

A NEW SPECIES OF RAINFROG (GENUS *ELEUTHERODACTYLUS*) FROM THE SERRANÍA DE TABASARÁ, WEST-CENTRAL PANAMA AND REANALYSIS OF THE *FITZINGERI* SPECIES GROUP

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ABSTRACT: We describe a new species of rainfrog of the *Eleutherodactylus fitzingeri* species group from central Panama. This species is most similar to members of the *E. melanostictus* subgroup and can be distinguished from other members of the *E. fitzingeri* group from Lower Central America by a combination of characters, including a large supraocular tubercle, barred thigh pattern, a granulate venter, marked sexual dimorphism in the tympanic membrane, and basal toe webbing. We analyzed a data matrix of 24 allozyme, morphological, and karyological characters, following the phylogenetic analysis of Miyamoto (1986), and included four additional characters. The 12 species of the *E. fitzingeri* group are included, in addition to the new species. The relative phylogenetic position of two species, *E. emcelae* and *E. phasma*, are proposed for the first time. The new species is hypothesized to be a member of the *E. melanostictus* subgroup, which contains the predominantly montane species *E. melanostictus*, *E. rayo*, *E. emcelae*, *E. monnichorum*, and *E. cuaquero*.

Key words: Anura; *Eleutherodactylus fitzingeri* species group; Leptodactylidae; New species; Panama

A SERIES of distinctive and brightly colored *Eleutherodactylus* was collected in 1978 near the Continental Divide (Atlantic slope) north of El Copé, Coclé Province, Panama, principally by A. Jaslow and associates. Recently, field parties from Southern Illinois University under the direction of K. Lips collected additional material from the same locality, which is currently protected as part of the Parque Nacional G. D. Omar Torrijos H.

The specimens are referable to the Middle American clade (subgenus *Craugaster*) of the genus *Eleutherodactylus* (Lynch, 1986; Lynch and Duellman, 1997; Savage, 1987, 2002) by having the *e* condition of the mandibular adductor musculature and a karyotype of $2n = 22$ (J. E. DeWeese, personal communication).

Miyamoto (1986) proposed the first explicit phylogenetic hypothesis for the then 10 known species within the *Eleutherodactylus fitzingeri* group based on a cladistic analysis of 20 allozyme, morphological, and karyological characters. Since then, two additional species, *E. emcelae* (Lynch, 1985) and *E. phasma* (Lips and Savage, 1996), have been included in this group and further information regarding the morphological variation among species is now

available. In addition to including the three additional species, our reanalysis of the data matrix of Miyamoto (1986) involved minor coding adjustments, changes in character state variation, and the addition of four new characters. Our goals were to evaluate the previous hypothesis of Miyamoto (1986) using the new characters and to determine the placement of *E. emcelae*, *E. phasma*, and the new species described below.

MATERIALS AND METHODS

All specimens of the new species are represented in the type series and referred material and their information is included within the description. Museum acronyms follow Leviton et al. (1985). Where applicable CH and MVUP refer to specimens in the Circulo Herpetológico de Panamá and Museo de Vertebrados Universidad de Panamá collections, respectively. Characters listed for the other species of the *E. fitzingeri* group are based on material examined in the preparation of the following: Campbell and Savage (2000), Savage and DeWeese (1979, 1981), Lips and Savage (1996), Savage (1974, 1975, 1987, 2002); information in Lynch and Myers (1983), DeWeese (1976), and Lynch (1993); and examples listed in Appendix 1.

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Description of morphology follows the standards for the genus in Savage (1987) and Lynch and Duellman (1997), with modification of the terminology for the digital disk pads as detailed in the text. Measurements were taken as described by Lynch and Duellman (1997) and Campbell (1994). Standard measurements for frogs are abbreviated as follows: standard length, SL; head length, HL; head width, HW; width of upper eyelid, EW; interocular distance, IOD; eye length, E; tympanum length, TY; crus length, C; foot length, FL. The sex of adults was determined by the presence of secondary sexual features (tympanum dimorphism, male vocal slits and sacs, and male nuptial pads).

Phylogenetic Reanalysis

The cladistic analysis of Miyamoto (1986) for 10 species in the *E. fitzingeri* group forms the basis of the data matrix analyzed here (Table 1). Based on a reanalysis of specimens and information from the literature, we have modified the data matrix of Miyamoto (1986:table 4) with minor coding adjustments, changes in character state definitions, the inclusion of four new characters, and the addition of three species (*E. emcelae*, *E. phasma*, and the new species). A fourth operational taxonomic unit (OTU) is added to accommodate additional variation in *E. melanostictus* from Panama. Details of the changes in the data matrix of Miyamoto (1986) and a full character state list are in Appendix II. We have recoded characters 13 (heel tubercle) and 15 (supraocular tubercle) to conform with broader definitions applicable to the entire genus, following Savage (1987) and Lynch and Duellman (1997). Because no additional data are available for the original allozyme characters (1–11) of Miyamoto (1986), nine OTU's are coded with question marks. Four additional characters (21–24) are discussed in further detail below.

