

# Systematics and Distribution of the Mexican and Central American Rainfrogs of the *Eleutherodactylus gollmeri* Group (Amphibia: Leptodactylidae)

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## Abstract

The *Eleutherodactylus gollmeri* species group consists of three southern Central American forms (*E. gollmeri*, *E. mimus*, and *E. noblei*), two species (*E. chac*, new species, and *E. rostralis*) restricted to the Atlantic versant of upper Central America, and two forms (*E. laticeps* and *E. lineatus*) that occur in southern Mexico and northern Central America. To evaluate the intrageneric relationships of the *E. gollmeri* group, a review of jaw musculature and osteological, external morphological, and karyotypic features was undertaken. On the basis of this review, it is clear that the genus *Eleutherodactylus* is paraphyletic.

Differences in jaw musculature suggest that two major branches (I being Central American and II, South American-Antillean) may be recognized. The Central American stock contains two distinct lineages (1–2) in addition to the nominal genus *Hylactophryne*. The other major branch consists of four distinct lineages (3–6) of *Eleutherodactylus* and a number of allied genera. Previous attempts to cluster *Eleutherodactylus* species into monophyletic groups are shown to be based on unstable and homoplasious features of external morphology and osteology.

The *Eleutherodactylus gollmeri* group belongs to lineage 1 within the Central American stock and appears to be most closely allied to the *E. fitzingeri* group as redefined. A cladistic analysis of relationships among the members of the *E. gollmeri* group indicates that *E. noblei* is the most primitive extant species, while *E. chac* and *E. rostralis* are the most derived. Conversion of the cladogram of characters into an area cladogram suggests that the origin of northern and southern stocks within the group involved a vicariance event

(a marine barrier across Honduras), fragmenting the initial wide-ranging ancestral stock. Additional vicariance events associated with marine invasions and mountain building in the region appear to have led to the origins of modern species. After the removal of isolating barriers, some north-south (and south-north) dispersals contributed to establishing current distribution patterns.

## Introduction

Among the most beautiful and active denizens of the ground level stratum of the humid, evergreen forests of tropical Mexico and Central America are a series of medium- to large-sized frogs allied to *Eleutherodactylus gollmeri* (W. Peters). These animals are often diurnal and characteristically bound through the forest in a zigzag pattern of long leaps when disturbed, using surprise, speed, and evasive action to escape danger. Because of their cryptic coloration, these frogs may pass unnoticed by an observer until they seemingly explode out of the leaf litter directly underfoot and disappear with graceful, arching leaps into the underbrush. In common with most other members of the genus (one species out of the approximately 400 valid forms is known to be viviparous), these frogs lay large, encapsulated eggs out of water which undergo direct development into small frogs without a larval (tadpole) stage. Unlike most of their congeners, males of the *E. gollmeri* group apparently lack the ability to produce vocalizations that in others are utilized for spacing or to attract females in the breeding season. As a result, the stock's

reproductive behavior remains unknown, although in most forms the eggs probably are laid in the leaf litter.

Since my first fieldwork in Central America in 1960 I have been intrigued by members of the genus, especially the graceful representatives of the *Eleutherodactylus gollmeri* group that occur in Costa Rica. Early on I discovered that much confusion surrounded the status and distribution of the nominate form, then thought to range from Mexico to Panama, and its relationship to other putative species. For these reasons, after sufficient materials had been accumulated, I began a revisional study along the lines of my analysis of the situation in the *Eleutherodactylus rugulosus* group (Savage, 1975) shortly after that paper appeared. What seemed at that time to be a relatively straightforward systematics paper grew into a 10-year project. The principal delays in completion were the result of the extreme difficulty in recognizing distinct forms in the group because of the relatively few external morphological characters that could be used for analysis, and the continuously expanding amount of critical material from upper Central America that became available with each passing year. Additionally, in the interim, ideas regarding intrageneric relationships underwent a series of radical revisions (Lynch, 1976, 1986) and needed to be considered as well because of the controversial position of the *Eleutherodactylus gollmeri* group in these schemes. Hopefully, the finished project will compensate the patient (and impatient) students of *Eleutherodactylus* for the delay.

The present account follows in a general way the approach and methods utilized in my previous study on the *Eleutherodactylus rugulosus* group (Savage, 1975). The matter of intergroup relationships within the genus, however, is considered in much greater detail than in the previous work. As in that report, I have not listed museum numbers for every locality cited. The list of specimens examined is on file and will be supplied to anyone wishing to verify identifications.

## The *Eleutherodactylus gollmeri* Group

### Definition of the Group

Most members of the group are elegant, slender, narrow-headed (head width/standard length < 50%), long-legged frogs, but mature adults of one

species, *Eleutherodactylus laticeps* (A. Duméril), are more robust and appear to have moderately broad heads and moderately short legs. No bony supported cranial crests are present. Vomerine teeth in paired triangular patches are located between and behind choanae and are separated from one another on the midline by a distance less than the width of a single tooth patch. No vocal slits, sac, or nuptial thumb pads in males; no inguinal gland. Disks on all fingers; disks on fingers and toes never emarginate; usually one or more disk covers pointed, some disk pads swollen to cuspidate. First finger longer than second. Subarticular tubercles on fingers and toes projecting, usually raised at distal margin. No supernumerary tubercles on hands and feet. Accessory palmar tubercles present, rounded. A well-developed inner tarsal fold. Toes webbed at least basally. Venter smooth.

Frontoparietal and prootics distinct; pterygoids overlap alae of parasphenoid; prevomers in contact or narrowly separated.

Depressor mandibulae muscle with slips originating on the dorsal fascia, squamosal, and annulus tympanicus; an adductor mandibulae externus superficialis present; jaw musculature formula after Starrett (1968), DFSQAT + e.

Karyology: 2N = 20 or 22; N.F. = 36 in two examined species (*Eleutherodactylus laticeps* and *E. mimus* Taylor).

### General Characteristics

All members of the *Eleutherodactylus gollmeri* group resemble one another in sharing the following suite of features (group characteristics and features used for species definition are not included): canthus rostralis sharp, loreal region obtuse in cross section; upper eyelids smooth, with a definite series of low superciliary tubercles and one to three low supraocular tubercles; length of upper eyelid equal to interorbital distance; tympanum external, distinct (thin), round in males, ovoid and higher than wide in females (fig. 1); dorsum shagreened to finely granulate, often with one or more series of distinct tubercles, including a postorbital, a supratympanic, two or more paravertebrals, and two suprascapular tubercles on each side; sometimes a suprascapular fold running across back and a supra-axillary tubercle on each side; supratympanic ridge well developed; usually a dorsolateral ridge along each side from eye to axilla or beyond, very strongly developed in some forms (fig. 2). Dorsal surfaces of body and head gray or light tan



FIG. 1. Lateral view of head in *Eleutherodactylus gollmeri* group showing differences in color pattern and sexual dimorphism in tympanum. **Top**, dark eye mask; male tympanum size and shape; **bottom**, barred pattern; female tympanum size and shape.

to dark brown; sometimes uniform but most often with a complex hourglass- or X-shaped middorsal blotch, with smaller lateral blotches which are sometimes outlined by light; sometimes a dark

interocular or light interorbital spot; a series of small dark dorsal spots arranged in an X, a series of broad dark longitudinal stripes, some light fuzzy dorsal spots, a narrow middorsal light line and/or dark pelvic spots; usually a dark seat patch. Juveniles usually lighter than adults. Upper surfaces of limbs uniform or weakly to strongly barred, with alternating bands outlined by thin yellow lines and lighter interspaces; forearms usually with a distinctive dark transverse band; usually a distinct dark eye mask running from tip to snout through eye to shoulder or beyond and bordered above by a narrow light line; eye mask sometimes broken into a series of light-outlined lip bars and dark marks in supratympanic and axillary region (fig. 1). Posterior thigh surface usually uniform.

### Systematic Characteristics

The following section reviews in detail those features that exhibit substantial interspecific variation in the *Eleutherodactylus gollmeri* group. My comments (Savage, 1975) on the need for rigorous definition of character states and availability of comparative materials apply in all studies of the genus.

**DORSAL AND VENTRAL INTEGUMENT**—The upper surfaces of the body are essentially smooth (smooth in appearance to the unaided eye and touch) or granulate (weakly and uniformly granular). In some forms a definite dorsolateral ridge runs from the tympanum well back onto the body (fig. 2).

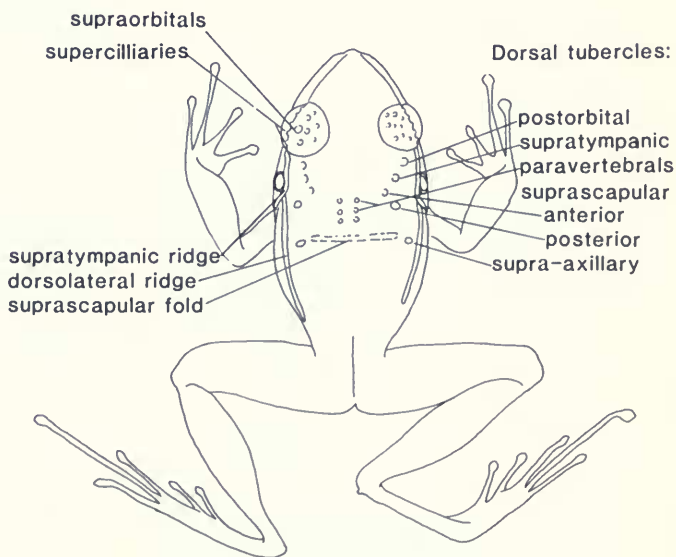


FIG. 2. Characteristics of dorsal integument in *Eleutherodactylus*. Note heel calcar on right heel.



**LYNCH**

**SAVAGE**

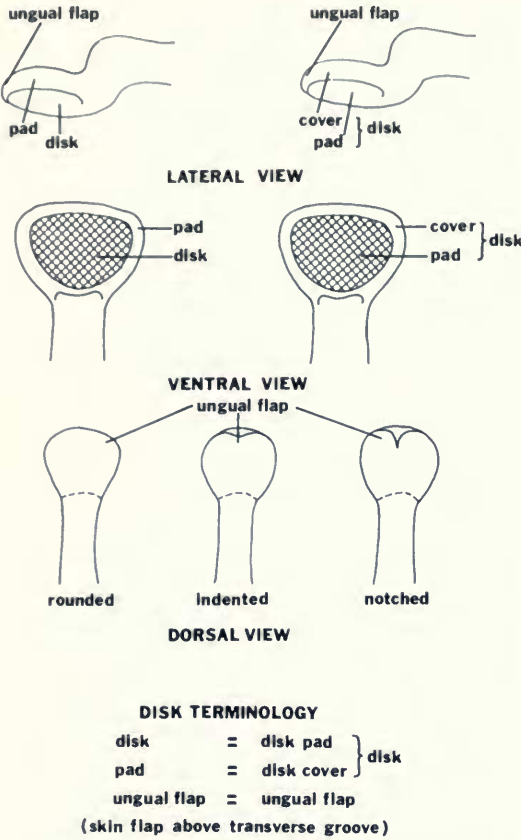
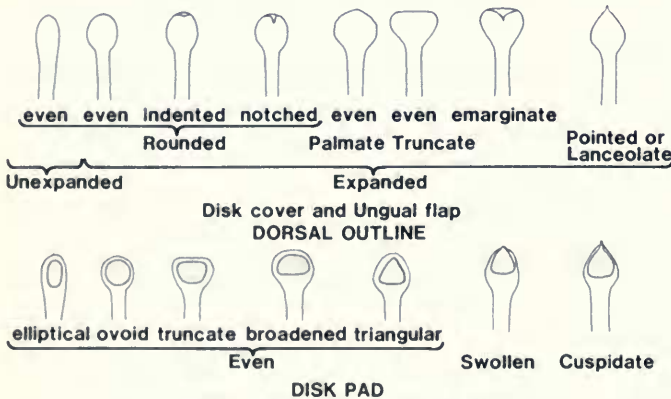


FIG. 3. Terminology for digital disk features in *Eleutherodactylus*.

The venter is smooth in all examples, but in large females of some populations the ventral disk tissue becomes thickened. The thickening and hypertrophy of the disk shows an ontogenetic trend, since young females lack this feature. In the very largest females, keratin appears to be laid down to produce a characteristic brownish color that overlays the disk surface.

**FINGER AND TOE DISKS**—As pointed out by Lynch and Myers (1983), Lynch has used an idiosyncratic terminology for basic disk characteristics in his myriad papers on the genus *Eleutherodactylus*. In my previous papers on the genus (e.g., Savage, 1974, 1975), I have used a more traditional terminology that is in essential agreement with the system followed by Lynch and Myers (1983). Since the differences in the two terminologies could cause confusion, Figure 3 shows their contrasting usage. In the system followed here, the term *disk* refers to the entire expanded structure on the end of the digit. The specialized ventral (subdigital) area of adhesive epithelium forms the *pad*. The dorsal area above the pad which is bounded by the circummarginal groove anteriorly and to some extent laterally, forms the *disk cover*. The more or less free anterior portion of the latter is the *ungual flap*. The relative size of the disk is significant. In most forms the disks are approximately the same size on all fingers and toes, but in one population the outer two fingers (III–IV) have much larger disks than the inner two (I–II).

The shapes of the disks on the fingers and toes often show significant differences between species in the genus. These differences are usually expressed in terms of the dorsal outline of the disk cover (ungual flap of Lynch, 1976) and the shape



**FINGER AND TOE DISK CHARACTER STATES**

FIG. 4. Standards for disk character states in *Eleutherodactylus*.










of the disk pad (fig. 4). Variation in these features in the *Eleutherodactylus gollmeri* group is relatively limited, but ranges from round and slightly expanded to slightly pointed disk covers, and from triangular, even to slightly cuspidate disk pads. Populations typically fall into one of the following categories:

- I. Fingers and toes—disk covers round, pads swollen
- II. Fingers—some or most disk covers slightly pointed to lanceolate, pads swollen to cuspidate  
Toes—disk covers rounded, pads swollen to cuspidate
- III. Fingers and toes—some or most disk covers slightly pointed to lanceolate, most pads swollen to cuspidate

**SUBARTICULAR TUBERCLES**—The tubercles under the joints of each finger and toe have three properties: basal outline, form, and profile. The different character states for each property are defined by illustration (fig. 5).

**HEEL, TARSAL, AND FOOT ORNAMENTATION**—The heel may be smooth, rugose, or granular. In some populations there are one to four obvious small pustular tubercles, while in others there are one or two relatively low to large conical tubercles

<u>BASAL OUTLINE</u>	<u>FORM</u>
○ round	
◌ ovoid	 flattened
◌ elongate	 projecting
◌ lanceolate	
<u>PROFILE</u>	
 globular	 obtuse
 conical	 pungent
	 pointed
Symmetric	Raised at Distal Margin

## DIGITAL TUBERCLES

FIG. 5. Standards for character states for subarticular tubercles in *Eleutherodactylus*.

## HEEL TUBERCLES

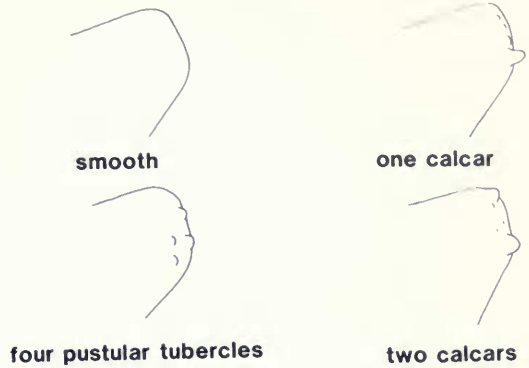


FIG. 6. Heel ornamentation in the *Eleutherodactylus gollmeri* group.

or calcars (fig. 6). While all members of the group have a distinct inner tarsal fold, some populations have a more or less well-developed series of two to six nonconical tubercles along the outer margin of the tarsal segment. The sole of the foot is smooth in some individuals, but several forms have a few (1–3) to several (4–7) very distinct plantar tubercles.

**TOE WEBS AND FRINGES**—Most members of the group have basal toe webbing with at least four phalanges of toe IV free of the web. These forms lack any sign of a toe fringe. One form has moderately webbed toes and a distinct fleshy fringe along all toe margins (fig. 7). Toe webbing for-

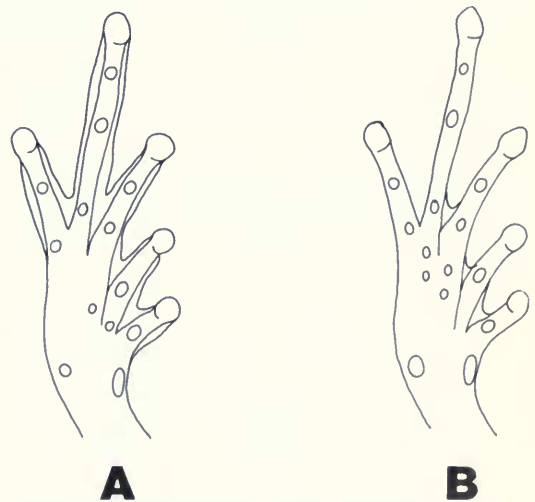


FIG. 7. Toe webbing and fringes in the *Eleutherodactylus gollmeri* group. A, moderate webbing and distinct fleshy fringes; B, basal webbing and no fringes.

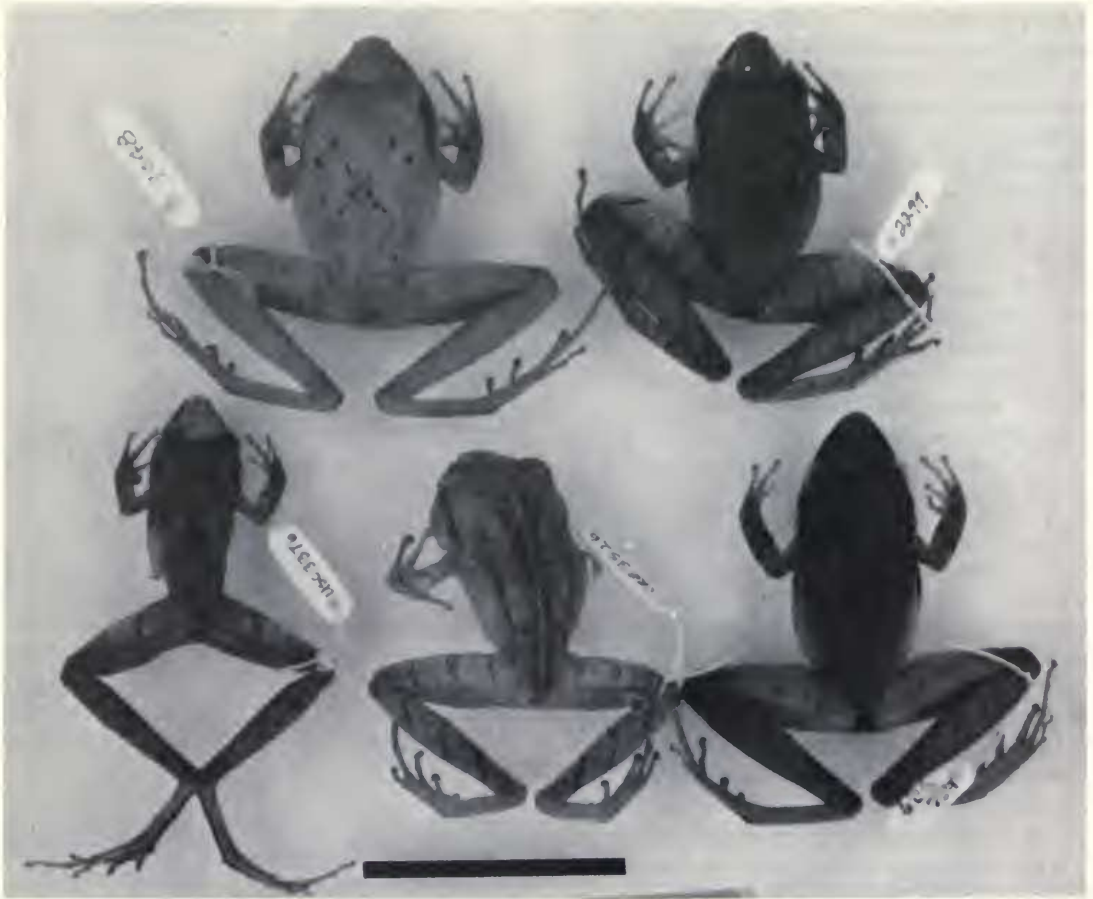


FIG. 8. Variation in dorsal color pattern in the *Eleutherodactylus gollmeri* group. **Upper left**, many pustules darkly pigmented and contrasting with light ground color; **upper right**, distinct dorsal dark figure; **lower left**, distinct light dorsal areas; **center**, hourglass-shaped dorsal dark marking; **lower right**, essentially uniform with paired paravertebral longitudinal dark areas. Specimens: *E. gollmeri* (upper left); *E. noblei* (center); other, *E. mimus*. Bar equals 40 mm.

mulae in the species accounts follow the system of Savage and Heyer (1969) as modified by Myers and Duellman (1982).

**COLORATION**—Seven features of coloration show evidence of populational consistency. These properties and their character states are described as follows:

1. While considerable variation in dorsal coloration is typical of most populations, one form consistently has the hourglass-shaped, dark, dorsal marking (fig. 8) which is only occasionally found in some other populations.
2. The posterior extent of the eye mask (fig. 9) seems constant for most samples. The mask may extend only to the tympanum ( $Z_3$ ) or a little beyond when continuous with the tym-

panic stripe; it may reach well beyond the axilla onto the body ( $Z_2$ ); or it may be reduced to a tympanic stripe above and behind the ear in individuals lacking an eye mask ( $Z_1$ ).

3. The pattern on the anterior surface of the thigh and lower limb is also relatively constant (fig. 10). In several populations the dorsal limb pattern is separated from the light ventral color by a dark brown stripe, serrate in dorsal outline, that runs along the anterior thigh surface for at least its distal one-third and continues around the knee as a distinct nonserrate dark line to the ankle (S). In other populations there is no distinct dark stripe along the thigh, but dark knee spots and a distinct dark stripe along the anterior surface of the lower leg are present (T). Finally, nei-

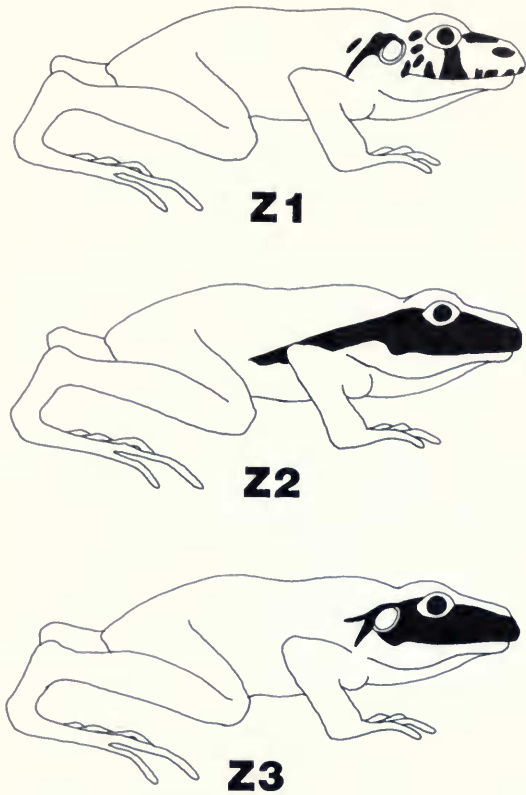


FIG. 9. Eye mask character states in the *Eleutherodactylus gollmeri* group (see p. 6 for descriptions).

ther a thigh nor a lower limb stripe is present, or at best is obscurely suggested, although dark knee spots may persist (U).

4. The presence or absence of a discrete, dark brown to black seat patch mark that contrasts strikingly with the dark pigment covering the posterior thigh, subanal, and posteroventral thigh surfaces is diagnostic of several populations (fig. 11). In forms having a dark seat patch mark, the mark is usually outlined by a light line to further contrast it with the adjacent areas. Some forms have the area above, lateral to, and ventral to the vent colored similarly to adjacent areas of the thigh region (A). In juvenile examples of these forms (under 20 mm in length), the subanal area may be somewhat darker than the adjacent thigh surfaces; a vague suggestion of a seat patch mark is indicated, and sometimes there is a concentration of dark pigment right at the vent opening in especially small individuals in these populations. Other populations may have a ring of dark pigment

around the vent (A'); a pair of distinct dark spots above and lateral to the vent, with the area immediately below the vent lighter than adjacent areas of the subanal and posterior thigh surfaces (the subanal region in these forms may be subtly outlined by darker pigment to suggest an obscure seat patch mark) (B); a dark, light-outlined, inverted V- or U-shaped seat patch mark, running from above the vent and downward for some distance to either side (C); a dark, triangular seat patch mark, with the apex above the vent and the darkest pigment along the lateral margins of the figure (D); or an essentially triangular dark seat patch mark with a very dark, round spot lateral to the apex of the figure on each side above the vent (E).

5. The posterior thigh surface is dark brown to reddish brown in most populations, but one population has the thigh area suffused with red in life. In large specimens of the largest species, there is some brown and yellow mottling on the lower posterior thigh surface, especially toward the midline.
6. The throat, venter, and undersurfaces of the forearm and thigh are usually nearly im-

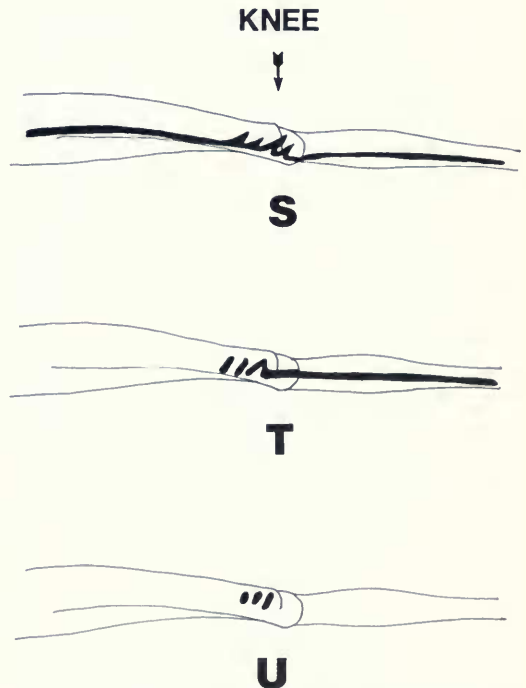


FIG. 10. Pattern on anterior surface of thigh and lower limb in the *Eleutherodactylus gollmeri* group; groin to left (see pp. 6-7 for descriptions).





FIG. 11. Standards for character states of dark seat patch marks in *Eleutherodactylus gollmeri* group.

maculate yellow (white in preservation). In some populations these surfaces are heavily mottled with brown pigment.

- Iris color (in life) is also distinctive. In most populations the upper half of the iris is bronze or yellow, but in some the upper portion is bright red. In all cases the lower half of the iris is dark brown.

