); upper Río Napipí below mouth Río Merendó (LACM 47179); upper Río Orogadó, jct. with Río Merendó (LACM 46676), above mouth Río Merendó (LACM 46639-46675, 47182); Río San Juan, 10-15 km. W Playa de Oro (USNM 147212); Río Truandó, below Sierra de los Saltos (LACM 50542); upper Río del Valle, 50 m. (LACM 73079-73081); Serranía de Baudó, ridges paralleling Río Yupe (LACM 46678); Sierra de Baudó (ANSP 25673); Tabor, 230 m., upper Río San Juan (AMNH 87100); Tadó, Río San Juan (LACM 46680-46682). **Córdoba:** 25 km. from mouth Río Esmeralda (LACM 114494-114496); Serranía de San Jerónimo, about 5 km. E Tierra Alta (LACM 114492). **Cundinamarca:** Finca El Cuchero, nr. Tocaima (USNM 144801); Sasaima, 1225 m. (ICN 3243). **Risaralda:** Pueblorrico, La Selva (FMNH 54230, 54417, 54608-54611); "Pueblorrico, Santa Cecilia, 800 m." [see fn. 18 in text] (FMNH 54385-54390, 54603, 54606, KU 145003-145005); Santa Cecilia (LACM 50465-50469, 50479). **Santander:** El Centro (FMNH 81763, USNM 147135-147137, 150458-150462, 150465-150470). **Sucre:** 4 km. E Tolu, Hacienda La Estanzuela (LACM 114493). **Tolima:** Mariquita (FMNH 81830-81832, USNM 144803-

144808). **Valle del Cauca:** Anchicayá, 500–600 m. (KU 152005–152008, LACM 50461–50463, MCZ 75053–75056, 86183); Buenaventura (KU 143935–143937, 154531, USNM 124175, 144810–144817, 150482–150487); vicinity of Buenaventura (BMNH 95.11.16.48–95.11.16.51 [reregistered as 1947.2.16.16–1947.2.16.19] syntypes of *Hylodes raniformis*); Cali (BMNH 95.11.16.52–95.11.16.53 [reregistered as 1947.2.15.83–1947.2.15.84] syntypes of *Hylodes raniformis*); about 13 km. W Dagua, Río Anchicayá drainage, 850–1200 m. (AMNH 88508–88513); Llano Bajo, 80 m. (KU 158589–158594); 1 km. W Loboguerrero, Quebrada de la Chapa, 620 m. (KU 143943–143953); Quebrada La Guinea, 2 km. E Cisneros, 400 m. (KU 143938–143942); Río Anchicayá, 8 km. W Danubio, 300 m. (INDERENA 40, 72, KU 168058–168079, LACM 50472, UVMP 1722); Río Calima, 15 km. NE Buenaventura (RMNH 18214); nr. Córdoba (USNM 145756–145768, 145770); Río Raposa biological station (USNM 151404–151406, 151416–151419, 151422, 151439–151441, 151443, 151445–151446, 151448, 151456); Río Zabaletas, 29 km. SE Buenaventura (KU 154530).

PANAMA: no specific locality (AMNH 41084).

Darién: Avelinos, Río Chico (AMNH 40985); nr. Avelinos, Río Chico (AMNH 39785–39786, 39788–39789); nr. Avelinos, Río Chico, Dry Creek (AMNH 41177–41182, 41184, 41186–41190); 0.5 mile above Avelinos, Río Chico (AMNH 40954, 40956–40957, 40959–40960, 40964–40971, 40973); Camp Creek [nr. Yavisa along Río Chucunaque] (AMNH 40740–40741, 40766–40769, 40771–40773, 40776–40780, 40783–40784, 41146, 52159); Camp Creek, Camp Townsend (AMNH 40925, 40933, 40989, 40991, 40993, 40996, 41032, 41065–41066, 41132–41135, 41716–41722, 41725–41726); Chalichiman's Creek, upper Río Subcutí (AMNH 40513–40514, 40533); nr. mouth of Icuanaí (Isuanon) river (AMNH 41692); Laguna, 820 m. (KU 76250–76254, 76279–76286); Rancho Ahagadó (UMMZ 137842–137845, 137853); [Río] Canclones (UMMZ 137838–137839, 137847); Río Canclon(es) (UMMZ 137707, 137848); nr. mouth of Río Canclones (UMMZ 124518–124524, 137852, 137861–137862); Río Chucunaque (AMNH 40639); west bank Río Chucunaque (UMMZ 137706); Río Chucunaque, nr. camp and nr. 1st creek [between Río Chiatí and Río Subcutí] (AMNH 40618, 40637–40638, 40645, 41102) Río Chucunaque, camp below Río Canglón [=Canclones] (AMNH 41129); Río Chucunaque, mouth of Río Canglón [=Canclones] (AMNH 40592, 40594–40609, 40612–40613); Río Chucunaque, at Río Ilogandí, about 8 km. above Río Mortí, 150 m. (KU 114507); Río Chucunaque, mouth Río