Character 21.—Color pattern of the posterior surface of the thigh is one of the best field characters for species recognition in *Eleutherodactylus* (Savage, 2002). The following five states are represented in the *E. fitzingeri* group: (1) uniform, inconspicuous, minute, pale spots may be present proximally; (2) mottled, dull, pale, irregular spots, often fused to form a mottled pattern; (3) vivid pale colored spots on a dark background; (4) a mixture of

distinct, vivid, pale spots and vertical, pale lines formed by fusion of spots; and (5) dark vertical bars separated by regular pale interspaces.

Character 22.—Savage (1987) diagrammed and described a range of conditions for the shape of digital covers and pads found in the genus. In this scheme, rounded disk covers with uneven distal margins were classified as “indented” where there was a shallow concavity in the margin or “notched” where the indentation was V-shaped. To avoid confusion, the term “emarginate” was used to distinguish the condition in truncate disks where an indentation was present. There is more variation in the degree of indentation in truncate disks than recognized by Savage (1987). Thus, we have taken a cue from Myers and Donnelly (1997) and recommend that “retuse” be used where the truncate disk margin has a broad shallow concavity and that “emarginate” be restricted to truncate disk covers that are deeply notched. These correspond to the “indented” and “deeply notched” disks, respectively, of Myers and Donnelly (1997). As a result, three character states are recognized for the disk covers of Fingers II–IV: (1) rounded; (2) truncate, even; and (3) one or more retuse.

Character 23.—Three character states for the condition of the depressor mandibular musculature are recognized, as modified from Savage (1987) and Lynch (1993), and based on a re-examination of material in light of the ontogenetic sequence described by Hanken et al. (1997): (1) dfsq—origin from the dorsal fascia and otic process of the squamosal following Lynch (1993:fig. 2); dfsq of Starrett (1968) would apply where only a few fibers originate from the squamosal. Although Savage (1987) quoted the definition of Starrett (1968) for dfsq, all his references to the dfsq condition in *Eleutherodactylus* correspond to the first definition above; (2) dfsqAT—origin from the dorsal fascia plus otic process of the squamosal (and otic capsule), with a slip (sensu Hanken et al., 1997) from the annulus tympanicus. Savage (1987) coded this condition as DFSQAT. Although there are separate slips (sensu Hanken et al., 1997) from the dorsal fascia and squamosal-otic capsule, these have coalesced and are not distinguishable from the dfsq condition; and (3) dfsqat—origin from the dorsal fascia, otic process of the squamosal (and otic capsule) and annulus tympanicus without

differentiation of parts (see Savage, 1987:fig. 27; Lynch, 1993:fig. 3).

Lynch (1993:40) rejected the use of depressor muscle character states because "one cannot polarize the character ...". In the present analysis we have used this feature as ordered based on the ontogenetic sequence in Hanken et al. (1997).

Character 24.—Tympanic sexual dimorphism: (1) little to no difference; and (2) tympanum of males 15–40% larger than those of females. Some species of *Eleutherodactylus* show sexual dimorphism in tympanum size while others do not.

The data matrix (Table 1) was analyzed using parsimony with missing data scored as question marks. All phylogenetic analyses were performed using PAUP* (version 4.0b10; Swoford, 2002). Shortest trees were sought using heuristic searches with 10 random addition sequence replicates, TBR branch swapping, and 50 trees held at each step. Homoplasy levels (e.g., character incongruence) were evaluated with the consistency index (Kluge and Farris, 1969), excluding uninformative characters, and the retention index (Farris, 1989, 1990). A nonparametric bootstrap analysis (Felsenstein, 1985) was used to evaluate confidence in the reconstructed trees. Using the heuristic search option in PAUP*, 100 bootstrap replicates were performed. Bootstrap values of $\leq 50\%$ are not reported, and clades with values of $\geq 70\%$ are considered strongly supported (Hillis and Bull, 1993).

We used the same outgroups (*E. escoces* and *E. rugulosus*) as Miyamoto (1986) but his samples for *E. rugulosus* are from the species *E. ranoides* following Campbell and Savage (2000). Monophyly of the *E. fitzingeri* group was assumed (following Lynch and Duellman, 1997; Lynch and Myers, 1983; Miyamoto, 1986; Savage, 1987), and the ingroup taxa were constrained by loading a constraint tree into the analysis.

The analysis treated five allozyme and six of the eight multistate morphological characters as ordered. The allozyme characters Cbp-1, Gdh-A, G-3-pdh-A, S-Icdh-A, and Pk-A were found to have intermediate allelic combinations (Miyamoto, 1986:table 2) and ordered using step matrices (Mabee and Humphries, 1993; Mardulyn and Pasteels, 1994; Appendix II). Of the eight multistage morphological

characters, 12, 13, 15, 17, 22, and 23 were ordered because they represent morphological transitional series. We refer to this analysis as *scaled*, following the terminology of Wiens (2000), where step matrices are used to weigh the cost of transition between states. This method for analyzing allozyme data isn't without its shortfalls, with congruence analyses demonstrating that it performs worse than frequency-based coding methods (Wiens, 2000). However, we choose the scaled method because allelic frequencies were not presented in Miyamoto (1986) and the raw data were unavailable. Of the nonfrequency parsimony methods, Wiens (2000) found that the scaled method had the best overall performance.