**SIZE AND PROPORTIONS**—Within the genus *Eleutherodactylus*, several general categories based on the size of adults may be recognized:

huge	> 85 mm
large	60–85 mm
moderately large	45–60 mm
medium	30–45 mm
small	20–30 mm
pygmy	< 20 mm

Because of sexual dimorphism, males usually belong to the next smaller category than that of females of the same species. Frogs of the *E. gollmeri* group are medium to large members of the genus.

In the species accounts, standard lengths are given in millimeters; all other measurements are in percentages of standard length. Few, if any, measurements besides head width and hind limb length seem to distinguish populations within the genus. My experience also indicates that the relative proportions for most morphological features routinely recorded by workers on *Eleutherodactylus* rarely differ within the same general species group (*sensu* Savage, 1975, 1976). Lynch and Duellman (1980) reach a similar conclusion in their study of 45 Andean species belonging to several diverse species groups in the genus. For these reasons I provide a range of variation for the measurements used, utilizing a style of notation—12 (37–43.2–49)—where the number outside the parentheses is the number (N) of examples, the first value inside the parentheses is the minimum, the second the mean, and the last the maximum. It is not my intent to imply a greater significance to these values than they deserve, so I eschew the presentation of standard deviation and standard error values.

Available samples of most populations consist primarily of juveniles and subadult females. Adult males usually comprise a very small percentage of any sample, and fully mature females are not well represented in most cases. The limitations of mensural data based upon such small samples of adults further support the concept followed here, that proportional features are best expressed by ranges. The recent work of Lee (1982) on the almost random effects of time in preservative on morphometric variability in anurans, and his conclusion that the variability exceeds that often used to distinguish between related species, further supports this view. Standard length differences for adults among populations remain useful in distinguishing related but similar forms.

## The Southern Species

Three distinct species, *Eleutherodactylus gollmeri*, *E. mimus*, and *E. noblei* Barbour and Dunn, occur in the region from extreme eastern Honduras to eastern Panama. These forms are readily distinguished on the basis of relative finger disk size, presence or absence of one or two well-developed heel tubercles (calcars), amount of toe webbing, fringing, and coloration. Some past confusion regarding the identity and distribution of these species stems from the allocation of a number of juvenile *E. noblei* and several *E. mimus* to *E. gollmeri* by E. R. Dunn. Although Dunn (in Dunn & Emlen, 1932) recognized the differences between *E. gollmeri* and *E. noblei*, he subsequently misidentified specimens of the latter in several museums as *E. gollmeri*. His concept of *E. gollmeri* was further a composite which included examples of what was described as *E. mimus* by Taylor (1955).

The accounts presented below are based on an examination of all available specimens of the group from the area, with the aim of clarifying the status of and correct distribution for the three forms.

1. *Eleutherodactylus gollmeri* (W. Peters). Figures 8, 14.

*Hylodes gollmeri*: W. Peters, 1863 (holotype: ZMB 3168, an adult female; Panama: "Veragua" = western Panama, see Rivero, 1961, p. 173).

*Lithodytes lanciformis*: Cope, 1878 (lectotype, by present action: USNM 32324, a young male; west coast of Central America).

*Eleutherodactylus humeralis*: Fowler, 1916 (holotype: ANSP 19593, a female; Costa Rica: Limón: Guapiles, 262 m).

*Eleutherodactylus goldmani*: Noble, 1924 (holotype: USNM 54033, a female; Panama: Panamá: Cerro Brujo, ± 600 m).

DIAGNOSIS—*Eleutherodactylus gollmeri* may be easily distinguished from the two other members of the group (*E. mimus* and *E. noblei*) that overlap its geographic range. It differs most significantly from *mimus* (features for the latter species in parentheses) in its one or two well-developed heel calcars (absent), lack of well-developed toe fringes (present), basal toe webbing (moderate), and dark seat patch mark, almost always consisting of a pair of dark spots above and lateral to the vent and never forming an inverted V or U (dark seat patch mark an inverted V or U that extends ventrally below level of vent).

*Eleutherodactylus gollmeri* and *E. noblei* are also trenchantly distinct. The disks on the outer two fingers (III–IV) are distinctly larger than those on the inner (I–II) two of *E. noblei*; it also lacks heel tubercles, has several (4–7) distinct plantar tubercles and lacks a dark seat patch mark. In contrast, *E. gollmeri* has all finger disks about the same size, one or two well-developed calcars, no distinct plantar tubercles and has distinct dark seat patch marks. *Eleutherodactylus gollmeri* cannot be confused with the completely allopatric species *E. laticeps* of northern Central America and adjacent Mexico, since the latter (features for *E. gollmeri* in parentheses) has the heel smooth or granular (definite calcars), no dark seat patch mark (present), and the anterior thigh uniform (a distinct dark stripe present).

*Eleutherodactylus gollmeri* most closely resembles the upland Mexican and Guatemalan populations referred to *E. lineatus*, which has very strongly developed outer tarsal tubercles and a triangular dark seat patch mark that is continuous with the dark area on the thigh's posteroventral surface, while lacking the dark stripe along its anterior surface (in *E. gollmeri* the outer tarsal tu-

bercles are weak, the seat patch mark is usually a pair of separate dark spots above the vent that are always well-separated from the posteroventral dark thigh surface by a lighter area, and a distinct dark stripe is present along the anterior thigh surface).

*Eleutherodactylus gollmeri* may be separated from the allopatric species *E. rostralis*, of Atlantic-versant Guatemala and Honduras, by morphology and coloration. The latter name has sometimes been placed with *E. gollmeri*, but *rostralis* and its smaller ally, *E. chac* (see its species account below), have 1–4 pustular tubercles on the heel versus 1–2 conical calcars in *gollmeri*. In addition, *E. gollmeri* has a distinct dark line along the anterior surface of the thigh (absent in *E. rostralis*), while the dark seat patch mark usually is a pair of dark spots located above and lateral to the vent and always separated from the dark area on the posteroventral thigh surface by a light area (dark seat patch mark triangular, continuous with posteroventral dark thigh area, and usually with a pair of dark spots lateral to the apex of the seat patch mark in *E. rostralis* and *E. chac*).

SUMMARY OF CHARACTERISTICS—Snout subelliptical in dorsal outline; from side, snout rounded and protruding well beyond lower jaw. Vertical diameter of tympanum in males greater than orbital diameter, about equal in females. Dorsum smooth but usually a series of well-developed tubercles (supratympanic and suprascapular); no suprascapular fold; no distinct dorsolateral glandular ridge. Finger disks barely expanded, all about same size, inner fingers (I–II) with rounded disk covers and swollen disk pads, outer two (III–IV) with lanceolate disk covers and cuspidate disk pads. Subarticular tubercles on fingers and toes ovoid, projecting, and obtusely raised (pungent in juveniles). Thenar tubercle elongate, palmar ovoid and usually bifurcate; a few distinct accessory palmar tubercles. One or two distinct heel calcars; toe disks barely expanded, rounded to pointed; some disk pads cuspidate. No fleshy toe fringes. Toes with basal webbing, modal toe webbing formula: I 2–2½ II 2–3¼ III 3–4 IV 4½–3 V. A distinct elongate raised inner and a small round outer metatarsal tubercle; inner tarsal fold and an outer row of very weak tarsal tubercles present; no plantar tubercles.

DISTINCTIVE FEATURES OF COLORATION—A narrow light middorsal line usually present. Dark eye mask extends beyond axilla onto body; occasional specimens lack eye mask and have a series of dark



FIG. 12 (upper left). *Eleutherodactylus chac*, southwest Santo Tomás, Izabal, Guatemala; courtesy of Linda S. Ford.

FIG. 13 (upper right). *Eleutherodactylus lineatus*, KU 181173, 3.8 km southeast Purulha, Baja Verapaz, Guatemala; courtesy of Jonathan A. Campbell.

FIG. 14 (lower left). *Eleutherodactylus gollmeri*, Fila Comadre, Limón, Costa Rica; courtesy of R. Wayne Van Devender.







FIG. 16. *Eleutherodactylus noblei*, La Selva, Heredia, Costa Rica; courtesy of Maureen A. Donnelly.



FIG. 15. *Eleutherodactylus mimus*, La Selva, Heredia, Costa Rica; courtesy of R. Wayne Van Devender.

lip bars and a supratympanic mark. A definite serrate dark stripe on anterior thigh surface continues as a distinct dark stripe along anterior margin of lower leg. Seat patch mark almost always a pair of dark brown spots above and lateral to vent; sometimes spots fused or extended ventrally for a short distance, discontinuous from dark posterior thigh surfaces. Posterior thigh surface rust-colored in life, brown in preservative, not suffused with red in life. Sole of foot and underside of tarsus uniform dark brown. Undersides of forearm, thighs, throat, and venter nearly immaculate. Iris chestnut red in life.

**COLOR VARIATION**—Variation was analyzed in detail for a single sample of 92 individuals (CRE 232, 234, 235, 237) from El Silencio de Sitio Mata, Cartago, Costa Rica, which encompassed the range found within the species. The most common pattern (47%) consists of a light brown to medium brown ground color, with a thin yellow middorsal stripe; black posterior suprascapular pustules, often with light centers; and a pair of more or less well-developed, short, elongate, paravertebral dark areas near midbody (fig. 8). A similar pattern, lacking the suprascapular spots, comprises 10% of the sample, while a third variant, in which the paired paravertebral dark areas are broken up into three or four pairs of discrete dark spots, occurs in 4% of the sample. In many individuals, the pattern consists of a more or less well-developed contrasting dark figure (fig. 8) and a series of one to four large roundish obscure light spots scattered anterior to the figure (27%). Within this subsample 60% of the individuals have dark posterior suprascapular spots, but these are lacking in the remaining 40%. A striking variant (fig. 8) has a rather light dorsal ground color with a series of very distinct black spots scattered on the dorsum (7.6% of the sample). These include the posterior suprascapular spots and usually several in the paravertebral area, but some may be present elsewhere. Three frogs having this pattern have the side of the head barred; the other four have dark eye masks (fig. 1). All examples in this sample have a narrow interorbital dark line and an upper snout somewhat lighter in color than adjacent areas.

**MEASUREMENTS (IN MM)**—Adult males 10 (30–32.6–36.5) in standard length, adult females 4 (45–48.3–54); smallest juvenile 9. Head width 40–41.4–43 in males, 41–44–47 in females; hind limb 194–200–207 in males, 204–212–220 in females.

**REMARKS**—The original description (Peters, 1863) of this form was based on an example (ZMB

3168) presumed to have been collected from Caracas, Distrito Federal, Venezuela. Although Dunn examined the type in 1928–1929 and realized that it was conspecific with Central American species (Dunn & Emlen, 1932), it was Rivero (1961, p. 173) who determined the probable source of the erroneous data. He concluded that the locality data associated with the syntypes (ZMB 3387, 3 examples) of *Phryndium crucigerum* Lichtenstein & von Martens (1856) had been inadvertently exchanged with those for the type of *Hylodes gollmeri*. Since the former is now regarded as a distinct species of *Atelopus* endemic to the Cordillera de la Costa of Venezuela and the latter is known only from lower Central America, this deduction seems valid. In addition, even today, types in the Berlin Museum are identified by numbered paper slips that are placed in the appropriate jars but are not attached to the specimens. It is almost certain that the types of *Eleutherodactylus gollmeri* were collected by Josef Warszewicz, whose activities I have reviewed elsewhere (Savage, 1970, 1972) and who collected other herpetological material from areas where *E. gollmeri* is known to occur.

Because of the type locality confusion, most authors called this species *lanciformis* between 1878 and 1932. Reexamination of the syntypes of this name confirms their identity with *Eleutherodactylus gollmeri*. They share with this form the heel tubercle, webbing, and coloration features that distinguish it from other members of the group. For the sake of nomenclatural stability, USNM 32324, a young adult male 24 mm in length, is herewith designated the lectotype of the name.

In 1916 Henry Weed Fowler described a new species in this complex as *Eleutherodactylus humeralis*, from the lowlands of Costa Rica. Dunn and Emlen (1932) regarded this name as a synonym of *E. gollmeri*. Allocation of the name has been one of the most difficult tasks of this review. The female holotype (ANSP 19593) is 33 mm in standard length and exhibits, as far as can be determined, the typical features of *E. gollmeri*. Nevertheless, the locality data create a problem, since *E. gollmeri* is known only from above 600 m in elevation in Costa Rica, north of the Talamanca Valley near the Panama boundary. The type locality of *E. humeralis* is in lowland northeastern Costa Rica at 262 m. All other specimens of this group from northwestern Costa Rica taken from 0–600 m are examples of the related but distinctive species *E. mimus*. In fact, the latter form is known from the type locality of *E. hu-*

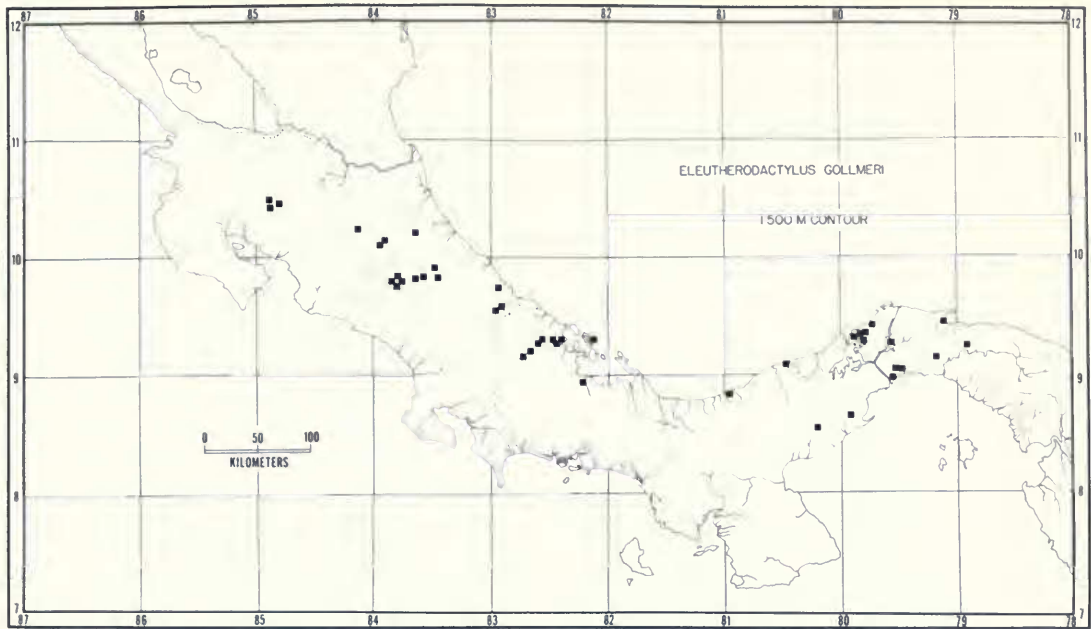


FIG. 17. Geographic distribution of *Eleutherodactylus gollmeri*. The dotted line indicates the 1500 m contour.

*meralis* at Guapiles based on a single subadult specimen (MCZ 7968).

The situation is compounded by the condition of the holotype, which appears to have partly dried out since Fowler's description, as the hindlimbs and feet are desiccated and brittle. Careful examination and direct comparisons with well-preserved examples of similar-sized *Eleutherodactylus gollmeri* and *E. mimus*, from Costa Rica, convince me that the type of *E. humeralis* belongs here. Although obscured by the damage caused by loss of fluid, a remnant of the heel calcar is evident and no suggestion of well-developed toe fringes is present. Finally, the dark seat patch mark typical of *E. gollmeri* is present, rather than the inverted or U-shaped mark of *E. mimus*. For these reasons I regard *E. humeralis* as a synonym of *E. gollmeri*.

The altitudinal distributions of *Eleutherodactylus gollmeri* and *E. mimus* in northeastern Costa Rica, exclusive of the Guapiles records, are 640–1500 m and 15–640 m, respectively. Very few records for *E. mimus* from 250–640 m are known, and it may be that the two species overlap more extensively than available material suggests. In extreme southeastern Costa Rica and Panama, where no *E. mimus* are known, *E. gollmeri* occurs down to a few meters above sea level.

Some geographic variation in the rugosity of the

dorsum and the degree of development of the heel calcars is suggested in the material at hand. Generally speaking, examples from southwestern, central, and eastern Panama tend to have the dorsum more tuberculate than Costa Rican examples. Many of these individuals have two well-developed heel tubercles, one large calcar on the distal portion of the heel and a second smaller one in the proximal area. The heel is more rugose in these examples as well. In most Costa Rican examples the dorsum is finely shagreened and only the distal heel calcar is developed. Examples from northwestern Panama and lowland southeastern Costa Rica are intermediate in these features.

Although Dunn and Emlen (1932) and Meyer and Wilson (1971) cite the range of this form as extending from Guatemala to Panama, the species is restricted to Costa Rica and Panama. All presumed Nicaraguan records for the species are based on juvenile *Eleutherodactylus noblei* or *E. mimus*. Honduran frogs referred to this form belong to three other species, *E. chac*, *E. laticeps*, and *E. rostralis*.

**DISTRIBUTION**—Evergreen forests of the lowlands and premontane slopes of eastern and central Panama (10–850 m), northwestern Panama (10–1450 m), and lowlands of adjacent extreme southeastern Costa Rica and the premontane zone



of northeastern Costa Rica (50–1500 m); one record from the lowlands (262 m) of northeastern Costa Rica at Guapiles (fig. 17).

**LOCALITIES—COSTA RICA:** **Alajuela:** Isla Bonita; **Cartago:** Altos Piedras Grandes; Cachí; Guabata; Moravia de Chirripó; Navarro; El Silencio de Sitio Mata; La Suiza; Tapanti; **Guanacaste:** El Silencio de Tilarán; San Bosco; **Limón:** Bambú; Comadre; Guapiles; Suretka; El Tigre; **San José:** La Hondura, La Palma. **PANAMA:** **Bocas del Toro:** 4.8, 5, 12.8 km W, 11 NW, and Almirante; Isla Bastimentos; Río Changena; La Loma; N slope Cerro Pando; **Coclé:** El Valle de Antón; **Colón:** Brazos del Medic, Río Cuango; SW slope Cerro Bruja, 3.5, 4 km SE; Río Coclé de Norte, Río Guanache; Puerto Pilon; Santa Rita ridge; **Panamá:** Cerro Azul; Cerro Bruja; Cerro Campana; btwn. Candalaria and Peluca Stations; Índio; kms 9, 11.7, 18, 22.6, El Llano-Cartí rd.; Madrona; 4.8 km N and Altos de Pacora; Panamá Viejo; Río Silugandi; Finca La Sumadora; **San Blas:** Niceusa; Camp Summit; **Veraguas:** Mouth Río Concepción.

## 2. *Eleutherodactylus mimus* Taylor. Figures 8, 15.

*Eleutherodactylus mimus* Taylor, 1955 (holotype: KU 37128, an adult male; Costa Rica: Guanacaste: San Bosco: 5 km NNE Tilarán, 64 m).

**DIAGNOSIS—**This species is uniquely distinct from all other members of the group in having substantial toe webbing (enclosing the basal subarticular tubercles on toes I–IV), well-developed fleshy toe fringes, and the characteristic inverted V- or U-shaped dark seat patch mark. In addition, the absence of definite heel tubercles or calcars separates *Eleutherodactylus mimus* from *E. chac*, *E. gollmeri*, *E. lineatus*, and *E. rostralis*, which have one or more distinct heel tubercles or calcars. *Eleutherodactylus mimus* may be further distinguished from the two other members of the group lacking heel tubercles: (a) *E. noblei* (features for *E. mimus* in parentheses), which has the outer two finger disks III–IV much larger than those for fingers I–II (about same size); and (b) *E. laticeps*, which has only basal toe webbing (substantial webbing), lacks a dark stripe on the anterior thigh surface (present), and lacks the inverted U- or V-shaped dark seat patch mark (inverted U- or V-shaped dark seat patch mark present).

**SUMMARY OF CHARACTERISTICS—**Snout pointed in dorsal outline; from side, snout rounded and protruding well beyond lower jaw. Vertical diameter of tympanum about equal to diameter of

orbit in males, smaller than orbit in females. Dorsum essentially smooth except for paired supratympanic and suprascapular tubercles; a definite supratympanic ridge; no distinct dorsolateral ridge; no suprascapular fold. Finger disks on I–II rounded, III–IV slightly expanded, only slightly broader than digits; disk pads swollen. Subarticular tubercles on fingers and toes round, projecting, and globular. Thenar tubercle ovoid to elongate, palmar tubercle bifurcate or cordate; two to three low accessory palmar tubercles. No heel calcar. Moderate rounded toe disks enclosed in a definite toe fringe that is continuous with webs; toe pads swollen. Toes extensively webbed, modal toe webbing formula: I 1– $\frac{3}{4}$  II 2– $\frac{3}{2}$  III 2 $\frac{1}{2}$ – $\frac{3}{4}$  IV 4– $\frac{2}{2}$  V. A distinct raised elongate inner and a very small round outer metatarsal tubercle; tarsus smooth except for inner tarsal fold; no outer row of tarsal tubercles; 0–3 plantar tubercles. Ventral disk thickened and darkened in large females (55+ mm).

**DISTINCTIVE FEATURES OF COLORATION—**A thin, middorsal light line invariably present. Dark eye mask always extending well posterior to axilla. A serrate dark line along anterior surface of thigh and continuing as a distinct, even dark stripe from knee to ankle. An inverted dark V- or U-shaped seat patch mark discontinuous from dark posterior thigh surfaces. Posterior thigh surface brown, not suffused with red in life. Undersides of forearms, thighs, throat, and venter nearly immaculate. Iris yellow in life.

**COLOR VARIATION—**The range of variation for this species is encompassed in a sample of 34 frogs from La Selva, Heredia, Costa Rica. The dorsal ground color varies from tan to medium brown. The upper surface of the snout is usually lighter than the body and bounded posteriorly by a narrow black interorbital line, and frequently this area is gray to almost white. Most individuals have a distinct dorsal dark figure (fig. 8), with one to three large, more or less obscure, light spots and distinct black posterior suprascapular spots (26%). Others lack the light spots (23%), while a few (8%) lack the light snout and light dorsal spots.

Most other examples have an essentially uniform dorsum color with black suprascapular spots and paired paravertebral longitudinal dark areas (12%) with paravertebral dark areas but no suprascapular spots (15%); or without paravertebral dark areas but with suprascapular dark spots (12%); or with suprascapular dark spots and several light dorsal spots (3%).

**MEASUREMENTS (IN MM)—**Adult males 11 (30–34.4–37) in standard length, adult females 10 (45–



FIG. 18. Geographic distribution of *Eleutherodactylus mimus*.

52.0–58); smallest juvenile 14. Head width 36–37.4–38 in males, 37–39.4–42 in females; hind limb 184–190–195 in males, 195–205–215 in females.

REMARKS—*Eleutherodactylus mimus* has been confused with *E. gollmeri* by previous workers. All records of *E. gollmeri* from Nicaragua and most records from the Atlantic lowlands of northeastern Costa Rica (except for the type of *E. humeralis* from Guapiles) are based on *E. mimus*. *Eleutherodactylus gollmeri* is not known to range north of the Tilarán-Arenal region of northeastern Costa Rica, which marks the northern boundary of the continuous cordilleras where *gollmeri* is found. *Eleutherodactylus mimus* is essentially a

lowland species while, in most of Costa Rica, *E. gollmeri* occurs at higher elevations, although it is found near sea level in extreme southeastern Costa Rica and adjacent areas of Panama.

DISTRIBUTION—Evergreen lowland and premontane forests on the Atlantic versant from eastern Honduras (500 m), through Nicaragua (100–940 m), to central Costa Rica (15–640 m) (fig. 18).

LOCALITIES—COSTA RICA: **Alajuela**: Boca de Arenal; **Guanacaste**: Arenal; Finca San Bosco; 5 km NNE Tilarán; **Heredia**: 4–6 km E and Puerto Viejo; Río Frío; La Selva; **Limón**: Bri-Bri; La Castilla; Guapiles. **HONDURAS**: **Olancha**: 40 km E Catamacas. **NICARAGUA**: **Matagalpa**: 19 km N and Matagalpa; **Zelaya**: Musawas on Río Huaspu.

3. *Eleutherodactylus noblei* Barbour and Dunn.  
Figures 8, 16.

*Eleutherodactylus noblei*: Barbour and Dunn, 1921  
(holotype: MCZ 7827, an adult female; Costa Rica:  
Limón: Guapiles, 262 m).

DIAGNOSIS—This form is distinct from all other members of the group in having the disks on the two outer fingers (III–IV) much larger than on the inner fingers (I–II). It is further distinguishable from *Eleutherodactylus chac*, *E. gollmeri*, *E. lineatus*, and *E. rostralis* by its lack of heel tubercles (one to three distinct tubercles in the latter species). In addition, *E. noblei* cannot be confused with the other two members of the group also lacking large heel calcars (*laticeps* and *mimus*), since it has toe webbing (only a trace in *laticeps*), although less than in the moderately webbed *E. mimus*, and lacks well-developed fleshy toe fringes (present in *mimus*).

SUMMARY OF CHARACTERISTICS—Snout pointed in dorsal outline; from side, snout rounded and protruding well beyond lower jaw. Vertical diameter of tympanum about equal to orbital diameter in males, less than orbital diameter in females. Dorsum weakly granulate; dorsal tubercles weakly developed or absent or, when present, usually only supratympanic or anterior suprascapular tubercles evident; suprascapular fold usually present; a well-developed dorsolateral glandular ridge from eye nearly to groin. Finger disks on I–II about as broad as digit, round to weakly pointed; disks on fingers III–IV distinctly larger than those on fingers I–II, palmate, about twice as broad as digits; disk pads on I–II weakly swollen, on III–IV even. Subarticular tubercles on fingers and toes rounded, projecting, and obtusely raised. Thenar tubercle elongate, about half as large as bifurcate palmar tubercle; no definite accessory palmar tubercles. No heel calcar. Toe disks moderately rounded, only slightly wider than digits; toe pads cuspidate. No fleshy toe fringes. Toes with basal webbing; modal webbing formula: I 2<sup>+</sup>–2<sup>+</sup> II 2<sup>+</sup>–3<sup>4</sup>/<sub>4</sub> III 3–4<sup>4</sup>/<sub>4</sub> IV 4<sup>4</sup>/<sub>4</sub>–3 V. A distinct elongate inner and a very small ovoid outer metatarsal tubercle; tarsus smooth except for inner tarsal fold; several (4–7) distinct plantar tubercles. Ventral disk thickened and darkened in largest females (55+ mm).

DISTINCTIVE FEATURES OF COLORATION—A thin middorsal light line is usually present. Usually a distinct brown hourglass-shaped mark on back which may be outlined by a light border; usually

a series of dark stripes in dorsolateral and/or flank region. Dark eye mask always extending well posterior to axilla, although obscure or faded in some specimens long in preservative; usually no distinct dark line along anterior thigh surface, usually none along lower leg. No dark seat patch. Posterior thigh surface uniformly brown or gray, suffused with red in life. Undersides of forearms, thighs, throat, and venter usually immaculate; a few examples with heavy flecking of brown, especially on throat and under limbs. Iris gold in life.