Metetí (AMNH 40686–40689, 40705–40709, 40711–40712, 40724–40727, 40729, 40928); Río Chucunaque, about 7 km. above Río Mortí, 150 m. (KU 114504–114506, 114508–114509); Río Chucunaque, about 10 km. below Río Subcutí, 120 m. (KU 114499–114503); Río Chucunaque, first camp above Río Tuquesa (AMNH 41116, 41119–41120); below Río Clarita, on Río Chucunaque (UMMZ 137846, 137866); Río Chucurú (AMNH 40621, 40625–40626); Río Cupe, about 12 km. SSW Boca de Cupe, 90 m. (KU 114573); Río Jaqué, 1.5 km. above Río Imamadó, 50 m. (KU 114493–114494, 114496–114497); Río Subcutí, Río Chucunaque (AMNH 40564, 40799–40820, 40822–40823, 40825, 40827–40829, 40834, 40836–40839, 40842, 40846, 40849–40851, 40854); Río Tacarcuna, 3 km. E Tacarcuna [see under Tacarcuna below] (KU 76264); Río Tuirá at Río Mono, 130 m. (KU 114515–114530); Río Ucurgantí, about 7 km. above mouth, 30 m. (KU 114510–114514); between Río Ucurgantí and Río Metetí (UMMZ 137840–137841); Tacarcuna, 550 m. [abandoned Cuna village site on Río Tacarcuna, upper Río Pucuro drainage] (KU 76255–76262, 76265–76270, 76272, 76274–76278, 76287–76291); Three Falls Creek [nr. Yavisa] (AMNH 41012–41014, 41687–41688, 41691–41698, 41704, 41709–41710, 41712, 41714); nr. Yavisa (AMNH 41138–41144); creek above Yavisa (AMNH 41049–41051). **Panamá:** Altos de Majé [now an island in Bayano Lake] (AMNH 88720–88740); between Río Silugandí and Flora de Laguna (UMMZ 124527–124528); Río Silugandí at Pan-Am. highway (UMMZ 124525–124526, 137641, 137643, 137645–137646, 137650, 137652–137653, 137656–137657, 137659–137663, 137665, 137667 [2], 137680–137682, 137684–137685, 137695–137697, 137700–137701, 137703, 137705, 137709 [3], 137716–137717, 137721 [4], 137722, 137724, 137728, 137730–137731, 137734, 137738–137739, 137741). **Pearl Islands, Bay of Panama:** Isla San José (AMNH 98420, USNM 120356–120357, 120360, 120362–120366, 120371, 120374, 120378, 120398, 120400–120401). **San Blas:** Camp Sasardí, 12 m. (KU 114534–114569, 117360–117361 [skeletons]).

Eleutherodactylus zygodactylus

COLOMBIA: **Chocó:** north slope Alto del Buey, 300–420 m., Serranía de Baudó (LACM 73158–73159); Mutis (USNM 151291); Tabor, 230 m., upper Río San Juan (AMNH 87099). **Risaralda:** "Pueblo Rico, Santa Cecilia, 800 m." ([in Depto. Caldas at time of collecting; see text fn. 18] FMNH 54356, 54602); N Santa Cecilia (LACM 50532–50534). **Valle del Cauca:** Anchicayá, 55 km. NW

Cali (MCZ 75057); Buenaventura–Cali road, km. 16 (ICN 6393–6396); 13 km. SE Llano Bajo, 375 m. (KU 168517); Río Anchicayá, 8 km. W Danu-

bio, 300 m. (ICN 4944, INDERENA 41, KU 168518 [holotype], KU 168519–168551, 170093 [skeleton]).

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