RESULTS

The frogs from El Copé agree in the following characteristics that are shared with species referred to the *E. fitzingeri* group (sensu Savage, 2002): relatively narrow heads (33–41% of standard length); long snouts; cranial crests absent; Finger I usually longer than Finger II; Toe III longer than Toe V, tips of both toes reaching some distance beyond penultimate subarticular tubercle on toe IV; vomerine tooth patches triangular in outline, situated posterior and mediad to choanae, barely separated medially; tympanum prominent; vocal slits, internal subgular vocal sac and nuptial thumb pads present or absent in adult males; disks on all digits expanded, some disk covers retuse (indented); disk pads not cuspidate; toes usually webbed at least basally; venter smooth or granulate. However, the frogs from El Copé are distinct from all previously recognized members of the *E. fitzingeri* group in having a unique combination of features that leads us to describe them as

Eleutherodactylus tabasarae, sp. nov.

Holotype.—UMMZ 167648 (Field Number AGK 4362), an adult male from 9.7 km NNW El Copé, on the continental divide at sawmill, La Pintada District, Coclé Province, Panama, 600–800 m (8° 40' 04" N, 80° 35' 6" W), obtained by Barry Hammel and Kathy Bub, 27 July 1978.

Paratypes.—All from La Pintada District, Coclé Province, Panama; males: SIUC H7091 and H6964, approximately 200 m E of the



FIG. 1.—Female paratype of *Eleutherodactylus tabasarae* (SIUC H6971), SVL = 53.43; photo by K. R. Lips.

continental divide below the abandoned sawmill site (Atlantic slope), Parque Nacional G. D. Omar Torrijos H., El Copé; UMMZ 167550, 9.7 km NNW El Copé on continental divide at sawmill (600–800 m); females: SIUC H6971 (Fig. 1) and H7067, approximately 400 m NE sawmill site below continental divide (Atlantic slope), Parque Nacional G.D. Omar Torrijos H., El Copé, 709 m; UMMZ 148788, El Copé cloud forest; UMMZ 167592, 13 km N El Copé on continental divide (600–800 m); UMMZ 174680, 6.4–8 km NNW El Copé (400–600 m).

Referred material.—CH 4486, headwaters of the Río Piedras, Cerro Bruja, Portobello District, Colon Province, Panamá (730–800 m); MVUP 1140, Cerro Guagaral (Cerro Brewster), Parque Nacional Chagres, Panamá District, Panamá Province, Panamá (910 m).

Diagnosis.—A member of the *E. fitzingeri* group (sensu Savage, 2002) differing from all other species in the group by having the combination of basal toe webbing and a granulate venter. It is phenetically most similar to a species in the Cordillera Talamanca-Barú of Costa Rica and western Panama, *E. melanostictus*, which has a large heel tubercle but lacks toe webs and a tarsal fold. It differs from its allies *E. emcelae*, *E. monnichorum*, and *E. rayo* by having a granulate venter and the posterior surface of the thigh marked with distinct dark bars and in lacking a heel tubercle. It is distinguished from *E. cuaquero* by having marked sexual dimorphism in tympanum size and Finger II longer than Finger I (I longer than II in *E. cuaquero*). Superficially the new species resembles some species of the *E.*

cruentus and *E. cerasinus* groups (sensu Savage, 2002), but members of those groups have Toe V longer than Toe III, lack toe webbing, and have strongly areolate venters.

Description of holotype.—A moderate-sized species, adult males 29–33.7 mm in standard length, adult females 48.5–54.2 mm; dorsum granular with many tubercles and/or short ridges; flanks areolate with a few scattered tubercles; upper limb surfaces shagreened; venter granulate; surface of head granular; EW/IOD 7–114%; snout rounded in dorsal outline, profile acuminate; canthus rostralis moderately sharp, acuminate in dorsal outline; loreal region concave, upper lip not flared in cross section; vomerine tooth patches triangular, much larger than choanae, posterior and medial to choanae, barely separated medially; an enlarged tubercle near posteriormedial margin of upper eyelid; tympanum distinct but heavily pigmented, round in males, subelliptical in females, width 80–95% of eye length in males and 34–58% in females; annulus tympanicus prominent, upper portion slightly concealed by supratympanic fold in females; Finger II much longer than Finger I; relative finger lengths in decreasing order III > IV > II > I (Fig. 2); disks on Fingers II–IV expanded, more than twice as wide as digits; covers truncate, that on Finger IV retuse (indented); disk on outer two fingers much larger than disk on Finger II; disk pad on Finger I ovoid, on Fingers II to IV truncate; width of disk on Finger III about half diameter of tympanum in males, greater than width of tympanum in females; paired vocal slits and internal subgular vocal sac in adult males; subarticular tubercles under fingers round to ovoid, obtuse in profile with distal margin raised; no supernumerary tubercles; thenar tubercle elongate with distal margin slightly raised; palmar tubercle bifid, slightly larger than thenar tubercle; several small low accessory palmar tubercles; no nuptial pads in males; no series of ulnar tubercles; a single large heel tubercle absent; heel with several weak tubercles; toe disks smaller than finger disks, disk on Toe IV slightly larger than those on Toes III and V; disk covers and pads on Toes II to V truncate; cover rounded and pad ovoid on Toe I; relative toe lengths IV > III > V > II > I; tips of both Toes III and V reaching beyond penultimate subarticular tubercle on