MEASUREMENTS (IN MM)—Adult males 4 (43–48.5–53) in standard length, adult females 5 (58–62.3–66); smallest juvenile 17. Head width 40–42–46 in males, 41–42.8–45 in females; hind limb 160–181.5–198 in males, 160–178–193 in females.

REMARKS—Although Barbour and Dunn (1921) recognized and clearly defined this distinctive form, the latter identified a considerable number of juvenile *Eleutherodactylus noblei* as *E. gollmeri* over subsequent years. Reexamination of all Central American material seen by Dunn indicates that most previous records of *E. gollmeri* from Nicaragua are based on *E. noblei*, although a few are representatives of *E. mimus*. Similarly, a number of lowland Costa Rican records for *E. gollmeri* are based on *E. noblei* and *E. mimus*. *Eleutherodactylus gollmeri* occurs only from northwestern Costa Rica to eastern Panama. It does not occur in Honduras, Nicaragua, or southwestern Costa Rica and adjacent western Panama. *Eleutherodactylus noblei* occurs in all of these places, while *E. mimus* is restricted to the Atlantic versant from central Costa Rica to eastern Honduras.

Most *Eleutherodactylus noblei* are light tan in ground color (fading to pale gray in preservative), with the thigh region suffused with bright red; frequently the rest of the body is covered with a pinkish wash. A number of large females from widely scattered localities (Las Cruces, La Selva, and San Isidro de El General) in Costa Rica are extremely dark above, with extensive dark markings ventrally. The more typically colored frogs occur at the latter two sites, along with these morphologically identical individuals. Representatives of the dark chromas had bright red suffusions over the thighs in life, to further agree with other animals referred to this species.

DISTRIBUTION—Lowland and premontane evergreen forests from extreme eastern Honduras, south on the Atlantic versant through Nicaragua and Costa Rica, onto both slopes in central Pan-



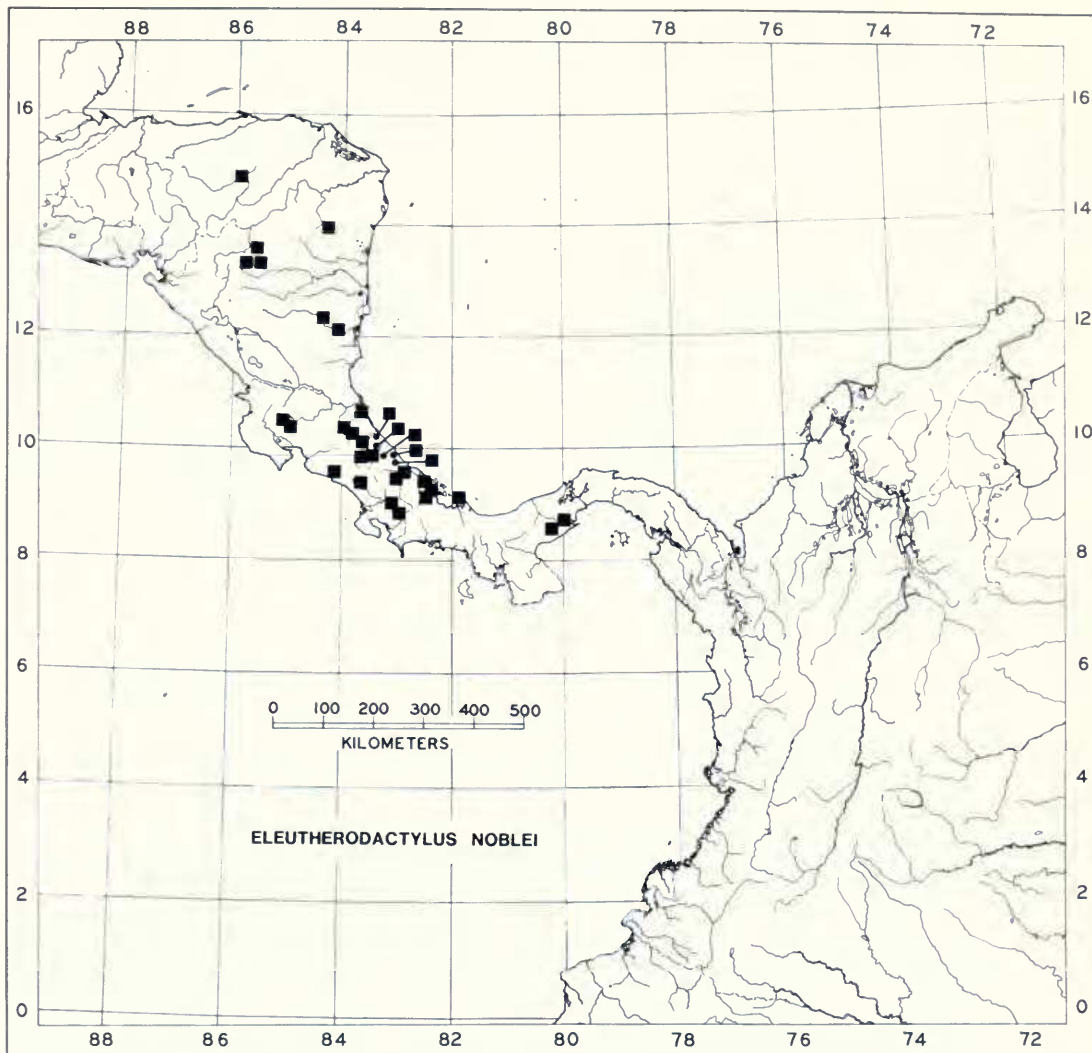


FIG. 19. Geographic distribution of *Eleutherodactylus noblei*.

ama, west of the Canal; also in the lower portion of the premontane zone of southwestern Costa Rica, 4–1200 m (fig. 19).

**LOCALITIES—COSTA RICA:** Cartago: Morehouse Finca; El Silencio de Sitio Mata; La Suiza; Guanacaste: El Silencio de Tilarán; Tilarán; Heredia: 6 km E Puerto Viejo; La Selva; Limón: 8 km SW Amubri; Batan; La Castilla; Los Diamantes; La Emilia; Guapiles; La Lola; Pandora; Penshurst; Suretka; Cerro Tortuguero; Vesta; Puntarenas: Las Cruces; Pozo Azul de Pirris; San José: San Isidro de El General. **HONDURAS:** Olancha: 2.5 km NW Catamacas. **NICARAGUA:** Mata-

galpa: La Cumplida; 19 km N and Matagalpa; Río San Juan: Río Escondido, 80 km W Bluefields; Zelaya: Eden Mine; Río Mico, 16 km W El Recreo. **PANAMA:** Bocas del Toro: 11 km N, 3 km W and Almirante; Río Changena; Bluefields, Peninsula Valiente; Coclé: El Valle de Antón; La Mesa, El Valle de Antón; Panamá: La Campana.

### The *Eleutherodactylus laticeps* Problem

The name *Hylodes laticeps* was proposed by A. Duméril (1853) for a single large (75 mm) female

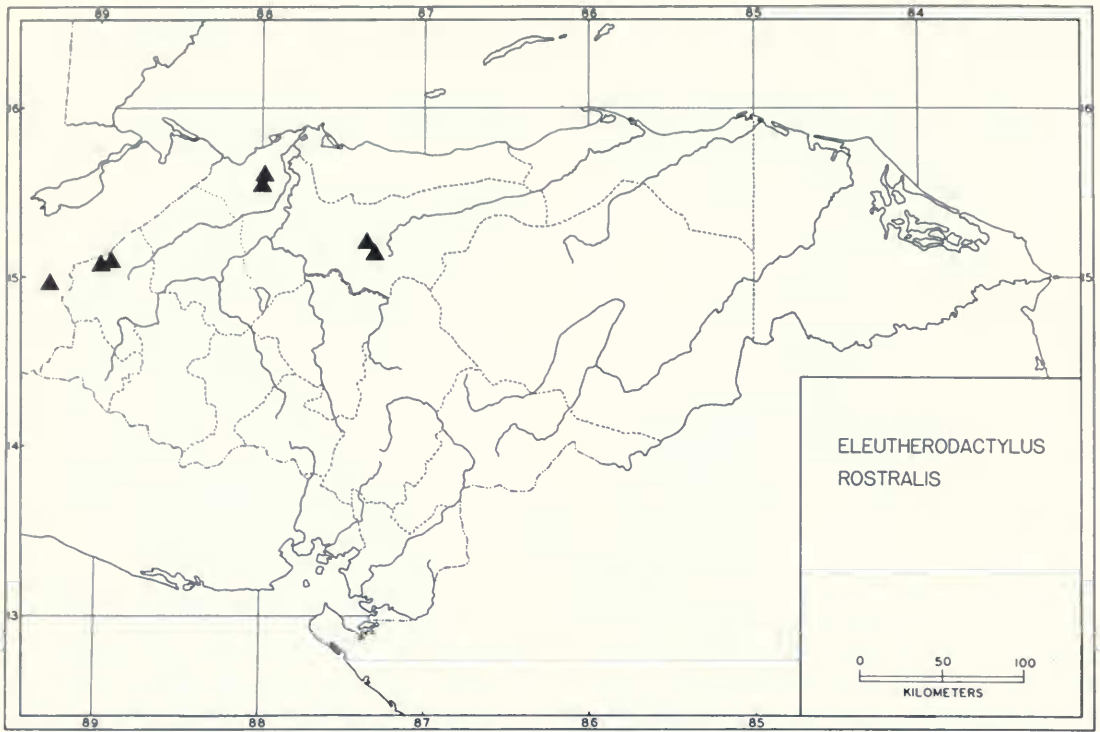


FIG. 20. Geographic distribution of *Eleutherodactylus rostralis*.

frog, with a broad head, short legs, barred lips, and ventral disk markedly thickened and somewhat darkened. The animal had been taken by Pierre-Marie Arthur Morelet during his visit to southern Mexico and Guatemala in 1847–1848 and labeled simply Yucatán, Central America. Although re-described by Kellogg (1932) and listed by Smith and Taylor (1948), no additional examples, besides the type, were reported prior to the discussion by Firschein (1951) of a second specimen (UIMNH 11301) from Palenque, Chiapas, Mexico, 244 m.

Two other examples, from the foothills of the Maya or Cockscomb mountains of Belize, formed the type series of a new species, *Eleutherodactylus stantoni*, proposed by Schmidt (1941). Stuart (1948) reported an additional example from Alta Verapaz, Guatemala. Both of these workers regarded *E. stantoni* as close to *E. laticeps* but having longer legs and, instead of lip bars, a dark eye mask. Firschein (1951) reexamined the latter frogs and, supplied with detailed notes on the holotype of *E. laticeps* by J. Guibé at the Paris Museum, concluded that the four examples represented two different species. He separated *E. laticeps* from *E.*

*stantoni* (contrasting features for *E. stantoni* in parentheses) on the basis of the presence of a transverse scapular fold (absent); short legs, the tibiotarsal articulation reaching to between eye and nostril when leg is extended forward (to snout or beyond), and unspecified color pattern differences. Since Firschein was not very familiar with other species of the *E. gollmeri* group from elsewhere in Central America, he regarded *E. laticeps* and *E. stantoni* as forming a distinct group.

Shreve (1957), in a paper apparently overlooked by most subsequent workers, recorded *Eleutherodactylus laticeps* from the Lacandón region of Chiapas, Mexico, about 80 km southeast of Palenque.

Stuart (1963) followed Firschein's (1951) conclusions, but Neill (1965), who examined an additional Belize specimen (MCZ 38000), now lost, disagreed. After comparisons with published descriptions, Neill concluded that his Belize frog was conspecific with the types of *Eleutherodactylus stantoni*, the Palenque specimen, and the type of *E. laticeps*. He was uncertain regarding the Alta Verapaz example, but used the name *E. laticeps* for the other four specimens. Lee (1980) followed

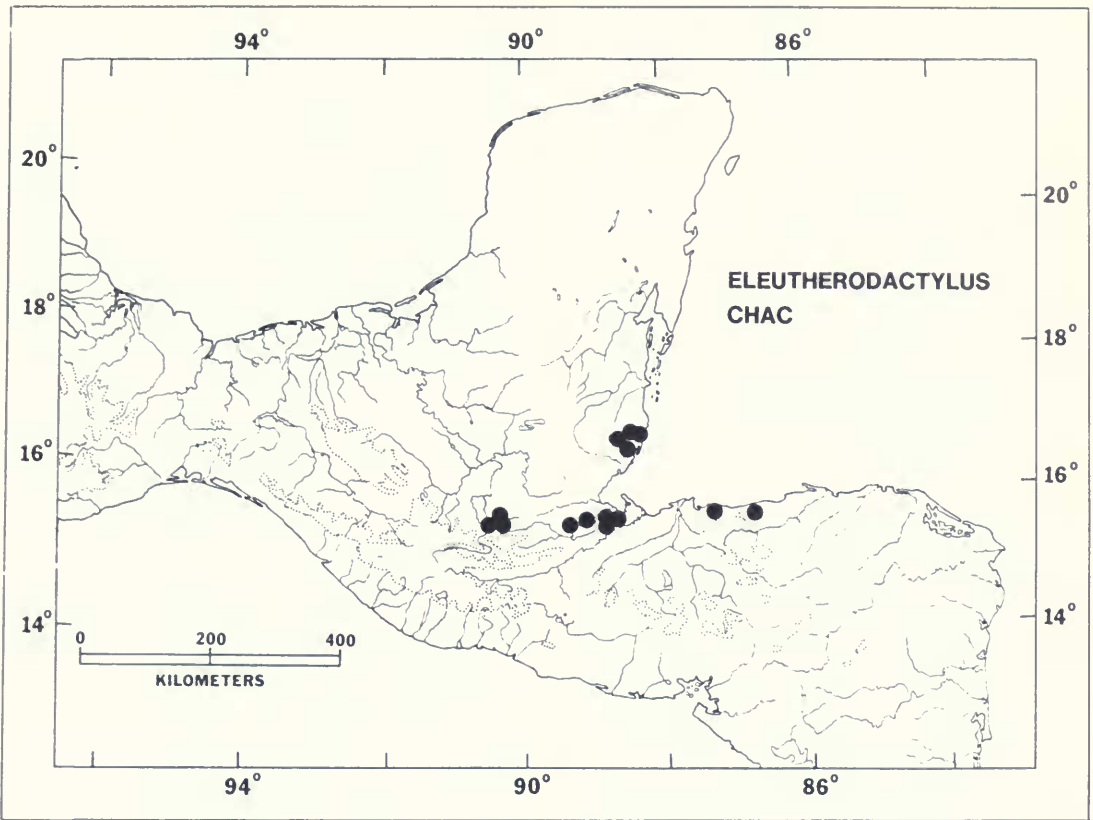


FIG. 21. Geographic distribution of *Eleutherodactylus chac*. The dotted line indicates the 1500 m contour.

Neill's (1965) conclusion that *E. laticeps* and *E. stantoni* are conspecific.

Meyer and Wilson (1971) reported a single female (USNM 21281) 70 mm in length, with locality data of "Honduras", as *Eleutherodactylus laticeps*. These authors emphasized the barred upper lip and the lack of a dark eye mask in this example to link it with the similarly marked type of that name. Presumably they regarded *E. stantoni* as distinctive in having a dark eye mask.

Lynch and Fritts (1965) described a new species, *Eleutherodactylus werleri*, on the basis of a single large male (43 mm in standard length) from the Los Tuxtlas region of Veracruz, Mexico. Although the describers and Lynch (1976) regarded this form as allied to *E. lineatus*, it differs from that form in lacking heel calcars and the dark seat patch mark. Reexamination of the holotype and only known specimen (UIMNH 42987) supports the surprising view that this frog is related to *E. laticeps* and *E. stantoni*.

In the course of the present study I have seen all examples involved in the problem as reported in the literature (except MCZ 38000, which is lost). I have also examined additional material from Honduras allied to *Eleutherodactylus laticeps* or *E. stantoni* but erroneously identified as *E. rhodopis* (Lynch & Fugler, 1965) and *E. gollmeri* (Meyer & Wilson, 1971). Finally, a beautiful living series of the population system from Alta Verapaz, Guatemala, and others from elsewhere in that country have been made available to me through the good offices of W. E. Duellman and D. B. Wake, of the Universities of Kansas and California (Berkeley), respectively.

These frogs are all clearly representative of the *Eleutherodactylus gollmeri* group as defined in this paper and further share the following combination of diagnostic characteristics: heel smooth or rugose, no dark seat patch mark, dorsum granulate and usually with a distinct suprascapular fold, and dorsolateral glandular ridges in living and well-



preserved animals. Frogs having these features occur as a system of eight allopatric populations, as follows (in order from north to south; numbers in parentheses indicate sample size):

- A. Volcán San Martín Pajapán, Veracruz, Mexico; 1219 m (1)
- B. Eastern Chiapas, Mexico; 244–950 m (6)
- C. Eastern Huehuetenango, Guatemala; 1200 m (4)
- D. Belize; 400–500 m (3)
- E. Alta Verapaz, Guatemala; 875–1600 m (25)
- F. Sierra de las Minas, Guatemala; 50–744 m (11)
- G. Lago de Yojoa Valley, Honduras; 750 m (22)
- H. Cordillera de Nombre de Dios, Honduras; 1270 m (1)

Three principal questions need to be answered in relation to this population system:

- 1. Which features of individual variation have contributed to misunderstanding the status of these frogs?
- 2. Is more than a single species represented by the system?
- 3. To which population or populations is the name *Hylodes laticeps* applicable?

Several features that are influenced by the nature and extent of preservation or show intrapopulation sample variation have been used as a basis for recognizing *Eleutherodactylus stantoni* as distinct from *E. laticeps*, or for combining the two nominal species. The two largest samples (E and G), from Guatemala and Honduras, respectively, provide data especially useful in evaluating the significance of these features: 1) dorsal granulation and fold and ridge development; 2) nature of the ventral disk; 3) head width; 4) leg length; 5) presence or absence of a dark eye mask; and 6) dorsal coloration.

In living, freshly or well-fixed examples, the dorsum is granulate or shagreened. Differences in description, preservation technique, and length of time since fixation are artifacts accounting for Firschein's (1951) use of this feature to separate *Eleutherodactylus laticeps* from *E. stantoni*. All available examples from Mexico, Guatemala, and Belize exhibit this feature, except one Alta Verapaz example (UMMZ 90958). Most of the Honduran frogs appear to have smooth dorsums, except on the very largest female (USNM 21281). Living and well-preserved specimens usually have the suprascapular fold indicated, and all examples have well-developed dorsolateral glandular ridges. The fold

is least obvious in young individuals and is barely suggested in most Lago de Yojoa Valley (G) specimens. The glandular dorsolateral ridges are best developed in large individuals and are least developed in the Yojoa series as well.

The excessive development of the ventral disk found in the holotype of *Eleutherodactylus laticeps* occurs in all large females (60–80 mm in length). Young frogs and adult males lack the extreme hypertrophy characteristic of large adult females. In addition, as the tissue of the disk thickens, keratin appears to be laid down on its surface to further thicken the skin and to produce a brown color overlying most of the disk surface. Examples from samples B and E, the large female labeled "Honduras", and the type of *E. laticeps* show maximum hypertrophy, keratinization, and darkening of the disk region. Since no adult females are represented in samples C, D, and F, it can only be assumed that a similar change in disk structure will be found when more material is available. In the Lago de Yojoa Valley series (G), the three largest females, 60–62 mm in length, show considerable thickening of the disk but no keratinization.

The degree of hypertrophy and keratinization of the ventral disk must be regarded as a sexually dimorphic, ontogenetic change that culminates with the extreme development seen in large females of 70–80 mm in length. No other member of the genus, insofar as I am aware, exhibits a comparable feature, and its presence supports the relatedness of the several samples in which it appears.

The trivial epithet *Eleutherodactylus laticeps*, the oldest name for these populations, emphasizes the relatively broad head found in the type and used by Schmidt (1941) and Stuart (1948, 1963) as one basis for recognizing *E. stantoni* as distinct. The feature is sexually dimorphic and, contrary to Schmidt (1941) and Neill (1965), it is large females, *not* males, that have the most broadened heads. In adult males the range of head width as a percentage of standard length is 34–39–43; in large females 50 mm or more in standard length, the range is 39–44–49. There are no significant differences in this feature among the available samples. The holotypes of both *E. laticeps* (75 mm in standard length) and *E. stantoni* (52 mm) are females, with head width proportions of 41 and 44, respectively.

The holotype of *Eleutherodactylus laticeps* has extremely short legs (161 of the standard length), while those of *E. stantoni* are much longer (190 and 185, in the holotype and paratype, both fe-

males, respectively). Firschein (1951) evaluated this difference by appressing the leg forward against the body and determining how far forward the tibiotarsal articulation lay. He characterized *E. laticeps* as having the joint reaching halfway between the eye and the nostril, as opposed to *E. stantoni*, where it extended anterior to the snout. Neill (1965) concluded that the apparent differences as determined by appressing the leg against the body were a distortion produced by the broad heads of the type of *E. laticeps* and the Palenque specimen.

The range of variation for this measurement is substantial for the two largest samples available. In the Alta Verapaz series (E), values are 4 (161–177–184) for males and 10 (158–175–192) for females. In the Yojoa sample (G), they are 2 (173–175–177) for males, 9 (169–182–197) for females. This variation encompasses the value for the types of *Eleutherodactylus laticeps* and *E. stantoni*. Occasional examples from elsewhere in the range of the populations reviewed here exhibit higher (up to 206 in males) or lower values (down to 151 in females).

What is even more interesting, however, is a comparison between large adult females, 65 mm in standard length, and younger subadult to mature females (40–65 mm). All of the relatively short-limbed examples in the series are in the former range with values of 9 (150–160–168), while the latter have relatively longer hind limbs and values of 23 (169–184–197). These data strongly suggest a differential growth rate in the body versus hind limbs (fig. 22), with the latter slowing down after a size of about 60 mm is reached. Significantly, the type of *Eleutherodactylus laticeps* is an old, large, relatively short-legged female, while that of *E. stantoni* is a young female with the relatively long legs of her age class.

Stuart (1948) and Firschein (1951) attempted to employ features of dorsal coloration to segregate *Eleutherodactylus laticeps* and *E. stantoni*, although none of their material approached the distinctive coloration of the holotype of the former, so beautifully figured by Duméril et al. (1854, pl. 99). Neill (1965) pointed out the similarity in coloration among the Belize and Palenque specimens, while noting some differences from the Alta Verapaz frog placed in *E. stantoni* by previous authors.

Interestingly, all of the presumed differences in dorsal patterns are represented by the fine series recently collected in Alta Verapaz, Guatemala (MVZ 159890–9905; JD 617–19, 621, 624). Specimens in this sample range in size from 17 to 79.8 mm

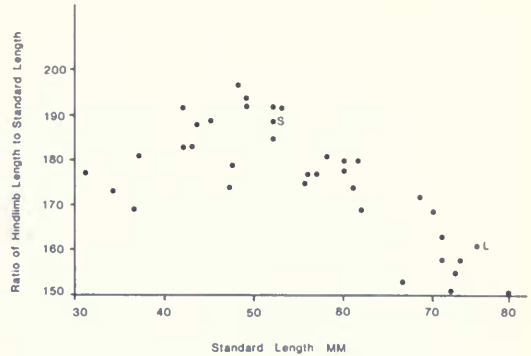


FIG. 22. Graphic representation of relationship between hind limb length and standard length in adult female *Eleutherodactylus laticeps*. S, holotype of the name *E. stantoni*; L, holotype of *E. laticeps*.

in standard length. Young individuals are light tan to gray with some darker markings. Adults are light gray brown to dark brown in ground color (fig. 23). Many are nearly uniform, with a few light spots and/or obscure dark markings. Others have definite large dark U's or inverted U-shaped marks on the back, which may occasionally fuse to form an hourglass-shaped figure. Some individuals have the dorsal surfaces covered with a series of small white spots, exactly as figured for the holotype of *Eleutherodactylus laticeps*. The arms and legs are strongly barred or the bars are obscured by darker pigment. Males tend to be uniformly colored, while variation in females is from uniform through strongly marked to light-spotted. While available material of most samples (A–F) falls within the limits of variation noted above, the Yojoa (G) population stands out. All frogs of this sample have a uniform, usually light tan, dorsum and obscure limb bars.

As is the case with other populations of the *Eleutherodactylus gollmeri* group, most specimens discussed here have a definite dark eye mask. Three specimens out of 21 (14.3%) in the Alta Verapaz sample lack the eye mask and have strongly barred lips, as do the type of *E. laticeps*, a male (MCZ 28246) from Chiapas, Mexico, and the large Honduras female assigned to *E. laticeps* by Meyer and Wilson (1971). Since the barred lip pattern is an occasional variant in other species in the group and it occurs as an individual variant in the largest population sample, it cannot be regarded as a feature of significance in diagnosing populational differences.

The evidence now at hand shows that the principal difficulties in past studies of frogs of this

series of populations derive from small sample size; individual variation, especially in ontogenetic changes; and the unique combination of characters in the female type of *Eleutherodactylus laticeps*. The large size (75 mm) of the latter, the consequently well-developed and darkened ventral disk, the sexually dimorphic very broad head and short hindlimbs, the presence of lip bars instead of a dark eye mask, and the white spotting in the dorsal pattern made it difficult to evaluate the type's relationship to smaller individuals and/or males. The fact that the type locality of *E. laticeps* was general (Yucatán) also encouraged a conservative approach, since the possibility seemed to exist that it represented a population from the peninsula that had not been resampled.

Be that as it may, the availability of new materials from southern Mexico and Atlantic-versant Guatemala has shown that the supposed differences between *Eleutherodactylus laticeps* and *E. stantoni* are products of ontogenetic, sexually dimorphic, or individually variable features. The presence of individuals in the Alta Verapaz, Guatemala, series that show both the extreme and intermediate conditions in all these features, leads me to conclude that samples B–F represent a single form. In addition, the large, robust female (USNM 21281) from “Honduras” clearly belongs with this species.

While my investigation was unable to discern any consistent feature that will separate sample G (Lago de Yojoa Valley, Honduras) from other populations, I am less comfortable in allocating them to the same form as B–F. The sample is extremely uniform in characters and is from an isolated upland lake valley, some 150–175 km southeast of the nearest Guatemala localities in the Sierra de las Minas and in the Alta Verapaz uplands, respectively. In addition, none of the females shows the extremely broad heads, short legs, or extensive disk modification seen in other samples. However, females of the same size as the maxima (60–62 mm) in the Honduras series, at other sites, usually show only a minimal thickening of the disk area.

It may well be that the large (70 mm) female with no additional locality data other than Honduras is from this population. It is clearly conspecific with the more northern samples (B–F) of this complex and shows extensive disk modification. Under the circumstances there seems to be no choice but to include the Yojoa population with others of this system. Additional material, especially of large adult females and/or the application of different techniques (e.g., electrophoretic) to the

study of this population are needed to confirm or deny the allocation made here.

A single male example (LDW 5607), 36 mm, from the Cordillera Nombre de Dios (sample H) along the northern coast of Honduras, agrees with the other Honduras specimens (sample G) in all significant features. The locality on Cerro Búfalo (1270 m) where this frog was taken is the highest known for *Eleutherodactylus laticeps*-like frogs in Honduras; population E occurs at higher elevations in Guatemala (to 1600 m).

The status of the single Veracruz, Mexico, frog (A) of this system is also a problem. Although originally described as a distinct form, *Eleutherodactylus werleri* (Lynch & Fritts, 1965), and thought to be related to the nominal forms *E. lineatus* and *E. macdougalli*, it closely resembles other *E. laticeps*-like frogs. The type of *E. werleri* is 10 mm longer than the largest male of definitive *E. lineatus* or *E. macdougalli* and, unlike them, lacks both heel tubercles and the dark seat patch mark. In these and other features it agrees with male examples of the *E. laticeps* system in every regard. There seems no alternative but to regard *E. werleri* as conspecific with populations B–F and probably G–H as well. The type of *werleri* is from an elevation of 1219 m, well within the altitudinal limits for *laticeps*-like frogs elsewhere in their range.

The third question raised by the original discussion (p. 20) regarded the applicability of the name *Hylodes laticeps* A. Duméril to these populations. Allocation of the name by past workers had been difficult, since the female holotype combined so many apparently unique features and the type locality was vague. In the previous pages of this section, I have demonstrated that all of the supposedly unique features of the type occur as sexually dimorphic or individually variable characters within the available samples. In addition, I have shown that the supposed differences between *Eleutherodactylus laticeps* and *E. stantoni* are related to ontogenetic and individual variation. Therefore, there seems no valid reason for these populations not to be regarded as a single species.

The matter of the correct type locality for *Eleutherodactylus laticeps* does not affect this conclusion. The collector of the holotype, Pierre M. A. Morelet, visited both Mexico and Guatemala during his expedition of 1847–1848. Although Firschein (1951) suggested that the type was collected well out on the Mexican portion of the Yucatán Peninsula and even restricted the type locality to Champotón, Campeche, Mexico, the species was then thought to occur only in Chiapas, Mexico,



and Belize, on the peninsula proper. Most records in Mexico and Guatemala are from the slopes of the uplands at the base of the peninsula. That this situation is not a collecting artifact is documented by the extensive Yucatán materials collected and/or examined by Lee (1980) in his analysis of the herpetofauna, without discovery of additional frogs of this kind. It seems almost certain from these data that Morelet's specimen came from somewhere other than the main portion of the Yucatán Peninsula. We know that he collected at several sites on the Atlantic versant of Guatemala, most especially in the vicinity of Cobán in Alta Verapaz. The types of two valid species named for him, *Agalychnis moreleti* and *Gerrhonotus moreleti*, were collected in Alta Verapaz and are known to occur in the mountains north of Cobán. Recent collecting in these same mountains has produced a series of frogs (population F) obviously conspecific with the type specimen. In fact, each of the supposedly unique features of the type is present in one or more large adult females from this series. For this reason I regard it as likely that the holotype was collected by Morelet in this region.

How the label containing the word Yucatán became associated with the type of *Eleutherodactylus laticeps* will always remain unknown. Perhaps Morelet used the term for a wider area than the Yucatán Peninsula proper. Perhaps a mix-up in locality data is involved. In any event restriction of the type locality for *E. laticeps* by Firschein (1951) to Champotón, Mexico, has no validity, since the species has never been taken closer to that place than 272 km to the south-southwest at Palenque. Fortunately, the designation has no legality as well, since type locality restrictions have no standing under the Rules of Zoological Nomenclature (Rec. 72 E).

In view of the above, members of the several discussed populations may be regarded as comprising a single species called *Eleutherodactylus laticeps*.

#### 4. *Eleutherodactylus laticeps* (A. Duméril). Figure 23.

*Hylodes laticeps* A. Duméril, 1853 (holotype: MNHN 509, an adult female; Central America: Yucatán; almost certainly an error for Guatemala: Alta Verapaz (near Cobán)).

*Eleutherodactylus stantoni* K. P. Schmidt, 1941 (holotype: UMMZ 80673, adult male; Belize: Cayo: Valentine, 400–500 m).

*Eleutherodactylus werleri* Lynch and Fritts, 1965 (ho-

lotype UIMNH 42987, adult male; Mexico: Veracruz: Volcán San Martín Pajapán, 1219 m).

**DIAGNOSIS**—*Eleutherodactylus laticeps* is the largest species in the *gollmeri* group with adult males 31–47 mm in standard length and adult females 55–80 mm. Frogs of this species can never be confused with *E. gollmeri*, *E. lineatus*, or *E. rostralis*, since they lack large heel calcars and have no dark seat patch mark (distinct calcars and dark seat patch marks in the latter forms). *Eleutherodactylus laticeps* differs from *E. chac*, the smallest species in the *E. gollmeri* group, by lacking the one to four pustular heel tubercles and triangular dark seat patch mark characteristic of the smaller form, in addition to being much larger.

*Eleutherodactylus laticeps* is distinct from *E. minus* in having minimal toe webbing and lacking fleshy toe fringes and a dark seat patch mark; the latter has substantial toe webbing, well-developed toe fringes, and a dark seat patch mark.

Although *Eleutherodactylus noblei* approaches *E. laticeps* in size, the two differ markedly in that the outer finger disks (III–IV) are much larger than the inner disks (I–II) in the former, while they are subequal in the latter species.

**SUMMARY OF CHARACTERISTICS**—Dorsal outline of snout rounded in females to subelliptical in males; rounded in profile and definitely protuberant in males. Vertical diameter of tympanum slightly greater than vertical diameter of orbit in males, about equal in females. Dorsum granulate, with at most a few low tubercles; usually a distinct suprascapular fold and a well-developed dorso-lateral glandular ridge. Finger disks barely wider than digits, covers rounded, pad even to swollen; subarticular tubercles on fingers and toes ovoid, projecting, and conical. Thenar tubercle subovoid, palmar tubercle rounded to cordate in form; palm covered by rounded accessory tubercles. No heel calcar. Toe disks barely expanded, cover round, some pads nearly cuspidate. No toe fringes. Toes with only a trace of webbing. A distinct large elongate raised inner and a moderate low rounded inner metatarsal tubercle; tarsus smooth except for well-developed inner tarsal fold. One to three plantar tubercles. Large females with the ventral disk thickened and darkened in color.

**DISTINCTIVE FEATURES OF COLORATION**—Dark eye mask usually present but extending posteriorly only a little beyond tympanum; some individuals without eye mask, which is broken up into definite dark lip bars and a tympanic dark mark. No definite stripe along anterior thigh surface, but a dark stripe from knee to ankle along anterior lower leg



FIG. 23. Variation in dorsal coloration in *Eleutherodactylus laticeps* from Alta Verapaz, Guatemala. The specimen on left approaches the holotype in dorsal pattern. Bar = 4 cm.

surface. No seat patch mark. Posterior thigh surface mottled with dark and light pigment. Undersides of limbs, throat, and venter with considerable dark mottling, especially in large females. Iris yellow in life.

**COLOR VARIATION**—Considerable pattern variation occurs in the sample of 31 adults and subadults analyzed. A common pattern (25%) is essentially a uniform dark brown dorsum without a middorsal light stripe. Most individuals with this pattern lack posterior suprascapular dark spots (7 of 8). In a large proportion (48%) of the sample, a middorsal dark figure, usually hourglass-shaped, is present. One example has the figure very distinctive and broken in two to form a U-shaped and inverted U-shaped pair of figures, while another has only the posterior portion of the figure present as a bottle-shaped figure. A narrow dorsal light stripe, continuous or restricted to the posterior one-half to one-third of the body, is found in about half of these individuals and is absent in the others. Dark, light-centered posterior suprascapular spots occur in almost all of these specimens.

A less common dorsal pattern (13%) is found

in some individuals, including the type of *laticeps*. These examples are mottled with dark brown and lighter colors (tan, gray, or white). They lack a middorsal light stripe and may have a suggestion of a dark figure middorsally. Dark posterior suprascapular spots may or may not be present.

Another pattern (9.7%) consists of an essentially uniform dorsum with the principal dorsal tubercles black in color to form a pattern of eight to 12 distinct small spots. A middorsal light stripe is present in one example (out of three) having this pattern.

Four specimens (13%) lack a dark eye mask and have the lips barred (fig. 1). Each of these examples has a different dorsal pattern. The holotype (MNHN 1547) is mottled. Another example (MVZ 159820) has the paired U-shaped figure described above, with a middorsal light stripe; a third (JDW 6196) has an hourglass-shaped figure, with a middorsal light stripe. The fourth (JDW 6193) has the light stripe and is marked with 10 discrete, small, black spots. The last three specimens are all from the same site (Finca Volcán, Alta Verapaz, Guatemala), where they were taken with 19 individuals having eye masks.

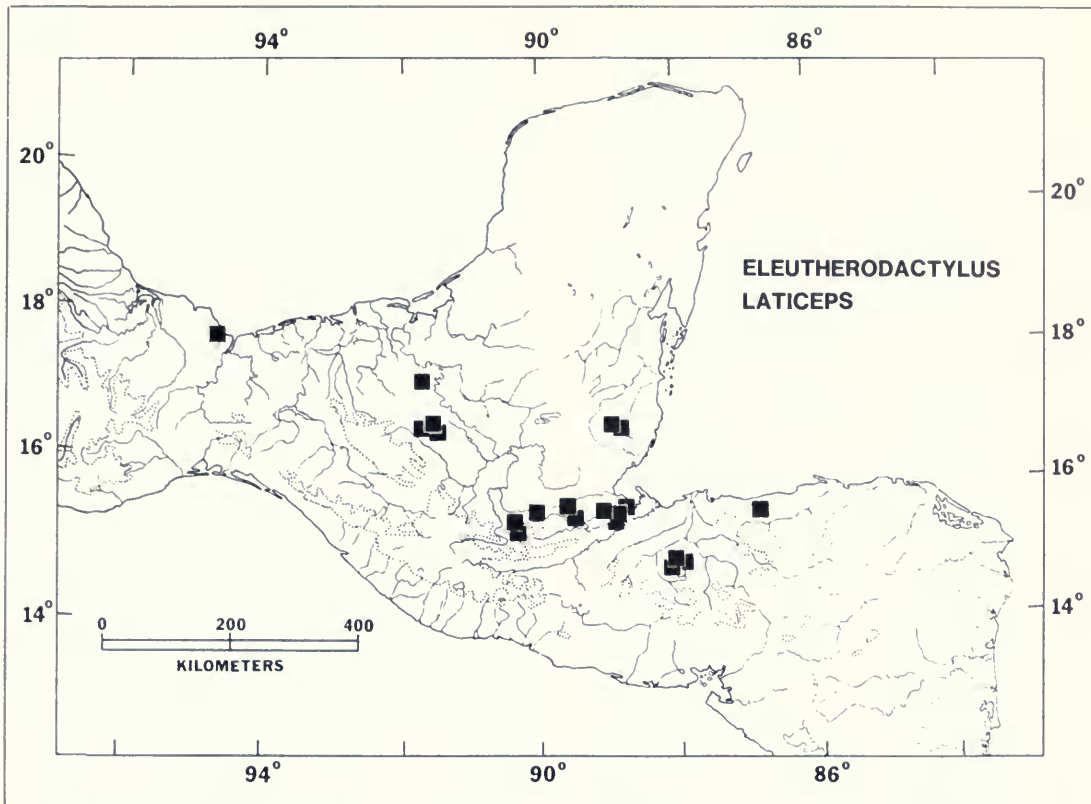


FIG. 24. Geographic distribution of *Eleutherodactylus laticeps*. The dotted line indicates the 1500 m contour.

**MEASUREMENTS (IN MM)**—Adult males 7 (31–38–47) in standard length, adult females 36 (55–61.6–79.8); smallest juvenile 18. Head width 34–38.5–43 in males, 34–41.8–49 in females; hind limb 177–180–206 in males, 150–171.8–197 in females.

**DISTRIBUTION**—Atlantic premontane slopes and some immediately adjacent lowland sites from eastern Chiapas, Mexico, south through Belize and Guatemala to western and northern Honduras; 50–1600 m (fig. 24).

**LOCALITIES**—**BELIZE:** Cayo: 8 km N Millinario; Valentine. **MEXICO:** **Chiapas:** Monte Líbano; Laguna Ocotol Grande; between Laguna Ocotol Grande and El Censo; **Veracruz:** Volcán San Martín Pajapán. **GUATEMALA:** **Alta Verapaz:** Finca Los Alpes; Finca Chichen; Finca Chicoyán, 1 km W Cobán; Finca Volcán; **Huehuetenango:** Finca Chiblac; **Izabal:** Los Amates; 4.8 km N Lago Izabal; 12.6 km W, 5.1, 11.8 km WSW Santo Tomás. **HONDURAS:** **Atlántida:** S slope

Cerro Búfalo; **Cortés:** 1.6 km SE El Jaral; Lago de Yojoa; **Santa Bárbara:** 8.8 km SE El Jaral.

### The Status of *Eleutherodactylus rostralis*

The Atlantic lowland and premontane populations of the *Eleutherodactylus gollmeri* group in Honduras, Belize, and Guatemala have been the source of considerable confusion for herpetologists. Much of the difficulty stems from Dunn and Emlen's (1932) reference of these populations to *Eleutherodactylus gollmeri*. In addition, most subsequent workers have not had access to the type specimens of *Hylodes rostralis* Werner (1896), a name whose allocation is critical to resolving the biological and systematic issues involved. Finally, some workers (Lynch, 1965a; Lee, 1980) have confused one representative of the *E. gollmeri* group in the region with the somewhat similar, but



distantly related, *Eleutherodactylus rhodopis*, which ranges south only to the base of the Yucatán Peninsula.

Dunn and Emlen (1932) regarded all Atlantic lowland frogs of the *Eleutherodactylus gollmeri* group from Central America, exclusive of *E. noblei*, as belonging to a single species. Earlier in the present paper I have demonstrated that typical *E. gollmeri* occurs only in Costa Rica and Panama, that Nicaragua specimens of *E. gollmeri* (*sensu* Dunn) are actually the distinct species *E. mimus*, and that the issue has been confused by identification of juvenile *E. noblei* from Nicaragua and lowland northwestern Costa Rica as *E. gollmeri*. The range of *E. gollmeri* is separated from the northern populations referred to that species by a hiatus of approximately 600 km, between northern Honduras and northwestern Costa Rica.

Schmidt (1941) erroneously referred material of northern "*Eleutherodactylus gollmeri*" populations from Belize to *E. rhodopis*, while Stuart (1941) regarded the northern frogs as distinct from southern *E. gollmeri* and called Guatemala examples *E. rostralis*. The issue at this point was very murky because Stuart (1948) seemingly changed his mind and called his small sample of *gollmeri*-like frogs from Alta Verapaz *E. rhodopis*. Stuart did suggest that two forms might be involved but left the matter uncertain.

Duellman (1963) and Stuart (1963) returned to Stuart's (1948) suggestion and concluded that *Eleutherodactylus rostralis* was distinct from *E. rhodopis* and allied to *E. gollmeri*. Lynch (1965a), on the other hand, in his unpublished opus on frogs related to *E. rhodopis* and *E. gollmeri* in Mexico and northern Central America, regarded northern "*E. gollmeri*" and/or "*E. rostralis*" as synonymous with *E. rhodopis*.

Meyer and Wilson (1971) reverted to calling the populations in Honduras *Eleutherodactylus gollmeri*, while Henderson and Hoever (1975) called the Belize samples *E. rostralis*. A final contribution to the confusion is the use of the name *Eleutherodactylus loki* (Shannon & Werler, 1955) by Lee (1980) for representatives of both the *E. rhodopis* complex and "*E. gollmeri*" (*rostralis*) samples from the Yucatán Peninsula. This arrangement was followed at the suggestion of Lynch, apparently based on his (1965a) manuscript.

Three principal questions must be answered in order to clarify the situation:

1. Are the *Eleutherodactylus gollmeri*-like frogs of northern lowland Central America distin-

guishable from *Eleutherodactylus rhodopis* and, if so, what are the distributions of the two forms?

2. Are the northern populations of *E. gollmeri*-like frogs distinguishable from typical *E. gollmeri* in lower Central America?
3. If the northern and southern populations of *E. gollmeri* (*sensu* Dunn & Emlen) are distinct, is the name *E. rostralis* available for the northern frogs?

Although a reading of the species account for *Eleutherodactylus gollmeri* in the previous section of this paper gives a preview of my answers to questions 2 and 3, a detailed analysis is required to substantiate my conclusions.

A central part of the problem regarding the lowland *Eleutherodactylus gollmeri*-like frogs of northern Central America is their relationship to *Eleutherodactylus rhodopis* Cope, a common and wide-ranging species of Mexico and northern Central America. For the region under discussion, two views have been variously advanced: (a) that the *E. gollmeri*-like frogs of Atlantic lowland Guatemala, Belize, and Honduras are conspecific with *E. rhodopis* (Schmidt, 1941; Stuart, 1948; Lynch 1965a) or its southern representative *E. loki* (Lee, 1980); or (b) that two species, *E. rhodopis* and an *E. gollmeri*-like form occur together in the area (Stuart, 1941, 1963; Duellman, 1963, and, by implication, Dunn & Emlen, 1932; Meyer & Wilson, 1971; Henderson & Hoever, 1975). Stuart, Duellman, and Henderson and Hoever use the name *E. rostralis* for the latter, while Meyer and Wilson follow Dunn and Emlen in using *E. gollmeri*.

In an attempt to reinvestigate the situation, I have examined all available material—frogs from the region variously identified as *E. rhodopis*, *E. loki*, *E. gollmeri*, or *E. rostralis* by other authors and additional recently collected specimens. These include all examples from Honduras, Belize, the Atlantic lowlands of Guatemala, and much comparative material from adjacent areas in Mexico. All examples seen by the various authors cited above from northern Central America, including all those mapped by Lee (1980) as *E. loki*, were examined.

My analysis of this material confirms and supports the conclusion of Duellman (1963) and Stuart (1963) that two superficially similar but distinct species occur in Guatemala. The two forms belong to two distinctive species series (groups *sensu* Lynch, 1976), one (A) to the *Eleutherodactylus rhodopis* series, and the other (B) to the *E. fitzingeri*

series (Lynch, 1976). As mentioned elsewhere (Savage & DeWeese, 1979; Savage, 1985) and as used here, a species group is defined as a monophyletic lineage within a species series. For reasons developed later in this paper, I regard the *E. gollmeri* group as a monophyletic cluster of allied species, closely allied to the *E. rhodopis* series and to the *E. fitzingeri* and *E. rugulosus* groups (*sensu* Savage, 1975, 1976; Savage & DeWeese, 1979) which were placed by Lynch (1976) in his *E. fitzingeri* series.

The characteristics used by Lynch (1976) to separate the *Eleutherodactylus rhodopis* lineage from the *E. fitzingeri* line (including the *E. gollmeri* group) are trivial and of dubious phylogenetic significance. Nevertheless it seems significant that species A agrees with *E. rhodopis* and its allies in having the first and second fingers equal in length and in lacking disks on the innermost fingers and toes, while species B agrees with the *E. fitzingeri* series (*sensu lato*) in having the first finger greater than the second and having disks on all fingers and toes. Although these features are occasionally ambiguous, especially determination of whether a disk groove is present in small or poorly or long-preserved material, other features unequivocally separate the two species in question as summarized in Table 1.

Species A agrees in every particular and is undistinguishable from *Eleutherodactylus rhodopis* (Cope, 1867; type locality Orizaba, Veracruz, Mexico, 1200 m) as usually defined by most herpetologists for Mexican and Pacific slope Central American material (Smith & Taylor, 1948; Mertens, 1952; Duellman, 1960; Lynch, 1965a; Stuart, 1963). The possibility exists that more than one species is represented within the substantial geographic and altitudinal range of the populations now subsumed under *E. rhodopis*, since there seem to be minor differences between Atlantic and Pacific slope samples and upland examples in the Isthmus of Tehuantepec region. However, all available specific names (*sallaei*, Günther, 1868; *plicatus* and *ventusus*, Günther, 1900; *beatae*, Boulenger, 1903; *dunni* and *mystaceus*, Barbour, 1922; *dorsoconcolor*, Taylor, 1941; and *loki* and *sanmartinensis*, Shannon & Werler, 1955) have type localities in the uplands of Veracruz, Mexico, and appear to be conspecific (Lynch, 1965a,b). For these reasons it is appropriate to regard the lowland Atlantic population of Guatemala as part of *E. rhodopis*.

The distribution of *Eleutherodactylus rhodopis* on the Atlantic versant includes premontane slopes

TABLE 1. Diagnostic comparisons of northern Central American problem species.

Species A— <i>rhodopis</i> group	Species B— <i>gollmeri</i> group
1. No toe webbing	1. Definite toe webbing
2. No tarsal fold	2. A distinct inner tarsal fold extending from inner metatarsal tubercle $\frac{1}{2}$ – $\frac{2}{3}$ length of tarsus
3. A conspicuous inner tarsal tubercle (sometimes divided) situated at about middle of tarsus	3. No inner tarsal tubercle
4. Heel smooth or with several low warts, no definite small tubercles	4. 1–4 definite well-developed small pustular tubercles
5. Subarticular, palmar, and thenar tubercles of hand strongly projecting, pungent	5. Subarticular, palmar, and thenar tubercles of hand relatively low, although obtusely raised
6. Accessory palmar tubercles well developed, projecting	6. Accessory palmar tubercles low, rounded
7. Subarticular tubercles under toes projecting, usually pointed	7. Subarticular tubercles under toes projecting, usually pungent
8. Plantar tubercles numerous, pointed	8. A few plantar tubercles
9. Iris bronze in life	9. Iris red in life
10. Adult lengths: males to 30 mm, females to 40 mm	10. Adult lengths: males to 27 mm, females to 39 mm

from northern San Luis Potosi south through Veracruz into Oaxaca and Chiapas, Mexico, and from the lowlands of Veracruz, Tabasco, and Chiapas into the Petén of Guatemala, Belize, and northwestern Honduras; and on the Pacific slope in Oaxaca and Chiapas southward through Guatemala to central El Salvador, 10–1700 m.

The range of *Eleutherodactylus rhodopis* in Atlantic lowland Central America is restricted to the Petén area of Guatemala, Belize, and adjacent northwestern Honduras, contrary to the statements of Smith and Taylor (1948), Stuart (1963), and Lynch (1965a, 1976). Definite *E. rhodopis* are known from the following localities: Piedras Negras, El Petén, Guatemala (USNM 116889–90), Santa Cruz, El Petén, Guatemala (UMMZ 75378, 6 examples), Santa Teresa, El Petén, Guatemala (UMMZ 75377), and Tikal, El Petén, Guatemala (UMMZ 117991); 2 km N Gallon Jug, Orange Walk, Belize (MCZ 37847); and mountains W San Pedro

Sula, Cortés, Honduras (FMNH 142147). All other records for this species from Atlantic-versant Central America are based on other forms. These include species B—see specimen records below; *E. bransfordii*—Cukra, Zelaya, Nicaragua (AMNH 7166–68, 91), Eden, Zelaya, Nicaragua (AMNH 7620–22), and Eden Mine Hill, Zelaya, Nicaragua (AMNH 7148–49); and *E. laticeps*—Lago de Yojoa, Cortés, Honduras (MSUM 4539). I have elsewhere (Savage, 1981a) pointed out the occurrence of *E. bransfordii* in extreme eastern Honduras.

Considerable confusion has existed regarding the presence of definitive *Eleutherodactylus rhodopis* in Honduras. Lynch (1965a) and Lynch and Fugler (1965) record it from the Omoa range to the west of San Pedro Sula based upon several examples (FMNH 4676, 4678–80, 4682–85, 4687–89, and 142147, originally included in the paratypic series of *E. milesi* as one of several examples numbered FMNH 4701). Meyer and Wilson (1971) reported that Lynch (pers. comm.) had changed his mind regarding these specimens and did not then believe that *E. rhodopis* occurred in Honduras. They did not review this material, but presumed that it represented what they were calling *E. gollmeri* in Honduras.

Reexamination of FMNH 142147, a female 28 mm in standard length, with well-developed oviducts and presumably an adult, shows that it agrees in every regard with Guatemala and Belize *Eleutherodactylus rhodopis*. The example is rather sunken and brittle, and the characteristic tarsal tubercle is somewhat obscure as a result but definitely present. Whether the remaining examples called *E. rhodopis* by Lynch (1965a) and Lynch and Fugler (1965) were of this form is moot. H. K. Voris of Field Museum informs me that all were lost, probably in the mails, in 1973.

The second form (table 1), species B, is a member of the *Eleutherodactylus gollmeri* group and is amply distinct from *E. rhodopis*. Within the *E. gollmeri* group, species B resembles the completely allopatric populations of *E. gollmeri* in lower Central America and has been associated with that form primarily by Dunn and Emlen (1932) and Meyer and Wilson (1971). The two allopatric populations differ as follows:

Species B—heel with one to four pustular tubercles; no distinct dark line along anterior thigh surface; the dark seat patch mark triangular and continuous with the dark posteroventral dark pigmentation of the thigh,

usually with a dark spot on either side of the apex of the triangle, above and lateral to vent; males to 27 mm, females to 39 mm in standard length.

*Eleutherodactylus gollmeri*—heel with one or two well-developed conical calcars; a definite serrate dark line along anterior thigh surface and dark seat patch mark; a pair of dark spots (sometimes fused) above and lateral to vent and separated from the dark posteroventral thigh pigmentation by a light area; males to 37 mm, females to 54 mm in standard length.

These differences combined with the approximately 600 km separation of the ranges of *Eleutherodactylus gollmeri* and the northern form lead me to regard them as separate species. The quest now remains to ascertain the correct name for the northland lowland population.

Werner (1896) proposed the name *Hylodes rostralis* for a member of the *Eleutherodactylus gollmeri* group from Honduras. E. R. Dunn examined the holotype (ZMB 13203) in Berlin during his museum tour of 1928–1929. On the basis of these observations, Dunn and Emlen (1932) placed *E. rostralis* in the synonymy of *E. gollmeri*. No subsequent worker was able to reexamine the type, since it was thought to have been destroyed during the Russian Revolution because it was originally located in the museum at St. Petersburg (Leningrad). Dunn and Emlen did not indicate that it had been transferred from Russia to Berlin. For this reason the correct application of the name *rostralis* has remained in doubt, although Stuart (1941) and Duellman (1963) used it for species B.

Fortunately, through access to Dunn's notes, kindly made available to me by R. F. Inger with the cooperation of Günther Peters of the Berlin Museum, I have been able to examine the holotype of *Hylodes rostralis* (ZMB 13203) and compare it directly to examples of all *E. gollmeri* group species.