toe IV; toes with basal webbing; modal webbing formula in males **I** 2-2 1/4 **II** 2-3 **III** 3-4 1/4 **IV** 4+-3+ **V**; in females **I** 2-2 1/4 **II** 2-3 1/4 **III** 3-4+ **IV** 4 1/4-3 **V**; subarticular tubercles under toes ovoid except elongate outer two on Toe IV, which have obtuse distal margins; supernumerary or planter tubercles absent; inner metatarsal tubercle ovate; outer metatarsal tubercle absent; low tarsal fold extends about halfway from base of Toe I to heel; no inguinal glands; ventral disk margin crossing venter anterior to level of groin. Depressor mandibulae muscle originates from the dorsal fascia, otic process of the squamosal (and otic capsule) and annulus tympanicus without differentiation of parts (dfsqt). Adductor (levator) mandibulae externus superficialis present; the condition of Starrett (1968), Lynch (1986), and Savage (1987).

Karyotype.—2N = 22, based on UMMZ 174680; no data on N. F. provided (J. E. DeWeese, personal communication).

Coloration in preservative.—Dorsal surfaces dark brown to tan with darker brown blotches and spots; a pair of dark suprascapular spots or blotches with pale outlines, followed by a large dark blotch that extends one-third to two-thirds the distance from the level of the axilla to the level of the groin; blotch bordered by light areas that give appearance of pale dorsolateral light stripes; flanks and groin with black to dark brown blotches on clear white ground color; head colored like body with definite dark interorbital blotch; side of head with five or six darker supralabial bars separated by light areas; smaller dark blotches corresponding to supralabial bars on margins of lower jaws; upper surface of arms with four or five dark brown blotches; anterior surfaces of thighs with vivid dark spots and/or bars contrasting with light ground color; posterior surfaces of thigh marked with vertical dark bars on light ground color; in some specimens, bars broken or parts offset; throat, chest, and venter immaculate white or with a few scattered large brown spots; lower surfaces of thighs light or with

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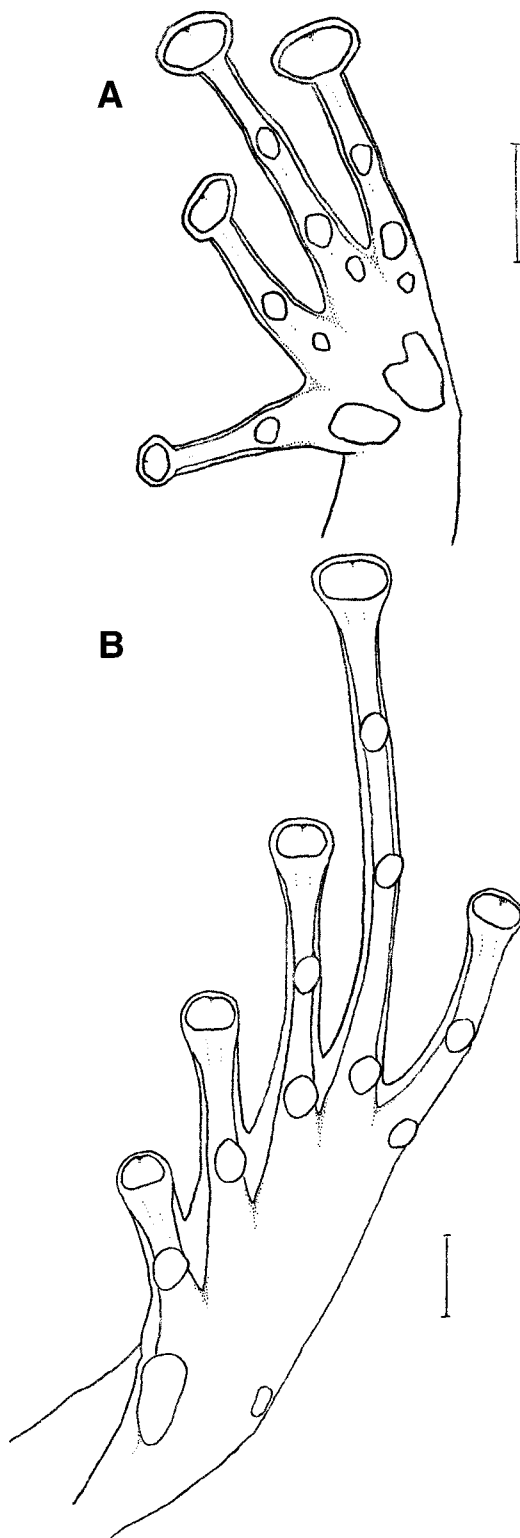


FIG. 2.—(Upper) Palmar view of left hand of holotype of *Eleutherodactylus tabasarae* (UMMZ 167648), scale = 2 mm; (lower) plantar view of left foot of female paratype of *Eleutherodactylus tabasarae* (SIUC H6971), scale = 2 mm.