Although soft and faded, the type (an adult female 42 mm in standard length) agrees in general characteristics with the *Eleutherodactylus gollmeri* group and exhibits the following diagnostic features: finger disks subequal; disks barely wider than digits, covers rounded, pads even to swollen; a series of two to three low pustular heel tubercles; basal toe webbing present but no fleshy marginal toe fringes; no obvious outer tarsal tubercles; no hourglass-shaped dorsal dark mark; and eye mask to tympanum (Z<sub>3</sub>). The type is so faded that little pattern can be seen, but several dark pigments



stand out: knee and leg marks similar to those typical of condition T (fig. 10) are suggested, and a pair of dark spots above and lateral to the anus, as in condition E (fig. 11), are present.

These features, especially the nature of the heel ornamentation and coloration, suggest that the holotype of *Eleutherodactylus rostralis* and of species B may be conspecific. The type of the former is trenchantly different from all other known members of the *E. gollmeri* group. The size of the finger disks (subequal) distinguishes it from *E. noblei*, which has enlarged disks on fingers III–IV. The presence of heel ornamentation and a dark seat patch mark separate the type of *E. rostralis* from *E. laticeps*, which lacks heel ornamentation and has no dark seat patch mark. *Eleutherodactylus mimus* is unique within the group and distinct from the holotype of *E. rostralis* in having extensive toe webbing and fleshy toe fringes, neither of which are present in the latter. Both *E. gollmeri* and *E. lineatus* have one or two very well-developed heel tubercles (calcars) and further differ from the type of *rostralis* in details of coloration, *E. gollmeri* principally in hindlimb pattern and *E. lineatus* in the seat patch mark.

Unfortunately the situation is more complicated than the above comparisons imply, when *Eleutherodactylus rostralis* or *gollmeri*-like material from Honduras is compared to species B and the type of the former. The first complication is that the type specimen of *Hylodes rostralis* is somewhat larger (42 mm) than any known representative of species B (maximum size 39 mm). The second is that several forms seem to be represented by Honduran frogs called *E. gollmeri* by Meyer and Wilson (1971). A number of these were discussed in an earlier section of this report and placed with *E. laticeps*.

The remaining series from Honduras are mostly from elevations between 100–1300 m and are larger in size (males to 36 mm, females to 58 mm in standard length) than Guatemalan examples of species B (males to 27 mm, females to 39 mm in standard length). In addition, the heel tubercles of the specimens are indistinct pustules, one to four in number; the outer edge of the tarsal segment is smooth or with one to five barely visible tubercles; and the upper eyelid has only a few posteriorly placed pustules. On the basis of these differences and a direct comparison of the holotype of *Eleutherodactylus rostralis* with all known members of the *E. gollmeri* group, I conclude that it is conspecific with Honduran upland populations. Al-

though very similar to one another in most features of external morphology and coloration, I further conclude that the upland populations to which the name *E. rostralis* must apply are distinct from the much smaller species B.

The following accounts distinguish between *Eleutherodactylus rostralis* and species B, which requires a new name. They are based upon examination of all available material from Guatemala, Belize, and Honduras, which has been called variously *E. gollmeri*, *E. loki*, *E. rhodopis*, or *E. rostralis* by previous authors, and includes all known examples from Atlantic-versant lowland and premontane slope areas.

##### 5. *Eleutherodactylus rostralis* (Werner)

*Hylodes rostralis* Werner, 1896 (holotype: ZMB 13203, an adult female; Honduras).

DIAGNOSIS—A medium to moderately large species within the *Eleutherodactylus gollmeri* group (adult males 30–36 mm, adult females 40–58 mm in standard length), *E. rostralis* can only be confused with its larger allies *E. gollmeri* and *E. lineatus* and the smaller *E. chac* within the group. Both of the former forms have one or two well-developed heel calcars which immediately separate them from *E. rostralis*, in which one to four small pustular heel tubercles occur. In addition, *E. rostralis* may be distinguished from *E. gollmeri* (characters for the latter in parentheses) by lacking a distinct stripe along the anterior thigh surface (stripe present) and in having a triangular dark seat patch mark that is continuous with the dark posterior thigh region (dark seat patch mark separated from dark area of posterior thigh). *Eleutherodactylus rostralis* also differs from *E. lineatus* (features in parentheses) in lacking well-developed outer tarsal tubercles (present) and in usually having paired dark round spots at the apex of the triangular dark seat patch mark (without paired dark round spots). *Eleutherodactylus rostralis* differs from its nearest ally, *E. chac*, in its larger adult size and its less pronounced heel and outer tarsal tubercles, as discussed above and summarized in Table 2. *Eleutherodactylus rostralis* (characteristics in parentheses) cannot be mistaken for *E. mimus*, which has extensive toe webs and fringes (absent); *E. noblei*, which has fingers III–IV with enlarged disks (not enlarged); or *E. laticeps*, which lacks both heel ornamentation and the triangular

TABLE 2. Summary of differences among members of the *Eleutherodactylus gollmeri* group.

Species	Enlarged outer finger disks	Moderate toe webs and fringes	Finger and toe disk formula	Heel ornamentation	Tarsal tubercles	Plantar tubercles	Dorso-lateral fold	Hind limb pattern	Seat patch mark	Iris color	Maximum size (mm)	
											♂	♀
<i>gollmeri</i>	...	...	III	1-2 calcares	Weak	0	...	S	B	Red	36.5	54
<i>mimus</i>	...	+	I	Smooth	...	0-3	...	S	C	Yellow	37	58
<i>noblei</i>	+	...	II	Smooth	...	4-7	+	U	A	Gold	53	66
<i>chac</i>	...	...	III	1-4 tubercles	Weak	4-5	...	T	E	Red	27	39
<i>rostralis</i>	...	...	III	1-4 weak tubercles	Smooth to very weak	2-4	...	T	D-E	...	35	58
<i>lineatus</i>	...	...	III	1-2 calcares	Strong	0-1	...	T	D	Bronze	32	47
<i>laticeps</i>	...	...	II	Smooth-rugose	...	1-3	+	T	A-A	Yellow	47	58

dark seat patch mark (heel pustules and dark seat mark present).

**SUMMARY OF CHARACTERISTICS**—Snout in dorsal outline subelliptical in males to rounded in females; rounded and protuberant in profile. Vertical diameter of tympanum about equal to diameter of orbit in both sexes. Dorsum weakly granulate but usually some well-developed paired tubercles; no suprascapular fold; no distinct dorso-lateral glandular fold. Finger disks slightly expanded, rounded on I-II, slightly pointed on III-IV, pads even (I-II) to cuspidate. Subarticular tubercles on fingers ovoid, projecting, and obtusely raised; on toes ovoid, projecting, and pungent. Thenar tubercle elongate, palmar ovoid and bifurcate; palm covered by well-developed rounded accessory tubercles. A series of one to four low heel pustules. Toe disks barely expanded, rounded to nearly pointed, some or all disk pads cuspidate. No fleshy toe fringes. Toe with basal webbing; modal toe webbing formula: I  $2^+ - 2\frac{1}{2}$  II  $2 - 3\frac{3}{4}$  III  $3 - 4\frac{1}{2}$  IV  $4\frac{1}{2} - 3$  V. A distinct elongate inner metatarsal tubercle; outer round, distinct, about half the size of inner; an inner tarsal fold and weak outer row of tarsal tubercles, present or absent; two to four plantar tubercles.

**DISTINCTIVE FEATURES OF COLORATION**—A narrow middorsal light stripe usually present, often only posteriorly. Dark eye mask extending as a narrow dark line beyond axilla onto body; occasional individuals lack eye mask and have a series of dark lip bars and a supratympanic mask instead. No definite dark line along anterior surface of thigh, although dark marks present on knee; an obscure dark line along anterior margin of lower leg. Dark seat patch mark triangular, with a pair of very dark spots (often round) on either side of apex, above and lateral to vent. Posterior thigh surface brown. Undersides of limbs and throat mottled with dark pigment. Iris probably bronze in life (Kodachrome slide).

**MEASUREMENTS (IN MM)**—The available sample of this species shows the following variation: adult male 35.5 in standard length, adult females 8 (40-46.6-58); smallest juvenile 15. Head width 39.4 in male, 42.8-42.3-43.1 in females; hind limb 163 in male, 157-177-191 in females.

**COLOR VARIATION**—The dorsal pattern for this species, based upon a series of 16 examples, varies from uniform medium brown, with or without posterior suprascapular dark spots, through a condition with a series of small dark spots arranged in an hourglass pattern, to an obscure hourglass to irregular dark figure on a lighter ground color.

The latter two types are the most common, each making up about 40% of the variation. An additional variant is found in one individual (LDW 6206: Cerro Azul, Copán, Honduras) with barred lips. This frog has several distinct black spots scattered over a uniformly lighter gray ground color. A thin continuous light middorsal stripe occurs in 63% of the examples and an incomplete posteriorly located stripe in 12%; a stripe is absent in 25% of the examples, including the one with barred lips.

**REMARKS**—The single known adult male (MCZ 17437) of this species, from the mountains west of San Pedro Sula in northwestern Honduras, is 35.5 mm in standard length, about 10 mm larger than the largest known male of the lowland species *B. Large*. Large females agreeing in every respect with the type of *Eleutherodactylus rostralis* are now known from several montane areas in Honduras. In addition, a single large female (CM 57745), 43 mm in standard length, is the only known example of the *E. gollmeri* group from the Guatemalan portion of the mountain chain that straddles the border between eastern Guatemala and northwestern Honduras (the Sierras Espiritu Santo and Merendon). This frog is clearly conspecific with the type of *E. rostralis*, which approaches the Guatemalan female in size.

**DISTRIBUTION**—Evergreen forests in the Atlantic-variant premontane zone of northern and western Honduras and adjacent Guatemala, 850–1300 m (fig. 20).

**LOCALITIES**—**GUATEMALA:** Zacapá: La Unión. **HONDURAS:** no other data; Copán: Montaña de Cerro Azul; below Quebrada Grande; Cortés: Sierra de Omoa, W. San Pedro Sula; Montañas de Santa Ana; Yoro: Monte Mataderos; Portillo Grande.

6. *Eleutherodactylus chac* Savage, new species.  
Figure 12.

**HOLOTYPE**—KU 186243, an adult male from 12.6 km W Santo Tomás, Izabal, Guatemala, 774 m.

**DIAGNOSIS**—The smallest species within the *Eleutherodactylus gollmeri* group (adult males 20–27 mm, adult females 31–39 mm in standard length), *E. chac* can only be confused with its larger allies *E. gollmeri*, *E. lineatus*, and *E. rostralis*. Both of the former two species have one or two well-developed heel calcares, in contrast to *E. chac*, which has one to four small pustular heel tubercles. In addition, *E. gollmeri* has a distinct dark stripe along the anterior thigh surface (absent in *E. chac*)

and the dark seat patch mark separated from the dark area on the posterior thigh surface (dark seat patch mark continuous with dark area on the thigh in the new species). *Eleutherodactylus chac* also differs from *E. lineatus* (characters for the latter in parentheses) in having less developed low outer tarsal tubercles (strongly developed), paired dark round spots at the apex of the triangular dark seat patch mark (without paired dark spots), and the iris red in life (bronze).

*Eleutherodactylus chac* is very similar to *E. rostralis* and is a smaller, lowland slope version of the latter upland species. Aside from the size difference (males to 36 mm, females to 58 mm in standard length in *E. rostralis* versus 26 and 39 mm, respectively, in *E. chac*), the new form has the heel pustules, outer tarsal tubercles, and eyelid tubercles more fully developed than in *E. rostralis*. The iris color in life for *E. chac* is red but is apparently bronze in *E. rostralis*, although this needs confirmation. *Eleutherodactylus chac* cannot be confused with *E. mimus*, which has extensive toe webs and fringes (absent in the new species); *E. noblei*, which has fingers III–IV with enlarged disks (not so in *E. chac*); or *E. laticeps*, which lacks heel ornamentation and a dark seat patch mark (heel pustules and a dark seat patch mark in *E. chac*).

**SUMMARY OF CHARACTERISTICS**—Snout subelliptical in dorsal outline in males to rounded in females; rounded and protuberant in profile. Vertical diameter of tympanum about equal to diameter of orbit in both sexes. Dorsum weakly granulate but usually with some well-developed paired tubercles; no suprascapular fold; no distinct dorsolateral glandular fold. Finger disks slightly expanded, rounded on I–II, slightly pointed on III–IV, pads even (I–II) to cuspidate. Subarticular tubercles on fingers ovoid, projecting, and obtusely raised; on toes ovoid, projecting, and pungent. Thenar tubercle elongate, palmar ovoid and bifurcate; palm covered by well-developed accessory tubercles. A series of one to four strongly developed accessory tubercles. A series of one to four strongly developed heel pustules. Toe disks barely expanded, rounded to nearly pointed, some or all disk pads cuspidate. No fleshy fringe on toes. Toes with basal webbing, modal webbing formula: I 2<sup>+</sup>–2½ II 2–3¼ III 3–4½ IV 4½–3 V. A distinct elongate inner metatarsal tubercle; outer round, distinct, about half the size of inner; inner tarsal fold and a distinct low row of outer tarsal tubercles; four to five plantar tubercles.

**DISTINCTIVE FEATURES OF COLORATION**—A narrow middorsal light stripe usually present. Dark



eye mask extending as a narrow dark line beyond axilla onto body; occasional individuals lack eye mask and have a series of dark lip bars and a supratympanic stripe instead. No definite dark line along anterior surface of thigh, although dark marks present on knee; an obscure dark line along anterior margin of lower leg. Dark seat patch triangular with a pair of very dark round spots on either side of apex, above and lateral to vent. Posterior thigh surface brown. Undersides of limbs and throat mottled with dark pigment. Iris chestnut red in life.

**COLOR VARIATION**—This little species is among the most variable in color pattern in the *Eleutherodactylus gollmeri* group. The dorsal ground color varies from yellow tan to dark gray brown. In the available sample of 46 frogs, excluding very small juveniles, most examples have an hourglass-shaped dark dorsal figure, within which there are a number of distinct darker small spots (20%), or have the figure restricted to the posterior portion of the body to form a bottle-shaped dark marking (22%). Most individuals in the former group have a complete narrow middorsal light stripe; those in the latter group have the stripe restricted to the posterior one-half to one-third of the body. A complete middorsal stripe is found in 62% of the total sample; 26% have a short stripe and 11% lack it. Other basic dorsal patterns (each comprising about 11% of the sample) include an essentially uniform one with a complete middorsal stripe; a pattern with short dark longitudinal paravertebral bars near midbody; and a series of small (4–6) paravertebral black spots or larger spots. Dark posterior suprascapular and/or axillary dark spots associated with the respective tubercles may (45%) or may not (55%) be present in any color phase but the uniform one. A few examples have large, dirty, white spots on the back (6%) and may be dull white on the upper snout surface (6%).

A high proportion (18%) of the series has a barred lip pattern (fig. 1). Two of these examples (KU 55921 and 186258, Sierra del Mico, Izabal, Guatemala, and Chinaja, El Petén, Guatemala, respectively) lack a middorsal light stripe and are mottled with brown and light tan. One (MVZ 160682, 2 km W El Estor, Izabal, Guatemala) has the typical bottle-shaped pattern but lacks any light stripe; three are marked with discrete dark spots (fig. 8), two (FMNH 49040, Belize; KU 186269, Sierra del Mico, Guatemala) lacking a middorsal light stripe, one (FMNH 35064, San Felipe, Izabal, Guatemala) having the stripe incomplete. One (KU

186256, Sierra del Mico, Izabal, Guatemala) has an hourglass-shaped dorsal figure and light stripe, while another (FMNH 49042, Belize) has light spots and the light stripe.

**MEASUREMENTS (IN MM)**—The holotype is 26 mm in standard length. Other measurements as a percentage of standard length are head length 46; head width 38; eye 13.5; eye to tip of snout 23; eye to nostril 13.5; vertical tympanum 13.5; hind limb 173; and tibia 56. The available series of this species shows the following variation: adult males 8 (20–23.9–27) in standard length, adult females 18 (29–34.8–39); smallest juvenile 12. Head width 38–43.3–48 in males, 40–43.4–47 in females; hind limb 173–181.2–196 in males, 161–188.6–203 in females.

**REMARKS**—Representatives of the new species have been associated with several allied or distantly related forms as reviewed above (p. 28). It differs from its closest relative, *Eleutherodactylus rostralis*, primarily in its smaller adult size, although the details of limb and eyelid tuberculosity support the separation. In addition, *E. chac* has a chestnut red iris in life, while field notes for *E. rostralis* suggest that its iris is bronzy. This supposed difference needs confirmation.

As currently understood, definitive *Eleutherodactylus chac* occurs at lowland and premontane sites at the base of the Yucatán Peninsula in Guatemala and Belize. In addition, seven examples from the northern lowlands of Honduras seem referable to this form. Unfortunately most of these frogs are immatures, but one adult male (MCZ 16190) and one adult female (MCZ 16189), both from Lancetilla, are best placed with this form. The male is slightly larger than the maximum size reported from Guatemala, at 27 mm in standard length. The fully mature female is 37 mm in standard length, which is near the maximum size for the species elsewhere.

The name *chac* is derived from the Mayan name for the rain god, whose beneficent downpours are essential to the lives of both rainfrogs and man in Central America.

**DISTRIBUTION**—Lowland and premontane evergreen forests of the Atlantic versant at the base of the Yucatán Peninsula in Guatemala, Belize, and northern Honduras, 30–775 m (fig. 21).

**LOCALITIES**—**BELIZE**: Double Falls; **Stann Creek**: Blue Creek; Bokowina; Silk Grass; **Toledo**: Maya Mountains: N slope; SW end Little Quartz Ridge. **GUATEMALA**: **Alta Verapaz**: Finca Chama; 3 km S, 5 km NW and Chinaja; **Izabal**: 2 km

W El Estor; San Felipe; Cerro San Gil; 5.1, 10.4, 12.6 km W Santo Tomás. **HONDURAS: Atlántida:** mts. above Corozal; Lancetilla.

### The *Eleutherodactylus lineatus* Population System

A series of allied populations sharing the features of subequal finger disks, one to two well-developed heel tubercles, basal toe webbing, strong outer tarsal tubercles, no dark stripe along anterior face of thigh, and a well-developed seat patch mark (D) occur at relatively high elevations in Guatemala, adjacent Chiapas and eastern Oaxaca, Mexico, and west of the Isthmus of Tehuantepec in Oaxaca and Veracruz, Mexico. The earliest name for frogs of this population system is *Hylodes lineatus* Brocchi (1879), based on a specimen (MNHN 4885) from the vicinity of Lago Atitlán, Quetzaltenango, Guatemala (Stuart, 1963). The known samples of this system seem to form a series of upland populations found along especially humid lower montane slopes (900–2000 m) that are isolated from one another by low-lying and/or sub-humid areas. Available examples may be grouped into the following populational clusters (fig. 25):

- A. Atlantic versant of montane Oaxaca, Mexico, N = 2 (900–1800 m)
- B. Uplands of southeastern Oaxaca, Mexico, N = 10 (1300–1400 m)
- C. Sierra Madre de Chiapas, Mexico, and adjacent southwestern highlands of Guatemala, N = 20 (1700–1900 m)
- D. Northern uplands of Chiapas, Mexico, N = 2 (1065–1900 m)
- E. Sierra de Cuchumatanes, Guatemala, N = 19 (1200–2000 m)
- F. Cerro Chitu, Alta Verapaz, Guatemala, N = 1 (1600 m)
- G. Sierra Xucaneb, Alta Verapaz, Guatemala, N = 2 (1410 m)
- H. Sierra de las Minas, Baja Verapaz, Guatemala, N = 20 (1650–1700 m)

In addition to the name *Eleutherodactylus lineatus*, three others have been applied to frogs from these populations: *Eleutherodactylus anzuetoi* Stuart, 1941 (populations E, G); *Eleutherodactylus macdougalli* Taylor, 1942 (population B); and *Eleutherodactylus werleri* Lynch and Fritts, 1965 (population A).

Stuart's *Eleutherodactylus anzuetoi* is based upon juvenile members of the complex from several lower montane situations in Atlantic-versant Guatemala. The types (UMMZ 89160, 19911–13) were recognized as distinct primarily because they were said to lack a tarsal fold and toe webs and because of their small size (15–23 mm in standard length). A reexamination of the types, another specimen referred to the nominal form by Stuart (1948), and comparison with fresh examples of populations E and G indicate that they are conspecific. The types are rather soft and faded after 40 years in preservative, but agree with Stuart's description while matching closely recently collected juveniles from Atlantic-versant Guatemala. Juveniles under 20 mm have barely a hint of toe webbing; the tarsal fold is weak but the diagnostic features of coloration and the strongly developed series of outer tarsal tubercles, emphasized by Stuart in his original description of *E. anzuetoi*, are typical for *E. lineatus*-like samples. The newly collected material (KU, MVZ, UTA) shows a gradual ontogenetic change from *E. anzuetoi*-like juveniles into adults typical of the *E. lineatus* population system. At around 20 mm in standard length, some indication of toe webbing is present and a short, weak inner tarsal fold may be seen in well-preserved fresh material. Small, juvenile *Eleutherodactylus* usually show less webbing than adults of the same species and frequently show little development of the tarsal fold.

*Eleutherodactylus macdougalli* was originally described by Taylor (1942) from southeastern Oaxaca, Mexico, on the basis of a single small (27 mm) male (UIMNH 15907). Additional specimens from the same general area agree in all ways with other *E. lineatus*-like samples. The occurrence of typical *E. lineatus* in extreme southeastern Chiapas, Mexico, 325 km southeast of the Oaxaca records and about 125 km northwest of the type locality of *E. lineatus*, in essentially the same range of mountains as *E. macdougalli*, suggests a possible continuity throughout this mountainous region. As a matter of fact there are no characteristics that may be used to separate individuals from either end of this mountain system (*E. macdougalli* to the east versus *E. lineatus* to the southwest) from one another, or from frogs of this system from intermediate sites in Chiapas and southwestern Guatemala.

*Eleutherodactylus werleri* was described on the basis of a single large (43 mm in standard length) example from the slopes of Volcán San Martín



Pajapán, Veracruz, Mexico (Lynch & Fritts, 1965). As previously discussed, this frog is conspecific with *E. laticeps* of southern Mexico, Guatemala, Belize, and Honduras. Subsequently, Lynch (1965b) associated the name *E. werleri* with two specimens of this stock (KU 86868–69, a male and female, respectively) from Atlantic-drainage northern Oaxaca. Examination of these frogs, 25 and 36 mm in standard length, respectively, shows them to differ in no significant way from typical *E. lineatus* from Guatemala, but they are distinct from the holotype of *E. werleri* in having two heel calcars and a well-developed dark seat patch mark (both are lacking in the type of *E. werleri*).

Because of the apparent but probably real disjunct distribution of the *Eleutherodactylus lineatus* population system, an attempt was made to distinguish the several allopatric units from one another. Nothing in the original or subsequent descriptions of frogs referred to the several nominal forms will serve this purpose. Examination of material from all population samples indicates no consistent differences among them.

Under these circumstances it seems best to regard this system as constituting a single morphological species comprised of a series of completely allopatric populations. It may well be that subsequent study of these populations utilizing other techniques (electrophoresis, microcomplement fixation, etc.) may demonstrate significant genetic differences among some of them. Until such a time only one species may be recognized based upon available data.

#### 7. *Eleutherodactylus lineatus* (Brocchi). Figure 13.

*Hylodes lineatus* Brocchi, 1879 (holotype: MNHN 4885; Mexico: Atitlán; almost certainly an error for Guatemala: Quezaltenango: vicinity of Lago Atitlán).

*Eleutherodactylus anzueto* Stuart, 1941 (holotype: UMMZ 89160, a juvenile; Guatemala: El Quiché: 2 km N Nebaj, 1985 m).

*Eleutherodactylus macdougalli* Taylor, 1942 (holotype: UIMNH 15907, an adult male; Mexico: Oaxaca: La Gloria, 12.9 km SE of Chimalapa, ± 1372 m).

DIAGNOSIS—*Eleutherodactylus lineatus* most closely resembles *E. gollmeri* of lower Central America and *E. rostralis* of Atlantic lowland northern Central America. From the former, *E. lineatus* differs most obviously in having a strongly developed series of outer tarsal tubercles; a more or less triangular-shaped dark seat patch mark with the darkest pigment along the margins of the figure; and a distinct dark stripe along the anterior

thigh surface versus, at best, weakly developed outer tarsal tubercles, the dark seat patch mark consisting of a pair of dark spots and both a definite dark and a serrate stripe along the anterior thigh margin in *E. gollmeri*.

*Eleutherodactylus rostralis*, in contrast to *E. lineatus* (characters for the latter in parentheses), has one to four small tubercles on the heel (one to two definite calcars) and a dark triangular seat patch mark surmounted by a pair of dark round spots (triangular and darkest above and lateral to the vent) but lacks well-developed outer tarsal tubercles (strongly developed).

SUMMARY OF CHARACTERISTICS—Snout subelliptical in dorsal outline in males to rounded in females, rounded and protuberant in profile. Vertical diameter of tympanum about equal to diameter of orbit in both sexes. Dorsum weakly granulate, with some well-developed paired tubercles; rarely an hourglass-shaped pair of longitudinal ridges; no suprascapular fold, no distinct dorsolateral fold. Finger disks slightly expanded, slightly pointed, pads swollen to slightly cuspidate. Subarticular tubercles on fingers and toes ovoid, projecting and globular. Thenar tubercle elongate, palmar ovoid and bifurcate; palm covered with well-developed accessory tubercles. One or usually two distinct heel tubercles (calcars). Toe disks slightly expanded, rounded to slightly pointed, most disk pads cuspidate. No fleshy toe fringes. Toes with basal toe webbing; modal toe webbing formula: I 2–2½ II 2+–3½ III 3½–4½ IV 4+–2¾ V. A distinct elongate inner metatarsal tubercle, a little less than half of outer, which is round, distinct; distinct inner tarsal fold and strongly developed row of outer tarsal tubercles; no more than one plantar tubercle.

DISTINCTIVE FEATURES OF COLORATION—A narrow middorsal longitudinal light stripe rarely present. Dark eye mask usually extends only to tympanum or a little beyond; occasional individuals lack eye mask and have a series of dark lip bars and a supratympanic dark mask instead. No definite dark line on anterior thigh surface, but dark knee marks present; a relatively obscure dark line along anterior surface of lower leg. Dark seat patch triangular, with darkest pigment above the anus and along upper lateral margins. Posterior thigh surfaces brown. Undersides of limbs and throat mottled with dark pigment in most examples, venter similarly marked in largest examples. Iris bronze in life.

COLOR VARIATION—Members of this species (sample N = 29) have a rather dark brown ground



color with three principal patterns: essentially uniform without a middorsal stripe and with or without suprascapular dark spots (17%); essentially uniform with a pair of paravertebral black spots near midbody, with or without a middorsal light stripe and with or without suprascapular spots (45%); and with a definite hourglass-shaped dorsal figure, without a middorsal light stripe and with or without dark suprascapular dark spots (38%). Two examples are somewhat intermediate between the last two patterns in having an obscure dorsal dark figure and paired midbody black spots.

Three examples have barred lips: two (MVZ 131715: 2 km NW Barillas, Huehuetenango, Guatemala; MVZ 134679: 10 km NE Barillas, Finca Chibac, Guatemala) with an hourglass-shaped dorsal figure, and one (MVZ 160659: S. Purlha, Baja Verapaz, Guatemala) with paired middorsal black spots. None of these has a middorsal light stripe, but suprascapular dark spots are present in two of them.

In most examples the eye mask reaches the tympanum or continues a little beyond ( $Z_3$ ). In a few the stripe reaches the axilla ( $Z$ ) and in three examples, beyond the axilla ( $Z_2$ ).

MEASUREMENTS (IN MM)—Adult males 7 (25–28.1–32) in standard length, adult females 15 (33–39.3–47); smallest juvenile 15. Head width 30–37.9–43 in males, 38–43.5–49 in females; hind limb 168–177.7–186 in males, 157–185.4–212 in females.

DISTRIBUTION—Lower montane evergreen forests of Atlantic-versant Oaxaca and Chiapas, Mexico, and Guatemala, and on the Pacific versant from eastern Oaxaca through Chiapas to southwestern highland Guatemala, 900–2000 m (fig. 25).

LOCALITIES—GUATEMALA: **Alta Verapaz:** Finca Chichen; above Finca Sumac; **Baja Verapaz:** 3.9, 4.8 km S Purlha and Union Barrios; **Huehuetenango:** 2 km NW and Barillas; Finca Chibac; Playa de Los Bendos, Río Ixcán; **El Quiché:** 2 km N Nebaj; **Quezaltenango:** Lago Atitlán; 13 km NNE Colombia; Finca Lorena. MEXICO: **Chiapas:** 12 km N Berriozal; 8 km S and Pueblo Nuevo; nr. Talquian; **Oaxaca:** Cerro Azul; Cerro Baul, Colonia Rodulfo Figueroa; La Gloria and Río Grande; btwn. La Gloria and Santa María Chimalapa; 11 km N and Vista Hermosa; N. Zanatepec.

## A Key to Species of the *Eleutherodactylus gollmeri* Group

- 1a. Disks on fingers subequal ..... 2
- 1b. Disks on outer 2 fingers (III–IV) markedly larger than those on inner 2 (I–II); males to 53 mm in standard length, females to 66 mm ..... *E. noblei*
- 2a. (1a) Toes with basal webbing, at most; no fleshy lateral toe fringes ..... 3
- 2b. (1a) Toes moderately webbed, with web between toes III–IV extending nearly to distal subarticular tubercle on toe III and halfway between the proximal and penultimate tubercle on toe IV; toes with conspicuous lateral fleshy fringes continuous with webs; males to 37 mm in standard length, females to 58 mm ..... *E. mimus*
- 3a. (2a) Heel with 1–4 distinct small pustular tubercles or 1–2 large calcars; a distinct dark line along outer thigh margin; most finger disk covers slightly pointed to lanceolate, with swollen to cuspidate disk pads; a distinct dark seat patch mark present ..... 4
- 3b. (2a) Heel smooth to rugose; no distinct dark stripe along outer thigh margin; finger disk covers round, with even disk pads; no distinct dark seat patch mark present, although sometimes some dark pigment around anus; males to 47 mm in standard length, females to 80 mm ..... *E. laticeps*
- 4a. (3a) 1–2 large heel tubercles (calcars) ..... 5
- 4b. (3a) 1–4 more or less distinct small pustular tubercles on heel ..... 6
- 5a. (4a) A distinct serrate dark longitudinal stripe along anteroventral surface of thigh; outer tarsal tubercles weak; dark seat patch mark a pair of dark brown spots above and lateral to anus, sometimes fused or extending ventrad for a short distance and discontinuous with dark posterior thigh surface; males to 36.5 mm in standard length, females to 54 mm ..... *E. gollmeri*
- 5b. (4a) No distinct longitudinal stripe along anterior thigh surface; well-developed tarsal tubercles; dark seat patch triangular and continuous with the dark area of the lower posterior thigh surface, and darkest pigment along the upper margins; males to 32 mm in standard length, females to 47 mm ..... *E. lineatus*

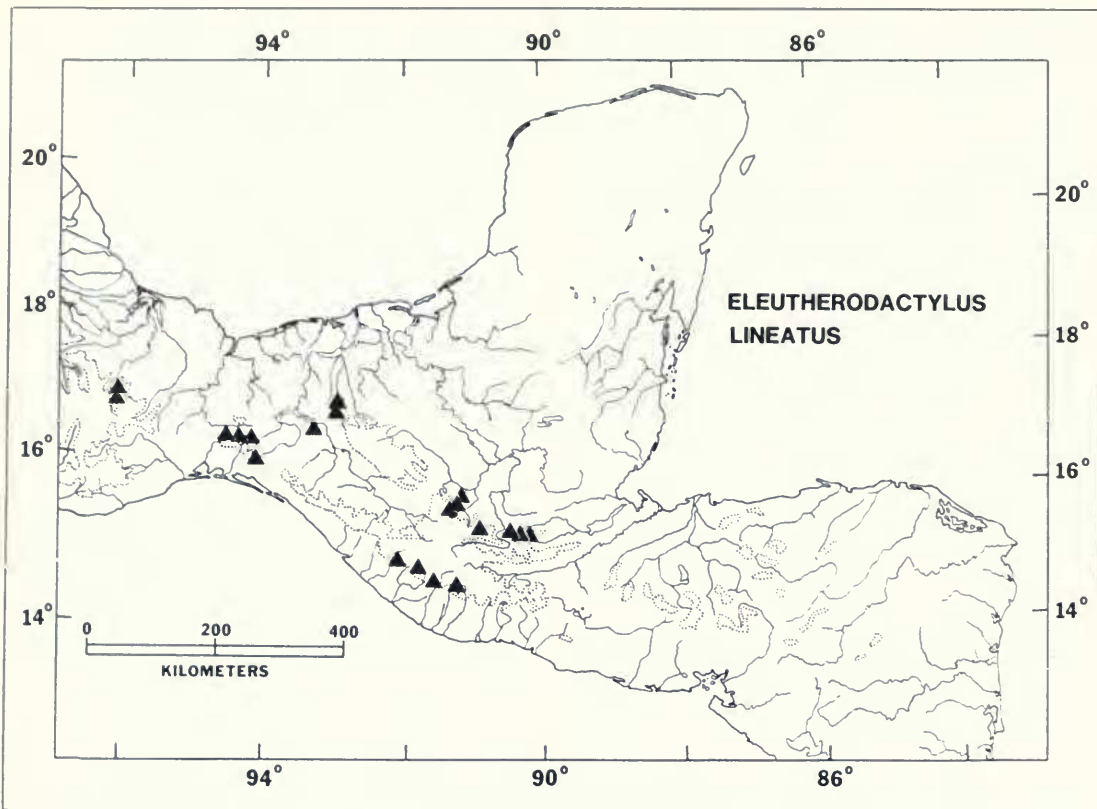


FIG. 25. Geographic distribution of *Eleutherodactylus lineatus*. The dotted line indicates the 1500 m contour.

- 6a. (4b) Heel pustules weak; row of outer tarsal tubercles very weak or absent; males to 36 mm in standard length, females to 58 mm ..... *E. rostralis*  
 6b. (4b) Heel pustules well developed; row of outer tarsal tubercles distinct; males to 27 mm in standard length, females to 39 mm ..... *E. chac*

### Distributional Patterns

In the following paragraphs, description of the ecologic occurrence of frogs of the *Eleutherodactylus gollmeri* group follows the modified Holdridge (1967) system of altitudinal zones, bioclimates, and associated vegetational formations outlined in an earlier paper (Savage, 1975). In this system members of the *E. gollmeri* group occur in three tropical altitudinal zones as defined by biotemperature (BT°) isophenes, but with approximate altitudinal limits indicated for Central America and southern Mexico as follows:

- Lowland—BT° = 24° C or more (0–500 m)  
 Premontane—BT° = 18–24° C (500–1500 m)

Lower montane—BT° = 12–18° C (1500–2500 m)

These zones correspond closely to what Stuart (1963) calls lowlands, moderate elevations, and intermediate elevations in Guatemala, respectively. Stuart (1950) and others have also referred to the lowest zone as lower tropical or the banana belt, the next highest zone as upper tropical or the coffee zone, and the final zone mentioned here as the subtropical zone. As pointed out by Stuart (1963), so-called “cloud forest” is typical on windward slopes in the latter zone. In drier situations in upper Central America and Mexico, oak-pine communities predominate in the lower montane zone.

The members of the *Eleutherodactylus gollmeri* group are restricted to evergreen forest sites in Mexico and Central America. In the southern portion of the range of the group, from eastern Honduras to eastern Panama, the distribution is primarily along the Atlantic versant. Exceptions include the occurrence of *Eleutherodactylus noblei* in southwestern Costa Rica and at scattered lowland localities on the Pacific versant of western Panama, and of *E. gollmeri* on the Pacific slope of central and eastern Panama (figs. 17–19).

*Eleutherodactylus gollmeri* has a relatively broad altitudinal range in the lowlands and on the premontane slopes of Panama. In Costa Rica the species is restricted to the lowland zone in the southeastern region, but is essentially a premontane slope form in the northeastern portion of the republic (640–1500 m, except for a record at Guapiles, Limón, 262 m). *Eleutherodactylus mimus* generally occurs at lower elevations than *gollmeri* in Costa Rica (15–640 m), where their ranges overlap geographically (figs. 17–18). Further to the north, in Nicaragua and Honduras, where *E. gollmeri* does not occur, *E. mimus* is found at higher elevations, mostly between 500–940 m.

The altitudinal distribution for *Eleutherodactylus noblei* resembles the pattern already described for *E. gollmeri*. In the southern portion of its range, *E. noblei* is essentially a lowland form, but in Costa Rica it ranges up to 1200 m in altitude along both slopes of the Cordillera de Talamanca and the Atlantic slope of the Cordillera de Tilarán. In Nicaragua and Honduras most records are from 500–900 m, but the species occurs near 100 m in elevation as well.

All three southern species have been recorded from one locale (Guapiles, Limón, Costa Rica). The three also are probably cosympatric in the El Silencio de Tilarán-San Bosco-Arenal area of Costa Rica, since they have been taken from closely adjacent sites along the continental divide northeast of Tilarán. Other sympatric co-occurrences are as follows: *Eleutherodactylus gollmeri*-*E. noblei*—El Silencio de Sitia Mata, La Suiza, Cartago, Costa Rica; Suretka, Limón, Costa Rica; 11 km NW and Almirante, Bocas del Toro, Panama; and El Valle de Antón, Coclé, Panama; and *E. mimus*-*E. noblei*—19 km N and Matagalpa, Matagalpa, Nicaragua; and La Selva, Heredia, Costa Rica.

The several northern Central American and Mexican members of the species group are completely allopatric to the southern forms. Their ranges are separated by a 125 km gap across north-

ern Honduras between the slopes south of Corozal (the eastern record for *Eleutherodactylus chac*) and the general area of Catacamas where *E. mimus* and *E. noblei* occur. The salient features of the geographic and altitudinal ranges of the four northern forms, which are also restricted to evergreen forests, follow (figs. 20–21, 24–25):

<i>E. chac</i>	Atlantic lowlands and premontane slopes of Guatemala, Belize, and northern Honduras, 30–775 m
<i>E. laticeps</i>	Atlantic lowlands and premontane slopes of southern Veracruz and Chiapas, Mexico, Guatemala, and Belize, 50–1600 m, and premontane areas of western Honduras, 750–1270 m
<i>E. lineatus</i>	Atlantic and Pacific upper premontane and lower montane zones of southern Mexico, 900–1800 m, and lower montane zone of Guatemala, 1200–2000 m
<i>E. rostralis</i>	Upper premontane areas of Atlantic-versant western Honduras and adjacent Guatemala, 850–1300 m

As may be seen from the above and the accompanying map (fig. 25), *Eleutherodactylus lineatus* occurs in the northern area at moderately high elevations, and its range extends well to the west of the Isthmus of Tehuantepec. It is completely allopatric to the upland form *E. rostralis* of Honduras and occurs at much higher elevations than *E. chac*, though their ranges approach one another in Guatemala.

East of the Isthmus of Tehuantepec, *Eleutherodactylus laticeps* (fig. 24) has a broad range from southern Mexico into Honduras at low to moderate elevations. The lower limits of the distribution of *E. lineatus* approach the upper limits for *E. laticeps* in northwestern Guatemala, and they are sympatric at Finca Chichen in Alta Verapaz, Guatemala (1100 m). *E. laticeps* and the much smaller *E. chac* occur together on the slopes of the Sierra del Mico in Guatemala and probably at nearby lowland sites (figs. 21, 24). Although the altitudinal ranges of *E. laticeps* and *E. rostralis* overlap in Honduras, no approach to sympatry is indicated by available data.

*Eleutherodactylus chac* and *E. rostralis* are altitudinally and geographically allopatric.



## Relationships and Evolution

The difficulties attending the evaluation of relationships in *Eleutherodactylus*, the most speciose genus of vertebrates, have been commented on at length by Savage and DeWeese (1979, 1981), Bogart (1981), Lynch and Myers (1983), and Savage (1985). The large number of forms (over 400 valid species) combined with the reoccurrence of the same character states of external morphology in distantly related species has subverted all attempts at recognition of natural subdivisions within the genus. Nevertheless, Lynch (1976) developed a most useful pragmatic scheme to cluster phenetically the species known at that time into 17 clusters (hereafter referred to as species series in the sense of Williams, 1976a,b; and Savage, 1985). During my study of Central American species of the genus (Savage, 1975, 1980, 1981b, 1985; Savage & DeWeese, 1979, 1981; Ford & Savage, 1984), I have attempted to recognize monophyletic stocks of closely related forms that now would be subsumed within one or the other of Lynch's series (most of which are probably polyphyletic). These units are the "species groups" of my past papers and this one, correspond to the assembly of Lynch and Duellman (1980), and are subdivisions within a series.

### Characters and Infrageneric Units

Several suites of characteristics have been utilized to establish species clusters within the genus. Lynch (1971) pointed out features of cranial morphology that seemed to separate most mainland members of the genus from their Antillean congeners. The former section of the genus he called the Beta group, the latter the Alpha group. Examination of his data and discussion indicates that the cranial characters actually divide the genus into two major and three minor sections, as follows:

#### I. Alpha section

1. Frontoparietal fused with otoccipital or prootic
2. No overlap between parasphenoid ala and the short median ramus of pterygoid
3. Vomers usually widely separated, small  
Distribution—Greater and Lesser Antilles and extreme northeastern South America

Similar genera—*Euparkerella*, *Sminthillus*, *Syrrhophus*, *Tomodactylus*

#### II. Intermediate section X

1. Frontoparietal fused with otoccipital or prootic (like Alpha)
2. Median ramus of pterygoid long, broadly in contact with anterior edge of parasphenoid ala (like Beta)
3. Vomers usually in contact or narrowly separated (like Beta)

Distribution—Ecuador (*Eleutherodactylus curtipes* group, Lynch, 1971; Lynch & Duellman, 1980)

#### III. Intermediate section Y

1. Frontoparietal and otoccipital or prootic separate (like Beta)
2. No overlap between parasphenoid ala and short median ramus of pterygoid (like Alpha)
3. Vomers usually in contact or narrowly separated (like Beta)

Distribution—Ecuador and Peru (*Eleutherodactylus acuminatus* and *E. cajamarcensis*); Hispaniola (*E. inoptatus* group, Schwartz, 1965; Lynch, 1976)

Similar genera—*Phrynopus*

#### IV. Beta section

1. Frontoparietal and otoccipital or prootic separate
2. Median ramus of pterygoid long, broadly in contact with anterior edge of parasphenoid ala
3. Vomers in contact or narrowly separated

Distribution—Mexico, Central and South America

Similar genera—*Barycholos*, *Holoaden*, *Hylactophryne*, *Ischnocnema*

#### V. *Eleutherodactylus rhodopsis* section

1. Frontoparietal and otoccipital or prootic separate (like Beta)
2. Pterygoid bent so that there is no overlap between parasphenoid and pterygoid, but median ramus of latter long
3. Vomers usually in contact or narrowly separated (like Beta)

Distribution—Mexico and northern Central America

Although Lynch (1971) emphasized his belief that the Alpha and Beta sections were natural, the intermediate sections X and Y suggest that the skull characters used in definition of the primary

groupings may be subject to parallelism. Lynch also regarded the *Eleutherodactylus rhodopis* section as part of the Beta section, because features 1 and 3 agreed with that unit and because the bent pterygoids have long median rami. In the accompanying chart (table 3) the included groups are placed into three divisions, Alpha, Beta, and a special division for *E. rhodopis* and its ally, *E. mexicanus*, enclosed in solid boxes under the Beta division for reference in evaluating other features.

That the dichotomous separation of the genus into two major sections on the basis of skull features is questionable is tacitly admitted by Lynch (1976), who places the *Eleutherodactylus curtipes* group (Intermediate X) and *E. acuminatus* and *E. cajamarcensis* (the South American part of Intermediate Y) within the *E. unistrigatus* series. The latter, multitudinous stock (containing about 100 valid species) is typically Beta in skull characteristics. In addition, Lynch (1976) suggested that the speciose Antillean *E. auriculatus* series (Alpha) and the *E. unistrigatus* series (Beta) are closely allied, based upon external morphology. This conclusion and the placement of the intermediate taxa support the idea that the derived skull features typifying the Alpha section (one involving a fusion of elements and two involving a reduction in element size) are homoplasious and have arisen several times in the evolution of the genus.

Partially because of the difficulties with osteological variation, but primarily because a dichotomous arrangement of the genus did not solve the practical problems of coping with 400 diverse species, Lynch (1976) subsequently devised a different approach to subdividing *Eleutherodactylus* into major clusters of similar forms. In this approach he emphasized two characters of external morphology (each with two character states) as a basis for dividing the genus into four infrageneric units (or sections). These features, the length of the first finger relative to the second and the texture of the skin of the venter, form the lynchpin of the system, as follows:

Section 1A—First finger longer than second; skin of venter smooth or feebly granular

Section 1B—First finger longer than second; skin of venter coarsely areolate

Section 2A—First finger shorter than second; skin of venter smooth

Section 2B—First finger longer than second; skin of venter coarsely areolate

On the basis of the use of a set of subsidiary features—presence or absence of cranial crests; rel-

ative head width; structure of the unguis flap; presence, absence, and shape of the disks; presence or absence of webbing; tympanic structure; vomerine tooth patch shape; and, in some cases, the cranial features previously described—Lynch divided the genus into 17 series and defined the 10 South American series in detail, including lists of referred species. He readily admits (1976, p. 6) that the recognized sections are probably no more than convenient subdivisions (i.e., are nonmonophyletic) but implies that the series are monophyletic.

While this arrangement fulfills the goal of grouping the plethora of species into a relatively small number of clusters, the emphasis on what I continue to regard as trivial “key” characters of external morphology (especially the features used in the establishment of the four sections) makes the system of dubious phylogenetic significance. The fact that these features and a number of the subsidiary ones show more variability within a number of the series than indicated by Lynch also suggests that the more speciose series are nonmonophyletic. Nevertheless, the Lynchian scheme provides a very useful framework for clustering *Eleutherodactylus* species into phenetic series. That many of the series are bound together by shared primitive character states and/or by homoplasy does not detract from their utility. The task now remains for the students of the genus to work toward a phylogenetically based system raised on shared-derived states and multiple character sets and to reflect evolutionary relationships more accurately, building upon the solid base provided by Lynch’s extraordinary efforts.

In this regard, my method of clustering species within the genus is doubtless a reflection of my focus on a smaller number of species (those of Mexico and Central America) than Lynch faced in devising his scheme for the entire genus or for South America alone. I worked up from a lower level to phenetically cluster species that are very similar in morphology and seemingly closely allied into species groups. As properly noted by Lynch and Myers (1983), a number of these groups have been defined solely by their contents (Savage, 1973, 1976, 1980), but other groups in my system have been formally defined (Savage, 1975; Ford & Savage, 1984). Species groups in this sense are comprised of a monophyletic stock of closely related forms, and for this reason I recently (1985) proposed that species groups (assemblies of Lynch & Duellman, 1980) of this kind be regarded as subunits within the Lynchian series. In this way both systems are integrated into a single scheme and

TABLE 3. Skull, jaw musculature, and karyotypic characters in *Eleutherodactylus*.

e		s			
dfsq, dfsqat	DFSqat	DFSQAT	DFSQ <sub>d</sub> AT	DFSQ <sub>d</sub>	SQ
<b>ALPHA</b>					
36 ALFREDI (2) 36,38,40 FITZINGERI (5) (36) 38 melanostictus 36 RUGULOSUS (10)	22 22 22 20,22		36 CUBAN AURICULATUS (2) 18 TOMODACTYLUS* (5) 22 42,46,50,52 P R AURICU- LATUS (11) 26 36 SYRRHOPHUS* (12) 26,30 36,38,40,44 CUBAN RICORDII (6) 28,32 36 SMINTHILLUS* 32 36,40,54 P R RICORDII (3) 30  NO DATA ON JAW MUSCLES: 32 dimidiatus 30		40 EUPAR- KERELLA 20
<b>BETA</b>					
36 HYLACTOPHRYNE* (2)	22		Intermediate skull: PHRYNOPUS*  36 diastema 20 (18) 46 altae 26 32,36,38,46 UNISTRIGATUS (5) 32,34,36 40 conspiciatus 34 GEOBATRACHUS* ISCHNOCNEMA* 22 BARYCHOLOS* PHYLLONASTES*	36 HOLO- ADEN* 18	
36 rhodopsis	18	cuauquero daryi 22 40 greggi monnichorum omilitimanus 36 GOLLMERI (2) 20,22 matudai 44 milesi 22 38 biporcatus 20 bufoniformis 22 36 bransfordii 18 36 podiciferus 18 hobartsmithi pygmaeus mausii	NO DATA ON DEPRESSOR CONDITION ALL WITH s:		
			38,44 BINOTATUS 22 44 DISCODALIS 22 PARVUS 22 38 sulcatus 22 38 holti 20 36 gaigeae 34 36 lanthanites 36		



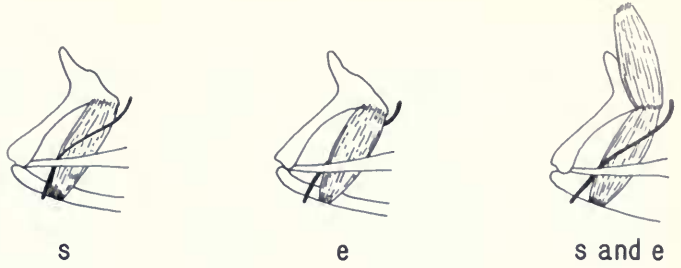


FIG. 26. Character of adductor mandibulae muscles in frogs (see p. 41 for explanation); after P. H. Starrett (1968).

the smaller clusters (groups) may be easily moved from one series to another as our knowledge increases or may require, since these series are more likely to be monophyletic than those currently recognized. While the integrated system will be useful for the taxonomic sorting of the many species, both the series and groups may be nonmonophyletic units in many cases, and a considerable re-shuffling of species and groups can be anticipated as a more phylogenetically based system evolves.

#### Jaw Musculature and Karyotypes as a Basis for Classification

As a contribution to the process, this seems a good place to review briefly the available data on jaw musculature and karyology that Savage and DeWeese (1979, 1981) suggested may provide a basis for resolving some aspects of the nonmonophyly of series and groups. Miyamoto (1981, 1983) has elucidated the significance of electrophoretic data as a basis for evaluating intragroup relationships. These data are ambiguous for most intergroup comparisons and will not be discussed further here. Following this review it should be possible to define more clearly the relationships of the *Eleutherodactylus gollmeri* group within the genus prior to treating its intragroup phylogeny.

The most consistent and evolutionarily significant aspect of the jaw musculature is the condition of the adductor mandibulae (Starrett, 1968; Savage, 1985; Lynch, 1986). Four states of this character (fig. 26) can be recognized in frogs, two of which occur in *Eleutherodactylus*: s + e, both an adductor mandibulae posterior subexternus and an externus superficialis present; s, only the subexternus present; e, only the externus superficialis present; o, neither present. Starrett (1968) reported the occurrence of the s + e condition in the *E. biporcatus* and *E. sulcatus* groups and in *E. bransfordii*, *E. hobartsmithi*, and *E. pygmaeus*, but Lynch (1986) and I have dissected additional ma-

terial and found the e-only condition in these groups and species.

The condition of the depressor mandibulae muscles also provides significant data for establishing relationships (fig. 27). Eleven patterns of depressor mandibulae origins are known in frogs (10 described by Starrett, 1968, and an additional one in this paper). Seven of these occur in the family Leptodactylidae and five in *Eleutherodactylus*. The conditions in the genus are: dfsq or dfsqat (Starrett, 1968, regarded these as two states; Savage & DeWeese, 1979, regarded them as variants), a single slip primarily from the dorsal fascia but with a few fibers from the squamosal (sq) or the squamosal and annulus tympanicus (sqat); DFSQat, two distinct slips from the dorsal fascia and squamosal with a few fibers from the annulus (this condition is recorded for any frog for the first time in the present paper); DFSQAT, three distinct slips, one each from the dorsal fascia, squamosal, and annulus; and DFSQ<sub>d</sub>AT, three distinct slips, with superficial slips from the dorsal, fascia, and annulus covering a deeper one from the squamosal (this condition appears superficially as DFAT; in species with a reduced auditory apparatus the formula is DFSQ<sub>d</sub>).

Of these conditions, dfsq and dfsqat are only known to occur in *Eleutherodactylus* and its close ally, *Hylactophryne*, among frogs. The DFSQ<sub>d</sub>AT condition is known to occur only in *Eleutherodactylus* and its close relatives (*Barycholos*, *Geobatrachus*, *Phyllonastes*, *Phyzelaphryne*, *Sminthillus*, *Syrrophus*, and *Tomodactylus*), the leptodactylid *Pseudopaludicola*, the myobatrachid *Geocrinia*, and all genera of the Dendrobatidae (Starrett, 1968). The latter family is usually considered a derivative from a leptodactylid ancestor.