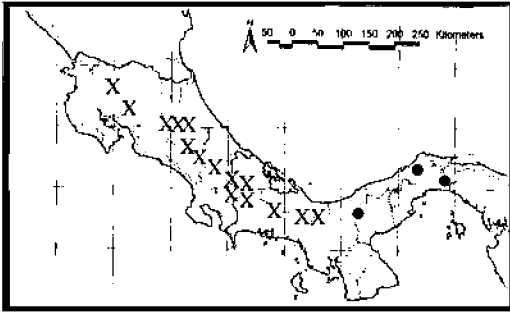


FIG. 3.—Distribution of *Eleutherodactylus melanostictus* (X) and *E. tabasarae* new species (●) in Costa Rica and western Panama; because of scale, a single symbol may represent more than one locality.

a few large dark brown spots marginally; calf and tarsal segments marked with distinct dark spots on ventral margins; soles uniform brown.

Coloration in life.—Upper surfaces cocoa brown, dorsum with medium-sized darker brown blotches interspersed with lemon yellow; blotches with red sprinkles and green lichenous patches; lips barred with brown and lemon yellow coloration; groin golden-yellow to orange with dark brown blotches; upper thigh surface barred with dark brown to black irregular bars interspersed with bright orange-red bars continuing onto anterior and posterior thigh surfaces; posterior calf and tops of feet similarly marked; chin, chest, and venter custard yellow; ventral surface of limbs bright yellow with scattered brown spots; iris silvery tan to golden above, lower half dark brown to black (Fig. 1).

Measurements of holotype (in mm).—SL 32.3; HL 13.5; HW 11.4; E 4.1; TY 3.9; C 18.9; FL 27.3; EW 3.9; IOD 3.9.

Measurements of type series as percentages of standard length.—HL 41–51; HW 35–41; C 48–59; FL 66–84.

Distribution and habitat.—The species is known from the Tropical Premontane Rainforest zone in the Serranía de Tabasará above El Copé, Coclé Province, west-central Panama (600–800 m) within the 25,000 ha Parque Nacional G. D. Omar Torrijos H., from the mountains of east-central Panama at Cerro Bruja, Colon Province (730–800 m), and the Serranía Piedras-Pacora, Parque Nacional Chagres, Panama Province (910 m) (Fig. 3). We follow Myers and Duellman (1982) in using the name Serranía de Tabasará for that

part of the western Panama massif (Cordillera Central) that forms the continental divide from the level of Laguna Fortuna, Chiriquí Province, eastward into Coclé Province in order to distinguish it from the Cordillera de Talamanca-Barú portion of the same mountain chain farther west in Panama. The collection area in the Serranía de Tabasará was selectively logged in the late 1970's, but both recent and historic collections of this frog were all made from the Atlantic drainage of the Río Guabal. All specimens of the new species were collected at night on vegetation up to 2 m above streams or above the forest floor near streams.

Remarks.—The composition of the *E. fitzingeri* species group has a checkered history after its proposal as an informal taxonomic group by Savage (1973). Some confusion derives from Lynch (1976) and Lynch and Myers (1983) who recognized a composite *E. fitzingeri* group including species from both of the two major mainland clades of the genus, subgenera *Craugaster* and *Eleutherodactylus* (sensu stricto) of Lynch (1986) and most subsequent authors. Savage (1987) proposed that the many groups, subgroups, or assemblies of species recognized by various authors within the two major clades could be organized into a system of "series" containing a number of species "groups". Although Lynch and Duellman (1997) opted not to use series as a subgeneric category, they defined an *E. fitzingeri* species group essentially the same in composition as that recognized by Miyamoto (1986) and Savage (1987). Their concept constitutes the *E. fitzingeri* species group in this paper as delineated by Savage (2002). Lynch (2000) removed *Eleutherodactylus andi*, *E. cuaquero*, and *E. emcelae* from the *E. fitzingeri* group to establish an *E. andi* species group. This action is not followed here as explained in the discussion section below.

With the addition of the new species, the *E. fitzingeri* species group now includes the following taxa: southwestern Ecuador to eastern Panama, *E. longirostris*; western Ecuador to eastern Panama, *E. raniformis*; western and north-central Colombia to northeastern Honduras, *E. fitzingeri*; northwestern Colombia to Costa Rica, *E. crassidigitus*; eastern Panama to Nicaragua, *E. talamancae*; montane western Panama, *E. emcelae*, *E. monnichorum*, and *E. tabasarae*; montane western Panama and