Heyer (1975) described the jaw muscle condition for two other presumed allies of *Eleutherodactylus*. The formulae for *Euparkerella* and *Iloaloden* are SQ + s and DFSQ<sub>d</sub> + s, respectively. The former condition is unknown elsewhere in the family although found in *Rhinoderma* (Starrett,

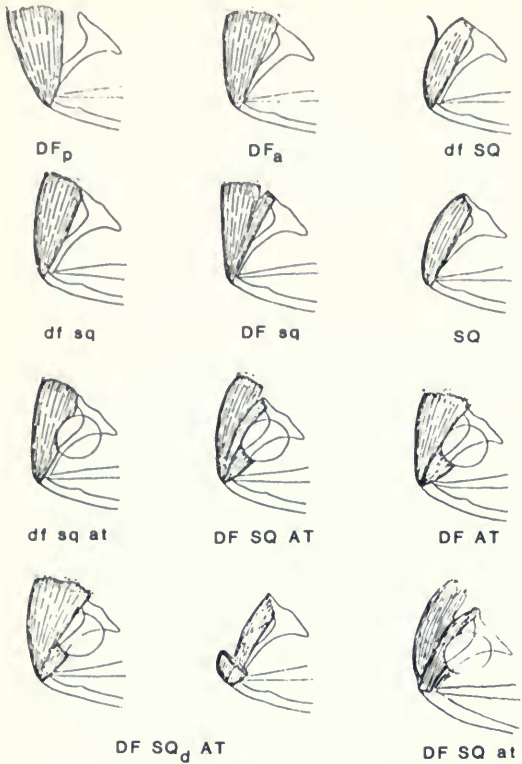


FIG. 27. Character states for depressor mandibulae musculature in frogs (see p. 41 for explanation); after P. H. Starrett (1968). In this diagram the notation for each condition separates the individual slip designations for clarity.

1968); the latter is obviously derived from the DFSQ + s condition.

Lynch (1986) has recorded the condition of the adductor mandibulae muscles in 219 species of *Eleutherodactylus* and the allied genera *Hylactophryne* (1 sp.), *Syrrhophus* (12 spp.), and *Tomodactylus* (5 spp.). As a result he corrected a number of errors in Starrett's (1968) classic study. Unfortunately, he did not record the condition of the depressor mandibulae. Nevertheless, Lynch's survey is of great significance to the discussion below.

On the basis of the features of the mandibular muscles, the species of *Eleutherodactylus* may be placed into four subdivisions (60 species examined by Starrett, 1968, and the present study; 240 species examined by Lynch, 1986, for the adductor condition only). Names in parentheses indicate other genera of the family Leptodactylidae sharing the jaw musculature characters.

1. dfsq or dfsqat + e only (*Hylactophryne*)
2. DFSQat + e only

3. DFSQAT + e only

4. DFSQ<sub>d</sub>AT + s only (*Barycholos*, *Geobatrachus*, *Holoaden* [DFSQ<sub>d</sub>], *Ischnocnema*, *Phyllonastes*, *Pseudopaludicola*, *Syrrhophus*, *Tomodactylus*)

It is important to note that Lynch (1986) corroborated Starrett's (1968) observation that *Hylactophryne augusti* has the e condition of the adductor jaw muscle contrary to Heyer (1975), who recorded the condition as being s. Other members of the genus (*H. occidentalis* and *H. tarahumarensis*) have the e condition according to Lynch (1986). Both Heyer and I have reexamined the specimen of *H. augusti* upon which his 1975 report is based and agree that it appears to have the s character state. This finding may be based upon an anomaly. For this reason I have accepted the preponderance of the evidence: the independent observations of Starrett (1968) and Lynch (1986); the occurrence of the e condition in other *Hylactophryne* (Lynch, 1986); and the detailed dissections and comparisons undertaken by Lynch, indicating that the e character state is typical of *Hylactophryne*.

Conditions 1–2 are unique to the Leptodactylidae among all anurans, while condition 4 is shared with some genera in the closely allied families Myobatrachidae and Dendrobatidae. Condition 1 is essentially unique to the *Eleutherodactylus* lineage, since *Hylactophryne* is usually thought to be derived from the former (Lynch, 1971). Condition 2 is unique to *Eleutherodactylus*.

The distribution of the jaw musculature features for the genus is summarized in the accompanying chart (table 3). In the chart, species groups are indicated in capital letters, with the number of species examined in parentheses. Where not all members of a nominal species group have the same condition, individual species names appear in lowercase letters. Several genera usually thought to be closely allied to *Eleutherodactylus* (Lynch, 1971) are also included in the chart and indicated by an asterisk (\*). Because Lynch's paper did not record the condition of the depressor mandibulae, his data were used to confirm the adductor condition but cannot be used to allocate species on this chart.

Significantly, members of several species series and groups defined on other morphological grounds share a common jaw musculature. Thus the *Eleutherodactylus auriculatus*, *E. ricordii*, and *E. unistrigatus* series (*E. diastema* and *E. unistrigatus* groups) all have a characteristic jaw muscle condition. The *E. biporcatus*, *E. sulcatus*, *E. rugulo-*

*pus*, *E. milesi-matudai*, *E. omiltimanus*, *E. gollmeri*, and *E. alfredi* groups similarly appear to be homogeneous in these features. On the other hand, the *E. fitzingeri* group (including *E. cuaquero* and the recently described *E. emcelae* [Lynch, 1985]) shows considerable variation in depressor muscle character states. The muscle features also lend considerable support to Lynch's (1976) suggestion that the mainland *E. unistrigatus* series (a Beta) and some members of the Antillean *auriculatus* series (an Alpha) may be closely allied. These data indicate that the Antillean *E. ricordii* series (an Alpha) may also be related to these two stocks.

In his 1976 paper, Lynch placed *Eleutherodactylus mexicanus*, *E. saltator*, *E. pygmaeus*, *E. hobartsmithi*, *E. sartori*, *E. rhodopis*, and *E. bransfordii* into the *E. rhodopis* series. Subsequently, Lynch and Myers (1983) referred the last named species to the *E. fitzingeri* series without comment. Similarly (1980), I placed *E. bransfordii* in the *E. gollmeri* group. These allocations are ambiguous, based upon jaw muscle features. *Eleutherodactylus mexicanus* is unique among known frogs in being DFSQat + e, and *E. rhodopis* has the dfsqat + e condition. *Eleutherodactylus bransfordii* and *E. podiciferus* resemble one another, the *E. gollmeri* group, and several members of the *E. fitzingeri* group in having the DFSQAT + e condition. Although Starrett (1968) recorded the condition for *E. hobartsmithi* and *E. pygmaeus* as being DFSQ<sub>a</sub>AT + s + e, Lynch (1985) has indicated Starrett was in error regarding the adductor character. I believe she inadvertently recorded the DFSQAT condition of these species as DFSQ<sub>a</sub>AT as well. On the basis of these features, the *E. rhodopis* series, including *E. bransfordii* and *E. podiciferus*, could be placed with the *E. fitzingeri* series or even in the *E. gollmeri* group within the latter series.

The data on jaw muscles, although incomplete, suggests that this feature is useful in defining natural groups and establishing evolutionary relationships within *Eleutherodactylus*. These data are somewhat in conflict with the skeletal groupings developed by Lynch (1971), but support (or at least do not conflict with) his 1976 groupings in many cases. They do indicate that at least some Lynchian series (Lynch, 1976; Lynch & Myers, 1983) are nonmonophyletic.

Karyological data (Bogart, 1973, 1981; DeWeese, 1976) may also shed some light on these matters (table 3). *Eleutherodactylus* has a considerable variation in 2N (diploid) chromosome values: 18, 20, 22, 26, 28, 30, 32, 34, 36. The *nombre*

*fundamental* (N.F.) as an indicator of the number of chromosome arms is also variable: 32, 36, 38, 40, 44, 46, 48, 50, 52, 56. Bogart (1981) and DeWeese (1976) have shown that species of the genus may be clustered using features of the karyotype, and that these clusters often conform to groupings based upon other characters. Miyamoto (1981, 1983) has also used these features for cladistic analyses of relationships within and among species groups. In the accompanying table (table 3), each species (lower case) or species group (capitals) has its N.F. (before the name) and 2N (after the name) indicator. Species or groups for which karyological data are available but for which there are no data on jaw musculature are included in an appropriate skull-based section (Alpha or Beta) below the dotted line.

DeWeese (1976) pointed out that mainland members of the genus fall into two major divisions based on karyology, those with 2N = 18, 20, 22 (I) and those with 2N = 26 or more (II). According to DeWeese, the former stock has favored minimizing segregational variability and has many biarmed chromosomes (BA). The latter (II) has maximized segregational variability and has more numerous acrocentric chromosomes. Thus, while the ranges of N.F. for the two groups overlap, there is no direct correlation between 2N and N.F.; they may be treated as different characters. Significantly, division I includes all species for which karyotypes are known from Mexico and 13 from upper Central America, whereas division II is centered on South America and lower Central America. South American division I stocks include sampled representatives of the *Eleutherodactylus biporcatus*, *E. sulcatus*, *E. binotatus*, *E. discodalis*, and *E. parvus* series of Lynch (1976) and the *E. diastema* group of Savage (1980). Lynch (1976) places the latter group within his *E. unistrigatus* series, but the karyological differences 2N = 20 in *E. diastema* (Bogart, 1973, reported 2N = 18 for this species, but DeWeese believes this is based on an error in identification) and 26, 32, 34, 36 in representatives of the *E. unistrigatus* group raise a question regarding that conclusion. It should also be noted that the *E. fitzingeri* series (Lynch & Myers, 1983) is almost certainly nonmonophyletic, based upon karyotypes. Most species referred to this series have 2N = 20 or 22. *E. bransfordii* and *E. podiciferus* have 2N = 18, while *E. conspicillatus* and *E. gageae* have 2N = 34 and *E. lanthanites* has 2N = 36. The former two numbers are from DeWeese (1976), the latter three from Bogart (1973). The latter author reports a 2N =



20 for *E. bransfordii*, but the identification of his specimen, which cannot be located, is questionable. John D. Lynch similarly has informed me that Bogart's identification of *E. conspicillatus* may be in error and may be based in part on *E. toftae*, a *E. unistrigatus* series form.

Comment is required on two mainland species in this regard. The karyotype of *Eleutherodactylus unistrigatus* is not known, although Lucca et al. (1974) described the karyotype of *E. unistrigatus holti* as  $2N = 20$ , N.F. 38, BA 18. This latter form is a distinct species (Heyer, 1985) and a member of the *E. lacteus* series (Lynch, 1976), a unit which is found only in southeastern Brazil and which is not related closely to the *E. unistrigatus* series. The karyotype of *E. altae* is unique among mainland members of the genus in having a high diploid number (26) and many (20) biarmed chromosomes. It resembles those Antillean *Eleutherodactylus* placed in a separate division in the next paragraph, although differing from them in the overall morphology of the karyotype.

The situation is somewhat more complicated in the Antilles than on the mainland (Bogart, 1981). Bogart suggested that four distinct stocks involving  $2N = 18, 26, 30$  and  $32$  (with  $28$  as a derivative) chromosome ancestors are represented. Several of these karyologies conform well to DeWeese's (1976) mainland divisions,  $2N = 18$  with I and  $2N = 28, 30, 32$  with II. *Eleutherodactylus dimidiatus* of Cuba ( $2N = 30$ ; N.F. 32; one biarmed chromosome pair) also belongs here (II). The others having  $2N = 26, 30$  do not. Eleven Puerto Rican species with  $2N = 26$  belonging to the *E. auriculatus* series have both high diploid numbers and many biarmed chromosomes. They may therefore be regarded as forming a third major karyotypic division (III) within the genus. These karyological data strongly suggest that the *E. auriculatus* series is nonmonophyletic. The Cuban species *E. auriculatus* and *E. varians* ( $2N = 18$ ; N.F. 36) belong to division I and differ markedly from the eleven Puerto Rican species ( $2N = 26$ ; N.F. 42, 46, 50, 52) which fall into division III. The differences within the *E. ricardii* group in karyology are also significant, as the three Puerto Rican forms have  $2N = 30$  and N.F. 36, 40, 54, in contrast to the five Cuban species with  $2N = 28$  or  $32$  and N.F. 36, 38, 40, 44, but they could be derivatives of a common ancestral stock.

Although the data on jaw musculature (60 species) and karyology (65 species) are incomplete, they point to several conclusions:

1. The skull characters emphasized by Lynch (1971) and as shown by him (1976) do not define monophyletic groups, and the Alpha condition seems to have developed several times by a fusion (between the frontoparietal and otoccipital) and reductions in element size (long to short median process of the pterygoid and large to small vomers)
2. At least six major lineages of *Eleutherodactylus* are indicated by a combination of jaw musculature and karyology, as follows (BA = number of biarmed chromosomes):
  - a. dfsq, dfsqat, DFSQAT + e; I ( $2N = 20, 22$ ); BA = 14, 16, 18, 20, 22 (*E. alfredi*, *E. biporcatus*, *E. fitzingeri* series, and *E. omiltilmanus* group)
  - b. dfsq, DFSQat, DFSQAT + e; I ( $2N = 18$ ); BA = 18 (*E. rhodopis* series)
  - c. DFSQ<sub>d</sub>AT + s; I ( $2N = 20$ ); BA = 16 (*E. diastema* group)
  - d. DFSQ<sub>d</sub>AT + s; I ( $2N = 18$ ); BA = 18 (Cuban *E. auriculatus* series)
  - e. DFSQ<sub>d</sub>AT + s; II ( $2N = 28, 30, 32, 34, 36$ ); BA = 0, 2, 4, 6, 8, 10, 12, 14 (*E. unistrigatus* and *E. ricardii* series)
  - f. DFSQ<sub>d</sub>AT + s; III ( $2N = 26$ ); BA = 16, 20, 24, 26 (*E. altae* and Puerto Rican *E. auriculatus* series)
3. The *E. unistrigatus*, *E. auriculatus*, and *E. fitzingeri* series of Lynch (1976) and Lynch and Myers (1983) are probably nonmonophyletic
4. Other eleutherodactyline genera fall into the following karyological divisions:
  - I. *Euparkerella* ( $2N = 20$ ; N.F. = 40; BA = 20)  
*Holoaden* ( $2N = 18$ ; N.F. = 36; BA = 18)  
*Hylactophryne* ( $2N = 22$ ; N.F. = 36; BA = 14)  
*Ischnocnema* ( $2N = 22$ ) and *Tomodactylus* ( $2N = 22$ )
  - II. *Sminthillus* ( $2N = 32$ ; N.F. = 36; BA = 4)  
*Syrrhophus* ( $2N = 26, 30$ ; N.F. = 36; BA = 6, 10)

#### A Phylogenetic Hypothesis

It seems evident from this discussion that the features of jaw musculature and karyology provide a promising basis for evaluation of the phyloge-

netic relationships among *Eleutherodactylus* as data on more species are accumulated. The principal difficulty with the use of these features lies in establishing those that are primitive and those that are derived. In the case of the adductor mandibularis muscles, Starrett (1968) and Heyer (1975) argue that the s + e condition is primitive and that the s-only condition is derived, through loss. The presence of the e-only state would similarly be considered a separate derived condition. Miyamoto and Tennant (1984) and Lynch (1986) argue that the s condition is primitive and the e derived. In addition, they regard the s + e state found in some other leptodactylid genera as derived. Their arguments seem persuasive and are followed here.

In the case of the depressor mandibularis muscle, the DFSQ<sub>d</sub>AT condition is clearly derived, while the DFSQAT state probably represents the primitive condition (Heyer, 1975), with DFSQat, dfsqat, and dfsq derived variants.

DeWeese (1976) indicated that karyological evolution in *Eleutherodactylus* has proceeded in two directions, from a primitive diploid number of 26 toward lower numbers (22, 20, 18) through centric fusion (division I), and toward higher numbers (28, 30, 32, 34, 36) through centric fission (division II). The former are further characterized by having a high number of biarmed chromosomes, the latter by having relatively few. It seems likely therefore that division III karyotypes are primitive (2N = 26; N.F. = 42, 46, 50, 52; BA = 16, 20, 24, 26) and divisions I and II are independently derived from II. On the basis of these evaluations it will be seen that of the six major lineages of *Eleutherodactylus* recognized above, all but one are defined by both a derived musculature and karyotype. Lineage 6 has a derived musculature but a primitive karyotype.

These features may be used to establish a tentative hypothesis of relationships among the six lineages (fig. 28). Since data for both jaw musculature and karyology are available for a relatively few species (ca. 12%) in the genus, this cladogram must be regarded as very preliminary and heuristic. It is, however, instructive to compare its salient features to Lynch's proposals (1976, 1985) regarding the relationship and classification of the eleutherodactylines (*Eleutherodactylus* and allied genera).

As pointed out in several previous papers by my associates and by me (Savage, 1980, 1981b, 1985; Savage & DeWeese, 1979, 1981; Ford & Savage,

1984; Savage, an earlier section of the present paper) Lynch's (1976) clustering of the species into series (groups) was an essentially phenetic one based upon "key" features of external morphology that we found to be variable within many of Lynch's nominal groups and probably homoplasious in different unrelated lines. The characters of relative length of the first as compared to the second finger (longer versus shorter), the texture of the abdominal skin (coarsely areolate versus smooth or feebly granular), and the condition of the unguis flap (even versus notched) used by Lynch to define his groups are particularly suspect in this regard. For these reasons we suggested that the features of jaw muscles and karyotypes seemed to provide a more promising foundation for a phylogenetically based classification than did external morphology.

The present analysis amply confirms the reservations cited above and leads to the following conclusions:

1. The genus *Eleutherodactylus* as presently recognized is paraphyletic
2. The Alpha versus Beta sections, based upon skull features as defined by Lynch (1971), form questionable monophyletic groups, since the derived Alpha condition would have to have evolved four times (once each in lineages 4, 6; in the ancestor of line 5; in *Sminthillus* and *Syrrhophus* and in *Tomodactylus*) to support Lynch's (1976) reservations regarding the significance of Alpha-Beta dichotomy
3. The *E. fitzingeri* series of Lynch (1976) as redefined by Lynch and Myers (1983) is clearly paraphyletic with one group (2N = 20, 22) associated with lineage 1 and *E. conspicillatus*, *E. gaigeae* and *E. lanthanites* (2N = 34, 36) only distantly related; since *E. conspicillatus* has the depressor condition DFSQ<sub>d</sub>AT, it (and probably its allies) belongs with lineage 5
4. The genus *Eleutherodactylus* consists of two major stocks, each defined by a jaw muscle synapomorphy: I by having the adductor condition e (including lineages 1-2 and *Hylactophryne*) and II by having the depressor condition DFSQ<sub>d</sub>AT (fig. 28)
5. Within the stock characterized by the DFSQ<sub>d</sub>AT depressor, three subdivisions are recognizable:
  - a. Those forms having the synapomorphy of division I karyotypes with 2N = 18,

20, 22, and many biarmed chromosomes (16, 18, 20); lineages 3–4, *Holoaden*, *Euparkerella*, *Ischnocnema*, and *Tomodactylus*

- b. A stock having the synapomorphy of division II karyotypes with  $2N$  usually 28–36 but, more significantly, always a small number of biarmed chromosomes (0–14); lineage 5, *Sminthillus* and *Syrrophus*
  - c. A lineage (6) defined by the pleisiomorphy of having division III karyotypes ( $2N = 26$ ; biarmed chromosomes 16, 20, 24, 26)
6. The broad-headed eleutherodactyls of the *E. sulcatus* series form a paraphyletic group, since one species has adductor condition *s* (*E. sulcatus*) and another *e* (*E. maussi*)

Lynch's (1986) recent review of the occurrence of the different conditions of the adductor muscle states in eleutherodactylines led him to a major revision of his previous position regarding the features of significance in clustering species of eleutherodactyline frogs. As a result of his analysis, he proposed that those species possessing the derived *e* condition formed a single monophyletic clade. Since this cluster of species has its distribution centered on Mexico and Central America, with a few forms in northern South America, he called it the Middle American clade to be referred to subgenus *Craugaster* Cope, 1862. All members of the following series and/or groups (à la Lynch, 1976, and Savage and associates, 1975–1985) would fall into this clade, according to Lynch: *Eleutherodactylus alfredi*, *E. gollmeri*, *E. milesi*, *E. omilimanus*, *E. rhodopis*, and *E. rugulosus*, along with the nominal genus *Hylactophryne*.

Lynch further concluded on the basis of the adductor character that his previously recognized *Eleutherodactylus biporcatus*, *E. fitzingeri*, and *E. sulcatus* series are paraphyletic since some members of each stock have the *s* condition and others *e*, although he acknowledged directly only the cleavage in the *E. biporcatus* and *E. sulcatus* clusters. He placed all forms previously referred to the *E. fitzingeri* series that have the *s* condition into the previously unrecognized *E. conspicillatus* group in the appendix.

Lynch also returned to his earlier idea that the fusion of the frontoparietal and prootic (one attribute of his Alpha section, 1971) is a synapomorphy shared by many *Eleutherodactylus* having the *s* condition of the adductor muscle. These states occur in many West Indian forms and the Mexican

and northern Central American genera *Syrrophus* and *Tomodactylus*. Insofar as known, no species having the *e* adductor state has the frontoparietal/prootic fusion but many forms lacking the fusion share the *s* condition (table 3). Unfortunately for this argument, my analysis (fig. 28) suggests that the fusion is a homoplasy that has arisen independently four different times.

Nevertheless Lynch concluded that his previous attempts to cluster species of this genus are seriously undermined by the jaw muscle and skull features, since they require that: 1) whichever condition of the ventral skin texture is derived, it must have evolved more than once; 2) whichever condition of the relative lengths of fingers I–II is derived, it must have evolved more than once; 3) the derived trait of a notched or indented unguis flap has evolved more than once; and 4) the derived condition of a broad head has evolved twice.

Each of these ideas will now be reviewed in the light of the present analysis, as summarized in the accompanying table and cladogram (table 3, fig. 28). There seems little problem with the recognition of the Middle American clade, since it is defined by the two synapomorphies of the adductor condition (*e*) and an advanced karyotype ( $2N = 18, 20, 22$ ;  $BA = 14, 16, 18, 20, 22$ ). It conforms to branch I of the cladogram and includes lineages 1 and 2 and *Hylactophryne*. In addition to the species listed by Lynch as belonging to this clade, the following forms may be included here based upon an examination of the jaw muscles: all members of the *Eleutherodactylus gollmeri* group discussed in this paper, *E. milesi* (DFSQAT + *e*), and *E. monnichorum* (DFSQAT + *e*). It is predicted that most species referred to this clade on the basis of jaw musculature and for which karyotypes remain to be described will have division I chromosome complements of  $2N = 22$  or less, with 14–22 biarmed elements.

Lynch confirmed my earlier suggestion (Savage, 1985) that his *Eleutherodactylus fitzingeri* series was paraphyletic, as further documented in an earlier part of this section. *Eleutherodactylus fitzingeri* and its allies belong to lineage 1, while most of the South American forms placed by Lynch prior to 1985 in this series probably belong in lineage 5. He also demonstrated an unexpected dichotomy within the broad-headed eleutherodactyls to show that both his *E. biporcatus* and *E. sulcatus* series are paraphyletic, since some species in each series have the *s* condition (*E. cerastes*; *E. cornutus* of the *E. biporcatus* series; and *E. ingeri*, *E. ruizi*, and *E. sulcatus* of the *E. sulcatus* series)



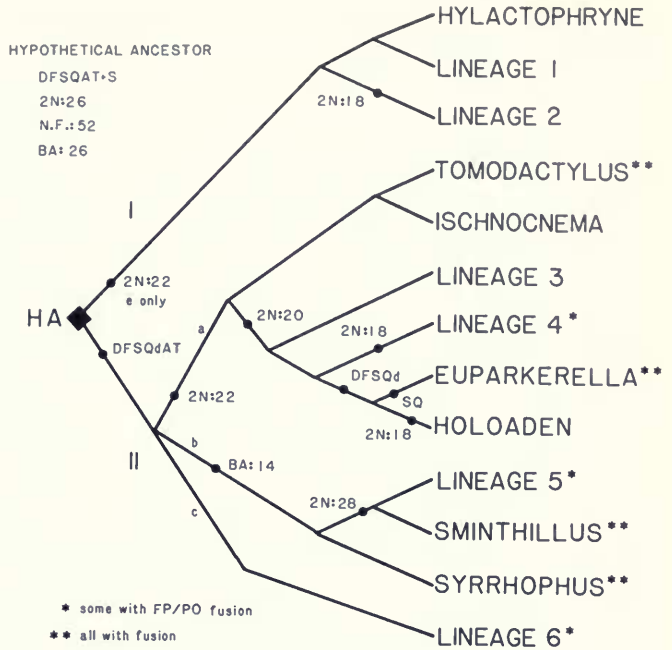


FIG. 28. Cladogram of relationships in *Eleutherodactylus* and associated genera based on features of musculature and karyology.

and others have the e condition (*E. biporcatus*, *E. bufoniformis*, *E. florulentus*, and *E. necerus* of the *E. biporcatus* series, and *E. maussi* of the *E. sulcatus* stock). Lynch concluded that the broad-headed *Eleutherodactylus* with the e condition belong with the Middle American clade (a reconstituted *E. biporcatus* group) and those with the s condition become a revamped *E. sulcatus* group by implication. Under this revision, the two groups of broad-headed eleutherodactyls are only distantly related.

The situation with the frontoparietal-prootic fusion has been discussed above (p. 44). As noted, this feature appears to be a multiply derived apomorphy (= homoplasious). In the cladogram (fig. 28), lineages and genera where this feature occurs in some species but not in others are indicated by an asterisk (\*) and in those where all members have the condition, by a double asterisk (\*\*).

Finally, it is gratifying to have Lynch confirm my long-held position that ventral skin texture, relative lengths of fingers, and the presence of emarginate disks have evolved several times within the eleutherodactyls and are an uncertain base upon which to establish relationships, phylogenies, or classifications. Fortunately the change in Lynch's emphasis supports the significance of jaw muscle features in the genus and suggests that the approach to classification championed in the pres-

ent paper is a most promising one for resolving the systematics of this diverse, speciose, and "difficult" group.

Unfortunately, the paucity of data on the condition of the depressor mandibulae and karyotypes in most species leaves many open questions regarding relationships within the lineages characterized by the s condition of the adductor muscles. It is tempting to predict that the derived DFSQ<sub>d</sub>AT condition of the depressor will be found in all species having the s adductor state. If this turns out to be the case, a South American-Antillean clade based on the derived depressor condition could be recognized and would correspond to branch II in the accompanying cladogram (fig. 28). In that event Lynch's (1976) *Eleutherodactylus lacteus* group would be associated with lineage 3, but his *E. binotatus*, *E. discodalis*, *E. parvus*, and *E. sulcatus* (as redefined in Lynch, 1986) groups would form a basal lineage on branch a, characterized by 2N = 20, 22; BA = 16, 18, 22. Schwartz's (in Lynch, 1976) Antillean *E. emiliae* group would form a part of lineage 5.

Because of the uncertainties regarding the available data, it is not possible to explore further the relationships of branch II stocks at this time, beyond calling other workers' attention to the principal lines (lineages 3–6) defined in this study. The picture for branch I is somewhat clearer, and a

proposed classification for this stock (the Middle American clade of Lynch, 1986) is presented below:

#### Section I

- Eleutherodactylus fitzingeri* series
  - E. alfredi* group (Lynch, 1976)
  - E. augusti* group (Lynch, 1968, 1976, as *Hylactophryne*)
  - E. fitzingeri* group\*
  - E. gollmeri* group\*
  - E. milesi* group (*E. matudai*, *milesi*)
  - E. omiltimanus* group (Ford & Savage, 1984)
  - E. rugulosus* group (Savage, 1975)\*
- Eleutherodactylus rhodopis* series
  - E. rhodopis* group\*

Citations indicate definition and content; asterisks (\*) indicate definition and content in the present paper.