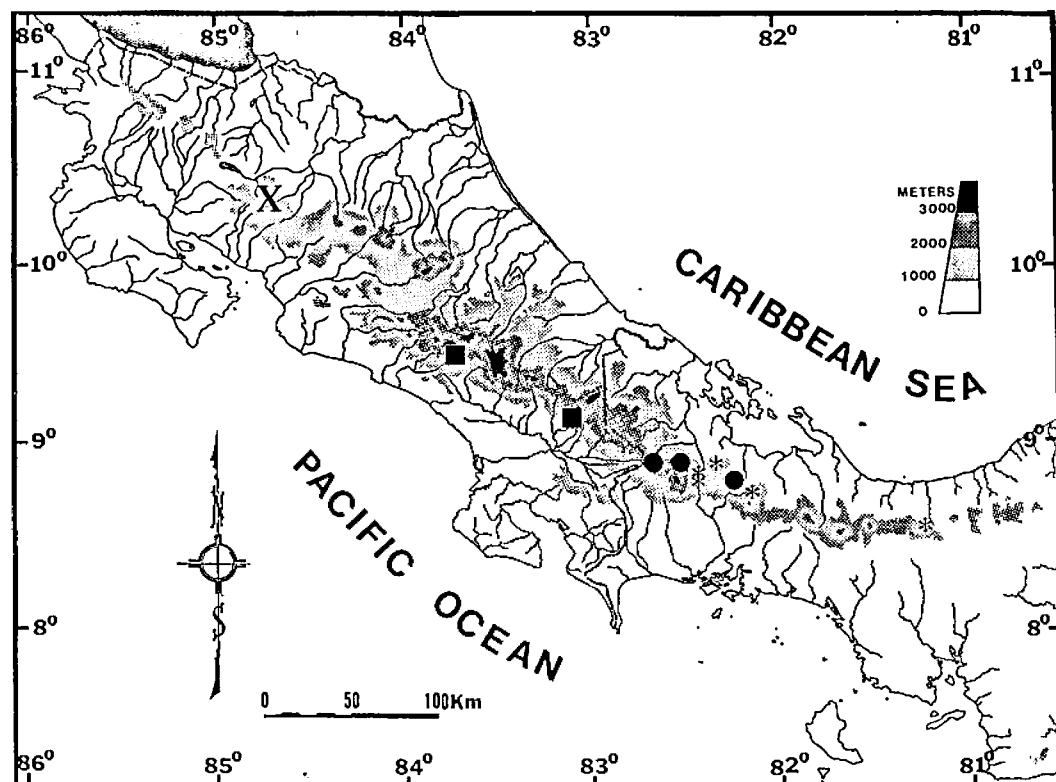


FIG. 4.—Distribution of four members of the montane clade of the *Eleutherodactylus fitzingeri* group, *E. cuaquero* (X), *E. emcelae* (●), *E. rayo* (■), and *E. monnichorum* (*); a single symbol may represent more than one locality.

Costa Rica, *E. melanostictus*; montane Costa Rica, *E. andi*, *E. cuaquero*, *E. phasma*, and *E. rayo* (Figs. 3, 4). We follow Lynch and Duellman (1997) in removing *E. bocourti* of Guatemala from the group. The specimen of the new species from Cerro Guagaral (MVUP 1140) was the basis for the record of *E. melanostictus* from the Parque Nacional Chiriquí by Ibáñez et al. (1994).

Phylogenetic relationships.—The 50% majority consensus tree (Fig. 5) from the scaled analysis summarizes the more common relationships of the 77 most parsimonious trees of 167 character steps each. These trees have a CI = 0.65 and a RI = 0.78. Bootstrap support for most clades is not strong, yet this is not surprising with a data matrix containing 21 OTU's and 24 characters (see Fig. 5; values below stems). Relationships supported in the consensus tree (see Fig. 5; nodes with 100%) place *E. tabasarae* in a clade containing the montane species *E. melanostictus*, *E. rayo*, *E. emcelae*, *E. monnichorum*, and *E. cuaquero*.

Eleutherodactylus melanostictus and *E. rayo* were found to be sister taxa, while *E. emcelae*, *E. cuaquero*, *E. tabasarae*, and *E. monnichorum* are sequentially removed from them. *Eleutherodactylus andi* is placed as the sister taxon to this montane clade, while the two *E. fitzingeri* OTU's and *E. raniformis* form an unresolved polytomy with respect to these. Among the remaining relationships supported in the strict consensus tree, *E. phasma* and *E. talamancae* are placed as sister taxa, in addition to the four samples of *E. crassidigitus*.

DISCUSSION

Eleutherodactylus tabasarae is a member of a clade containing the montane species *E. melanostictus*, *E. rayo*, *E. emcelae*, *E. monnichorum*, and *E. cuaquero* (Fig. 4). This group corresponds to the *E. melanostictus* subgroup following Miyamoto (1986), with the addition of the new species and *E. emcelae*. *Eleutherodactylus tabasarae* is diagnosed from other members of the *E. melanostictus* sub-

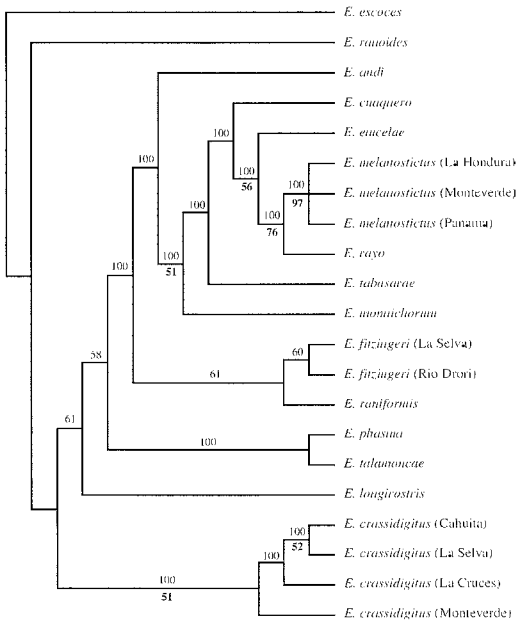


FIG. 5.—Majority rule (50%) consensus tree for species of the *Eleutherodactylus fitzingeri* group from the scaled analysis. Values above branches reflect the percentage of the 67 most parsimonious trees sharing the respective topology. Values below branches represent bootstrap values.

group by a combination of characters. Based on the phylogenetic analysis, *E. tabasarae* possesses three characters convergent with *E. melanostictus*: both species have a large supraocular tubercle and granulate venter and most populations of *E. melanostictus* (Savage and DeWeese, 1981) share a barred posterior thigh pattern with *E. tabasarae*. In addition, *E. tabasarae* has a distinct tympanum with marked sexual dimorphism, Finger II longer than Finger I, a tarsal fold, and basal toe webbing, but lacks a single well-developed heel tubercle. These additional characters are interpreted as retentions of ancestral states.

Miyamoto (1986) recognized three other subdivisions within the *E. fitzingeri* group: *E. crassidigitus* (monotypic), *E. talamancae* (monotypic), and *E. fitzingeri* (including *E. andi*, *E. fitzingeri*, *E. longirostris*, and *E. raniformis*). Compared with Miyamoto (1986), our analysis supports *E. crassidigitus* as monotypic and adds *E. phasma* as the sister taxon of *E. talamancae*. Contrary to Miyamoto (1986), our analysis places *E. andi* as the sister taxon to the *E. melanostictus* subgroup, rather than as a member of the *E. fitzingeri* subgroup.

Further, *E. longirostris* is removed from the *E. fitzingeri* subgroup, leaving only *E. fitzingeri* and *E. raniformis* as sister taxa (Fig. 5).

Savage (1973) suggested that an *E. melanostictus* group might be recognized. Although never defined in print, it was thought to include *E. melanostictus*, *E. monnichorum*, and *E. rayo*. Lynch (1976) and Lynch and Myers (1983) rejected this notion. Miyamoto and Tennant (1984) indicated that *E. melanostictus* was best considered a member of the *E. fitzingeri* group. Miyamoto (1986) later recognized an *E. melanostictus* subgroup within the *E. fitzingeri* group, containing *E. melanostictus*, *E. monnichorum*, *E. rayo*, and *E. cuaquero*. Lynch (1986) based his concept of the *E. melanostictus* group on the character of "notched" disks on some digits and included *E. melanostictus*, *E. monnichorum*, and *E. emcelae*. Savage (1987) pointed out that most members of the *E. fitzingeri* group have some emarginate disks on their outer fingers and did not recognize the *E. melanostictus* group, while citing similarities among *E. andi*, *E. cuaquero*, and *E. emcelae*.

Lynch (2000), apparently following up on Savage's (1987) comment, proposed an *E. andi* group for *E. andi*, *E. cuaquero*, and *E. emcelae*. These species were said to differ from others usually placed in the *E. fitzingeri* group in lacking strong sexual dimorphism in tympanum size. Examination of available material suggests otherwise. In most members of the *E. fitzingeri* group, males have a much larger tympanum than females, 1/2 to 3/4 the length of the eye compared to 2/5 to 3/5 the length the eye in females. The TY/E ratio for members of the putative *E. andi* group is:

	Males	Females
<i>E. andi</i>	2/3	1/2
<i>E. cuaquero</i>	2/3	2/3
<i>E. emcelae</i>	1/3	1/3

Moreover, *E. melanostictus* and *E. rayo* have the tympanum about 1/2 the eye length in both sexes.

The members of the montane clade (= *E. melanostictus* subgroup of the present paper) within the *E. fitzingeri* species group are known to range from the Cordillera de Tilarán of northern Costa Rica south and east through

the mountains of Costa Rica and western Panama to east-central Panama. The most basal species of the *E. melanostictus* subgroup, *E. monnichorum* (Fig. 4), occurs in the Cordillera de Talamanca-Barú in western Panama ESE to the Cerro Bollo region of the Serranía de Tabasará (1000–1856 m), about 140 km W of the localities for *E. tabasarae*.

The other members of the montane clade (Fig. 4) form a sublineage with *E. cuaquero*, restricted to the Cordillera de Tilarán (1500–1600 m), *E. emcelae* of the Cordillera de Talamanca-Barú of western Panama (1425–1525 m) and *E. rayo* endemic to the Pacific slope of the central area of the Cordillera de Talamanca-Barú in Costa Rica (1480–1820 m). Also in the *E. melanostictus* subgroup, *E. melanostictus* has a distribution encompassing most of the geographic and elevational range (1150–2700 m) of the entire subgroup. It is known to be sympatric, or is probably sympatric, with all other species in the montane clade except *E. tabasarae* (Fig. 3). It is, however, the only member of the clade to occur in the volcanic Cordillera Central of Costa Rica. The nearest record for *E. melanostictus* (USNM 297689–297692) to localities for *E. tabasarae* is in the Cerro Colorado region of the Serranía de Tabasará, about 140 km W of the type locality of the latter. The local endemics, *E. cuaquero*, *E. rayo*, and *E. tabasarae*, are probably the result of allopatric speciation because of orogenic effects from early Pliocene onward (Savage, 2002). *Eleutherodactylus emcelae* may also be a product of a similar process but has now come to overlap in distribution with *E. monnichorum*. The wide distribution and derived position of *E. melanostictus* indicates it is a recent product of this clade, not yet fractionated by orogenic or climatic fluctuations such as those so significant in the development of the montane lower Central American herpetofauna (Savage, 2002).

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APPENDIX I

Material Examined

Eleutherodactylus emcelae CRE 10529; *E. longirostris* LACM 46024; *E. talamancae* CRE 3635; *E. crassidigitus* CRE 3220; *E. escoces* CRE 4211; *E. cuaquero* UCR 4418; *E. monnichorum* UMMZ 69483-69484 (3 specimens), ANSP 21576-87, MCZ 10051-56, AMNH 124512, USNM 297693.

APPENDIX II

Allozyme, morphological, and karyological characters used in the phylogenetic analysis numbered as in Miyamoto (1986). Asterisk (*) indicates characters and sequence of states on which we conducted an ordered analysis. Changes are noted when coding differs from Miyamoto (1986:table 4). Allozyme characters (1-11) and determination of stepmatrix weightings are derived from Miyamoto (1986:table 2). See Materials and Methods for discussion of newly added characters (21-24).

- 1. Ak-A: two alleles recognized
- 2. Cpb-1: five allelic combinations ordered in a stepmatrix

	1	2	3	4	5
1	0	2	2	2	2
2	2	0	1	2	2
3	2	1	0	1	2
4	2	2	1	0	2
5	2	2	2	2	0

- 3. Ck-A: two alleles recognized
- 4. Gdh-A: three allelic combinations ordered in a stepmatrix

	1	2	3
1	0	2	2
2	2	0	1
3	2	1	0

- 5. G-3-pdh-A: four allelic combinations ordered in a stepmatrix

	1	2	3	4
1	0	1	2	2
2	1	0	2	2
3	2	2	0	3
4	2	2	3	0

- 6. M-1cdh-A: two alleles recognized
- 7. S-1cdh-A; four allelic combinations ordered in a stepmatrix. *Eleutherodactylus escoces* is coded with a question mark due to inconsistencies in the data matrix and character descriptions in Miyamoto (1986)

	1	2	3	4
1	0	1	1	2
2	1	0	1	2
3	1	1	0	1
4	2	2	1	0

- 8. Ldh-B: five alleles recognized. *Eleutherodactylus escoces* is coded with a question mark due to inconsistencies in the data matrix and character descriptions in Miyamoto (1986)
- 9. Pept-I: three alleles recognized
- 10. Pgm-A: three alleles recognized
- 11. Pk-A: five allelic combinations ordered in a stepmatrix

	1	2	3	4	5
1	0	1	2	2	2
2	1	0	2	2	2
3	2	2	0	2	2
4	2	2	2	0	2
5	2	2	2	2	0

- 12. *Canthus rostralis: (1) rounded; (2) moderately sharp; (3) sharp. Both *Eleutherodactylus escoces* and *E. ranoides* are coded as having a moderately sharp

- canthus rostralis based on a reevaluation of the diversity throughout *Eleutherodactylus*
- 13. *Single, large heel tubercle: (1) absent; (2) weak; (3) well developed. An intermediate state is added to recognize the condition found in *E. emcelae* and *E. monnichorum*
- 14. Relative lengths of Fingers I and II: (1) $I \geq II$; (2) $II > I$. *Eleutherodactylus cuaquero* has Finger I longer than Finger II (Savage, 2002)
- 15. *Supraocular tubercle: (1) absent; (2) weak; (3) well developed. An intermediate state is added to recognize the condition found in *E. monnichorum*
- 16. Tarsal fold: (1) absent; (2) present. *Eleutherodactylus talamancae* lacks a tarsal fold
- 17. *Toe webbing: (1) absent; (2) basal; (3) moderate; (4) strong. *Eleutherodactylus ranoides* has moderate toe webbing (Savage, 2002)
- 18. Tympanum: (1) distinct; (2) indistinct. *Eleutherodactylus cuaquero* has a distinct tympanum (Savage, 2002)
- 19. Venter: (1) smooth; (2) granulate
- 20. Karyology (N.F.): (1) 36; (2) 38; (3) 40. Character State 3 is modified to remove polymorphic condition. After reviewing DeWeese (1976), *E. crassidigitus* from Las Cruces has a N. F. = 38 and *E. crassidigitus* from Monteverde has a N. F. = 40
- 21. Posterior thigh pattern: (1) uniform; (2) mottled; (3) vivid pale spots; (4) vivid pale spots and stripes; (5) barred
- 22. *Disk covers of Fingers II–IV: (1) rounded; (2) truncate, even; (3) one or more retuse.
- 23. *Depressor mandibulae: (1) dfsq; (2) dfsqAT; (3) dfsqat
- 24. Tympanic sexual dimorphism: (1) little or none; (2) male tympanum 15–40% larger than female tympanum