The nominal genus *Hylactophryne* (Lynch, 1968, 1976) is a component of this section and could be recognized as a group (*Eleutherodactylus augusti* group) within Section I. This is the course advocated by Lynch (1986) to reduce paraphyly in *Eleutherodactylus*, although he continues to regard the several other usually recognized genera that make Section II paraphyletic as valid. For the time being it seems best to recognize that *Eleutherodactylus* is paraphyletic, that several lineages within the stock will be awarded generic status once a fuller evaluation of derived characters is made, and that there is no need to reduce currently recognized genera back into *Eleutherodactylus* only to have them reemerge in expanded form later on. *Hylactophryne* is precisely defined by a series of derived digital characteristics (Lynch, 1968, 1971, 1976), and for this reason it seems best to continue to separate it from other section I stocks that Lynch (1986) placed in his Central American clade. If the relationships implied by the accompanying figure (fig. 28) turn out to be correct, lineages 1 and 2 ultimately might be regarded as distinct genera.

#### The Status of the *Eleutherodactylus gollmeri* Group

The species placed in the *E. gollmeri* group in the present paper have been treated in a variety of ways by previous authors. Smith and Taylor (1948) associated one form (*E. macdougalli* = *E. lineatus*) with *Eleutherodactylus rhodopis* and its allies, while apparently regarding *E. laticeps* as

unrelated to any other form. Firschein (1951) and Lynch (1965b) followed this lead and recognized, respectively, *E. laticeps* and *E. rhodopis* groups within the genus. The former contained the nominal species *E. laticeps* and *E. stantoni*, the latter *E. rhodopis*, *E. lineatus*, and their presumed allies *E. anzuetoii*, *E. macdougalli*, and *E. werleri*. *Eleutherodactylus rostralis* was regarded as a synonym of *E. rhodopis* by Lynch. The latter author acknowledged a possible relationship of the *E. rhodopis* group to the lower Central American forms allied to *E. gollmeri*, which he regarded as a distinct species group. I (1973, 1976, 1980) clustered the southern Central American forms, *E. bransfordii*, *E. gollmeri*, *E. mimus*, *E. noblei*, and *E. podiciferus*, together as the *E. gollmeri* group.

Lynch (1976), in his effort to subdivide the genus *Eleutherodactylus* into cogent units, substantially revised his own and others' placement of the species previously referred to as the *E. rhodopis*, *E. laticeps*, and/or *E. gollmeri* groups. These units or series (as discussed on p. 39) were defined principally upon features of external morphology. Several clusters of Mexican and upper Central American species previously placed in the *E. mexicanus*, *E. pygmaeus*, and *E. rhodopis* groups by Lynch (1965a, 1970) were united into a single unit (the *E. rhodopis* series). The members of the *E. laticeps* group, the *E. gollmeri* group, and the species allied to *E. lineatus* were placed together with a diverse array of frogs, including the *E. fitzingeri*, *E. gaegeae*, and *E. rugulosus* groups (Savage, 1973), to form the *E. fitzingeri* series. *E. bransfordii* of Honduras to Panama was associated in this scheme with the *E. rhodopis* and not the *E. fitzingeri* series. Subsequently Lynch and Myers (1983) placed *E. bransfordii* and its lower Central American allies, *E. podiciferus* and the recently described *E. jota* (Lynch, 1981), in the *E. fitzingeri* series, without comment.

Several questions need to be addressed before any conclusions may be reached regarding the status of the *Eleutherodactylus gollmeri* group and its intergroup relationships:

1. Is the *E. gollmeri* group monophyletic?
2. If so, is the group referable to either the *E. rhodopis* or *E. fitzingeri* groups, as proposed by previous authors?
3. Or, may it constitute a distinct species group within one of the six lineages of *Eleutherodactylus*?

In answer to the first question, all members of the group share a common suite of external mor-

phological characteristics, skull structure, jaw musculature, and a derived karyotype (in the two species in which it is known), as outlined under the group definition (p. 2). Only a single morphological feature, the presence of expanded finger and toe disks, one or more of which have swollen or cuspidate disk pads, constitutes a shared derived character state. This latter feature and the raised and pointed subarticular tubercles distinguish *Eleutherodactylus gollmeri* and its allies from members of the *E. fitzingeri* and *E. rugulosus* groups (Savage, 1975, 1980) and from the *E. fitzingeri* series (Lynch, 1976). The *E. gollmeri* group closely resembles the frogs referred to the *E. rhodopis* group by Lynch (1976), but the latter stock has several derived features: unexpanded finger and toe disks, and no toe webs or tarsal fold, that separate them from the former.

The answer to the second question is more complicated. Although the available data on jaw muscles and karyology for many species referred to the *Eleutherodactylus rhodopis* and *E. fitzingeri* series (Lynch, 1976) are fragmentary, it is clear that the *gollmeri* group is allied to these stocks. The *E. fitzingeri* series is essentially equivalent to lineage 1 (fig. 28) and the *E. rhodopis* series (lineage 2) appears to be the sister group of lineage 1 plus *Hylactophryne*.

Lynch (1976) redefined the *Eleutherodactylus rhodopis* series to include the northern Mesoamerican species *E. hobartsmithi*, *E. mexicanus*, *E. pygmaeus*, *E. rhodopis*, *E. saltator*, and *E. sartori* and the Central American *E. bransfordii* and *E. podiciferus*. Subsequently Lynch and Myers (1983) transferred the latter two forms and their recently described ally, *E. jota* (Lynch, 1981), to the *E. fitzingeri* series. Although I (1973, 1976, 1980) regarded *E. bransfordii* and *E. podiciferus* as closely allied to *E. gollmeri*, the evidence from general morphology and karyology (table 3, fig. 28) convinces me that this is not the case. *Eleutherodactylus bransfordii* and *E. podiciferus* resemble *E. rhodopis* in having  $2N = 18$ ; N.F. = 36; BA = 18. In addition, the derived feature of morphology mentioned above as separating the *E. gollmeri* and *E. rhodopis* stocks are shared by the lower Central American forms. *Eleutherodactylus jota* from Panama and recently resurrected *E. stejnegerianus* (Miyamoto, 1983) from Panama and western Costa Rica apparently also belong with the *E. rhodopis* series.

As visualized here, this series includes the following species: *E. bransfordii* (Cope), *E. hobartsmithi* Taylor, *E. jota* Lynch, *E. mexicanus* (Broc-

chi), *E. podiciferus* (Cope), *E. pygmaeus* Taylor, *E. saltator* Taylor, *E. sartori* Lynch, and *E. stejnegerianus* (Cope). These species share the following features: chunky narrow heads (head width/standard length < 50%); short legs without bony supported cranial crests; vomerine teeth in paired triangular patches located between and behind the choanae and separated from one another on the midline by a distance less than the width of a single tooth patch, or vomerine teeth absent in some species; vocal slits and nuptial thumb pads present in adult males of some species; tympanum prominent; inguinal glands often present; fingers and toes without expanded disks; first finger equal to or longer than second; subarticular tubercles projecting or rounded; usually supernumerary tubercles on hands and/or feet; accessory palmar tubercles usually present; no tarsal fold although an inner tarsal tubercle or two present; no toe webs; mandibularis muscles DFSQat, DFSQAT + e; and  $2N = 18$ ; N.F. = 36; BA = 18 in three species. According to Lynch (1971, 1976) this stock differs from all other members of the genus in having the pterygoid bent so that there is no overlap between the parasphenoid and pterygoid, although the median ramus of the latter is relatively long.

It is quite clear that *Eleutherodactylus bransfordii* and its allies cannot be associated with the *E. fitzingeri* series *contra* Lynch and Myers (1983). But even with *E. bransfordii* and its allies removed from the *E. fitzingeri* series, the latter unit is non-monophyletic. Most Central American members of the stock have division I karyotypes ( $2N = 20, 22$ ) but the Amazonian species (*E. conspicillatus*,  $2N = 24$ , and *E. lanthanites*,  $2N = 36$ ) and *E. gaigeae* ( $2N = 34$ ) of lower Central America and northwestern Colombia have division II karyotypes. The latter three species almost certainly are not closely related to the low chromosome number species forming lineage 2, although as previously noted there remains the possibility of misidentifications on Bogart's part. This view was anticipated by Lynch and Myers (1983), who realized that their *E. fitzingeri* series was defined on the basis of shared primitive characters.

Lynch (1986), as discussed in the previous section on infrageneric units, has come now to the same conclusion based upon the adductor mandibulae musculature. Examination of the depressor condition (DFSQ<sub>a</sub>AT) in *Eleutherodactylus conspicillatus* confirms that conclusion.

The *Eleutherodactylus fitzingeri* series, minus the high chromosome number species with the s adductor condition (all probably related to *E. con-*



*spicillatus*), is comprised of six groups, as outlined at the end of the previous section. The *E. fitzingeri* group is closely allied to the *E. rugulosus* group (Savage, 1975), and I would expand the latter to include *E. anatipes*, *E. anomolus*, and *E. zygodactylus*, placed in the *E. fitzingeri* group by Lynch and Myers (1985). In addition I no longer regard *E. matudai* and *E. milesi* as members of the *E. rugulosus* stock, but place them in a separate group. The *E. fitzingeri* group proper (i.e., those species closely related to *E. fitzingeri*) share the following features: slender, narrow heads (head width/standard length < 50%); long legs without bony supported cranial crests; vomerine teeth in paired triangular patches located between and behind the choanae and separated from one another on the midline by a distance less than the width of a single tooth patch; vocal slits and nuptial thumb pads in adult males; tympanum prominent; no inguinal glands; disks on all fingers and toes; some disks on fingers usually emarginate, outer two expanded; first finger longer than second; subarticular tubercles on digits not projecting; no supernumerary tubercles on hands or feet; accessory palmar tubercles present; an inner tarsal fold; toes webbed at least basally; venter smooth; mandibularis muscles dfsq, dfsqat, DFSQAT + e; 2N = 20, 22; N.F. = 36, 38, 40; BA = 14, 16, 18, in five species. As presently defined, the *E. fitzingeri* group contains the following species: *E. andi* Savage; *E. bocourti* (Brocchi); *E. crassidigitus* Taylor; *E. cuaquero* Savage; *E. emcelae* Lynch; *E. fitzingeri* (O. Schmidt); *E. longirostris* (Boulenger); *E. raniiformis* (Boulenger); *E. melanostictus* (Cope); *E. monnichorum* Dunn; *E. rayo* Savage and DeWeese; *E. talamancae* Dunn.

Some time ago I suggested (1973) that an *Eleutherodactylus melanostictus* group might be recognized within the *E. fitzingeri* series. Although never defined in print, my concept of this nominal group was based upon the features of *E. melano-*

*stictus*, *E. monnichorum*, and *E. rayo*. Recently Lynch (1986) resurrected the group (although previously Lynch, 1976, and Lynch & Myers, 1984, had rejected the idea). Lynch argued that since *E. melanostictus* and *E. monnichorum* and his new species, *E. emcelae*, shared notched unguis flaps on some digital disks, this feature constituted a synapomorphy defining the group. Apparently Lynch overlooked the fact that most members of the *fitzingeri* group, including *E. andi*, *E. bocourti*, *E. cuaquero*, and *E. rayo*, have emarginate outer finger disks. In my opinion *E. andi*, *E. cuaquero*, and *E. emcelae* are allied species and somewhat separated from *E. melanostictus* and its closest allies. Nevertheless, I see no value in further subdividing the *E. fitzingeri* series at this time, especially since *E. fitzingeri* seems a close relative of *E. andi* and *E. cuaquero*.

Of the groups within the Middle American clade (branch I), only the *Eleutherodactylus fitzingeri* group, as reconstructed in the present paper, seems close to *E. gollmeri* and its allies. The latter stock differs from the former in four derived features (primitive character states for the former group in parentheses): swollen or cuspidate disk pads, projecting subarticular tubercles, no male vocal slits, and no male nuptial thumb pads (even pads, tubercles not projecting, vocal slits, and nuptial thumb pads present in males). The *E. gollmeri* group may therefore be regarded as a stock derived from an ancestor sharing these primitive features with *E. fitzingeri* and its close allies.

#### Intragroup Relationships, Evolutionary History, and Biogeography

Intragroup relationships were determined by constructing a cladogram using the summary of diagnostic features (table 2), with the *Eleutherodactylus fitzingeri* group as the outgroup. The nine characters were coded (table 4) according to the following transformation series:

	0	1	2	3
1. Outer finger disks	Enlarged	Subequal	...	...
2. Webs and fringes	Basal, moderate, no fringe	Moderate, with definite fringes	...	...
3. Finger disk formula	No swollen disks	I	II	III
4. Heel	Smooth	1-4 tubercles	1-2 calcars	...
5. Tarsal tubercles	Absent or very weak	Weak	Well developed	...
6. Dorsolateral fold	Absent	Present	...	...
7. Plantar tubercles	0-3	2-4	4-7	...
8. Hind limb pattern	U	T	S	...
9. Seat patch mark	Absent	C	B	D-E

TABLE 4. Systematic characters of the *Eleutherodactylus gollmeri* group.

Taxa	Characters								
	1	2	3	4	5	6	7	8	9
<i>fitzingeri</i> group	0	0	0	0	0	0	0	0	0
<i>chac</i>	1	0	3	1	1	0	2	1	2
<i>gollmeri</i>	1	0	3	2	0	0	0	2	1
<i>laticeps</i>	1	0	2	0	0	1	0	1	0
<i>lineatus</i>	1	0	3	2	2	0	0	1	3
<i>mimus</i>	1	1	1	0	0	0	0	2	2
<i>noblei</i>	0	0	2	0	0	1	2	0	0
<i>rostralis</i>	1	0	3	1	1	0	1	1	3

The resulting cladogram (fig. 29) was obtained from the character matrix by the Wagner procedure (Farris, 1970) and its global branch swapping option, following numerical procedures available in the PHYSYS computer package written by J. S. Farris and M. F. Mickevich. The DIAGNOSE algorithm was used to optimize the characters on the Wagner tree. This tree is the single best-fitting cladogram for the data, with a tree length of 24.00, a consistency index of 70.833, and an F-ratio of 9.39.

The cladogram indicates that none of the species included in the *Eleutherodactylus gollmeri* stock cluster to form subgroups. *Eleutherodactylus noblei* is the most primitive member of the group, since it retains several primitive character states shared with the outgroup, including enlarged outer finger disks, smooth heel, smooth tarsus, and uniform hind limb pattern. All other members of the group exhibit two or more derived states, compared to the outgroup. Evolution within the group has been stepwise, and for this reason the cladogram provides both a diagnosis of each taxon and a phylogenetic classification, without recourse to construction of formalized tables or listings.

The cladogram of relationships taken in concert with biogeographic data also provides clues to the evolutionary history of the group. Since this stock is exclusively Middle American in distribution, the detailed history of the Isthmian Link between North and South America (Savage, 1983) is not involved in interpreting its phylogeny. It appears that the basic stock of the group (and other subdivisions of lineage 3) was present in humid lowland tropical situations in Mexico and upper Central America at least by Miocene and dispersed southward from present-day Nicaragua onto the emerging Isthmian Link (now southern Nicaragua, Costa Rica, and Panama) as it was uplifted, be-

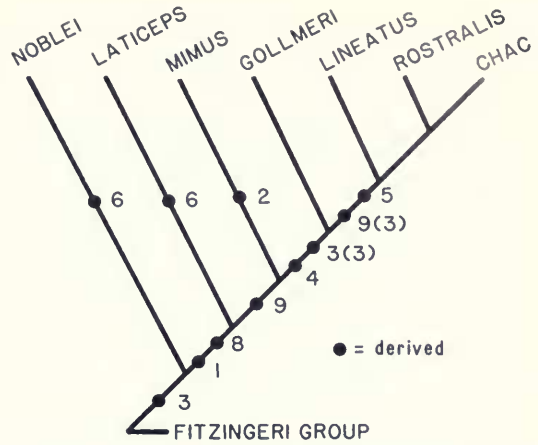


FIG. 29. Cladogram of relationships within the *Eleutherodactylus gollmeri* group.

ginning in that epoch. A common repetitive distribution pattern is indicated by the available data. Geographically the group occurs in two discrete clusters:

1. The southern species—*Eleutherodactylus noblei* (eastern Honduras, Nicaragua, Costa Rica, and western to central Panama), *E. mimus* (eastern Honduras to Costa Rica), and *E. gollmeri* (Costa Rica to the western portion of eastern Panama); the range of the former essentially encompasses the ranges of the last two species (figs. 17–19)
2. The northern species—*E. laticeps* (southern Atlantic slope Mexico, Guatemala, Belize, and northern Honduras), the three closely allied species *E. lineatus* (upland southern Mexico and Guatemala), *E. chac* (Atlantic lowland eastern Guatemala, Belize, and northern Honduras), and the upland *E. rostralis* (western Honduras and extreme eastern Guatemala); except for the Pacific slope and Atlantic drainage Oaxaca populations of *E. lineatus*, the range of *E. laticeps* essentially encompasses those of the other northern forms (figs. 20–21, 24–25)

This pattern suggests that an originally continuous ancestral range (Mexico–Nicaragua) was fragmented into two segments, one in eastern Honduras–northern Nicaragua, the other from north-central Honduras to Mexico. The distribution patterns and the cladogram of relationships further suggest that two ancestral populations, A (ancestor of *Eleutherodactylus noblei* and *E. lati-*

ceps) and B (ancestor of the remaining forms), were split by the same event (fig. 30). The northern fragment of A subsequently evolved into *E. laticeps*, the southern one into *E. noblei*. Similarly, the southern fragment of B (*E. mimus*-*E. gollmeri*) and its northern equivalent (*E. lineatus*-*E. rostralis*-*E. chac*) each underwent further fragmentation. This initial vicariance event ( $V_1$ ) must have been followed by dispersal of the southern populations of A and B southward onto the emerging Isthmian Link. A second vicariance event ( $V_2$ ) fragmented the southern portion of B, and somewhat later a third such event ( $V_3$ ) in the northern segment allowed further differentiation. In the south, dispersal southward by *E. mimus* and northward by *E. gollmeri* after the barrier responsible for  $V_2$  was removed produced the current pattern.

In the north the situation was somewhat more complex. It is apparent that the northern B ancestor was originally distributed in the lowland areas of what is now southern Mexico, Guatemala, and Honduras. This population seems to have been uplifted and fragmented by the mountain-building activities of Plio-Pleistocene times into two principal subdivisions, one in the emerging mountains of Guatemala and Mexico north and west of the Río Motagua Valley, the other in northwestern Honduras and immediately adjacent Guatemala, south and east of the valley. A third segment of the northern B ancestor is represented by present day *Eleutherodactylus chac*, which occurs in lowland and foothill situations in Atlantic slope Guatemala, Belize, and northern Honduras. Its probable origin was as an isolate along the slopes of the Sierra del Mico and/or Montañas Mayo; it subsequently expanded its range into the lowlands.

I have elsewhere (Savage, 1983) discussed at some length a general theory of biogeography that combines the best attributes of concordant dispersal and vicariance approaches. The essential features of this theory involve: 1) an initial concordant dispersal; 2) geographic fragmentation of the continuous range by barriers; 3) differentiation of the isolates (vicariance); 4) establishment of endemics; and 5) with barrier removal or loosening, concordant dispersal reoccurred. The evolutionary pattern outlined in the paragraphs above fits the general theory very well and implies one major dispersal event, followed by a major vicariance event ( $V_1$ ) and two minor ones ( $V_2$  and  $V_3$ ). A secondary dispersal event would also account for the overlapping ranges of *Eleutherodactylus gollmeri* and *E. mimus*.

While the specific scenario developed from a knowledge of the cladistic relationships of the *Eleutherodactylus gollmeri* group is plausible, it may be a unique pattern. Robust biogeographic theory (Rosen, 1978; Savage, 1983) is based not upon unique patterns but on concordant general patterns. Comparisons with other groups found in the same region are required to test the generality of the described pattern. Unfortunately, there appears not to be a single cladistic analysis of interspecies relationships for other taxa with comparable distributions in Mesoamerica, so that critical testing of the generality of the pattern must await future studies. Nevertheless, the pattern elucidated by the phylogeny of the *E. gollmeri* group offers several novel suggestions regarding the geographic events that have shaped biotic evolution in Central America. Since a major feature of robust theory is the ability to generate unexpected (novel) predictions (Rosen, 1978; Craw & Weston, 1984) relating to earth (geologic/climatic) history and patterns of distribution for unstudied groups (Savage, 1983), the present analysis may contribute as a step toward a detailed understanding of intra-Mesoamerican biogeography.

What are the novel predictions generated from the model (fig. 30)? Certainly the idea of southward dispersal from nuclear Central America onto the emerging Isthmus Link ( $T_3$ ) is not unexpected, as it conforms to a major general pattern long recognized and well documented (Simpson, 1950; Darlington, 1957; Marshall et al., 1979; Savage, 1983, to cite a few), nor is the separation of populations of this stock in the mountains north and south (*Eleutherodactylus lineatus* and *E. rostralis*, respectively) of the Motagua and Polochic fault zone of Guatemala. This pattern is also a common one discussed in some detail by Rosen (1978) and related to mountain building in Pliocene-Recent times, which fragmented many forms across this axis. The model, however, does contain three novel predictions regarding the shaping of current distribution patterns in Mesoamerica:

1. At  $T_2$  (probably early Miocene), a major vicariance event (barrier) separated the formerly continuous lowland ranges of members of the stock into northern and southern fragments. The barrier (probably a marine embayment) must have been located across what is now northeastern Honduras in the general region between the Río Aguan and the Sierra Agalta-Sierra Río Tinto axis, and may have been associated with the Coma-



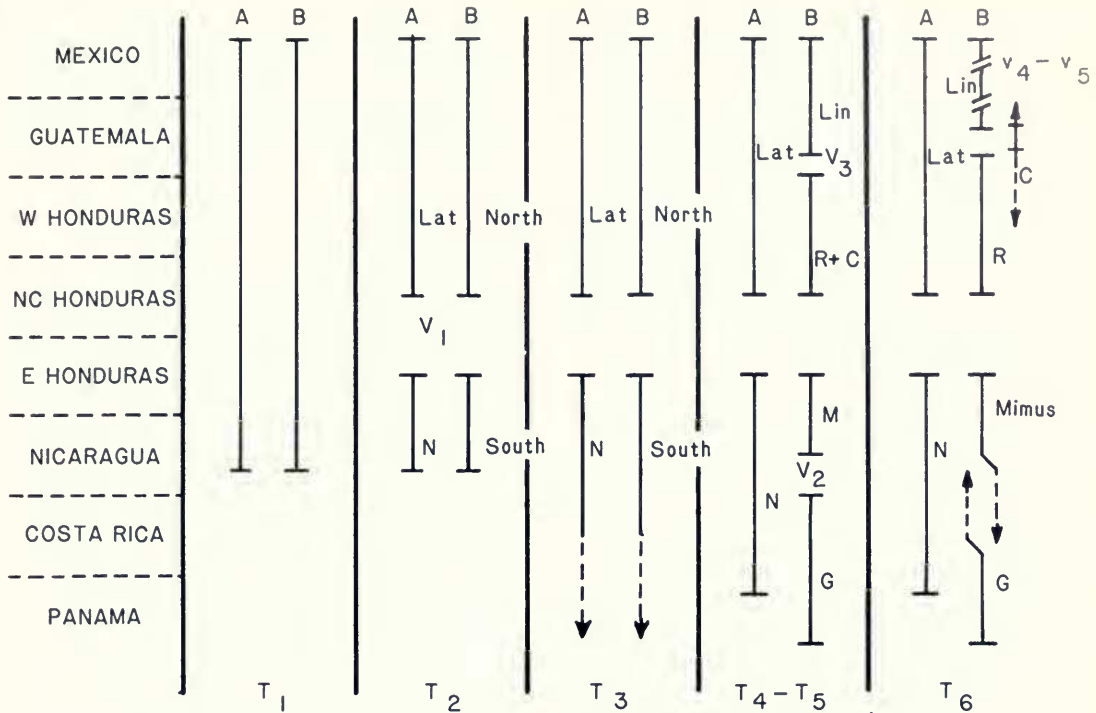


FIG. 30. Diagrammatic representation of evolution and biogeography of the *Eleutherodactylus gollmeri* group. C = *E. chac*; G = *E. gollmeri*; Lat = *E. laticeps*; Lin = *E. lineatus*; M = *E. mimus*; N = *E. noblei*; V = vicariant event; dashed line = dispersal (see p. 52 for additional explanation).

yagua Graben or Honduras Depression (Roberts & Irving, 1957) which runs from northeast to southwest and terminates at the Gulf of Fonseca. The physical barrier has subsequently been eliminated by uplifting of the northern Honduras coast and lowering of sea level. Nevertheless, the effects of this barrier are emphatic, since no sympatry occurs between northern and southern derivatives of the *Eleutherodactylus gollmeri* group.

- At T<sub>4</sub> (probably early Pliocene), a vicariance event separated the formerly continuous range of the southern B stock (fig. 26) into northern and southern fragments. The responsible barrier must have been located between present-day Nicaragua and southeastern Costa Rica. It may well have been associated with the Nicaragua Depression (McBirney & Williams, 1965) that runs from the Gulf of Fonseca southeastward to the Atlantic coast of extreme southern Nicaragua and northeastern Costa Rica, along the valleys of the Great Lakes and Río San Juan.

Conventional wisdom (Dengo, 1973; Vinson & Brineman, 1963) regards the Nicaragua Depression as a persistent marine trough interconnecting the Pacific and Atlantic into Pliocene and remaining as a marine embayment connected to the Caribbean until the end of Pliocene. The present model (fig. 30) predicts otherwise in implying that the region was land positive by mid- to late Miocene, was flooded by a marine intrusion from the Caribbean in early Pliocene, and ultimately became land positive again. The latter event allowed for the reunion of *Eleutherodactylus noblei* populations isolated to the north and south of the barrier and for the sympatric occurrence of the two derivative species (*E. gollmeri* and *E. mimus*) of the southern B stock.

- Probably beginning in T<sub>5</sub> (mid- to late Pliocene, if not earlier), certain populations of the northern B stock became fragmented by mountain building. Current distributions imply that a more or less continuous distribution of the B stock ancestor occurred over

much of lowland northern Central America, from present-day Veracruz and Oaxaca, Mexico, through Guatemala to northern Honduras. Fragmentation of this wide distribution by uplift of mountain ranges, with the fragments "riding" up with the mountains, appears to be responsible for the current montane distribution of *Eleutherodactylus rostralis* (fig. 16) and the many isolates of *E. lineatus* (fig. 25) and of *E. chac* (fig. 21), which is restricted to lower elevations but centered on the low mountains north of the Motagua fault region.

It is of course tempting at this stage of the discussion to list a series of distribution patterns for other groups of organisms that may resemble those of the *Eleutherodactylus gollmeri* group, to suggest that the three novel predictions are corroborated by other taxa. It must be remembered, however, that biogeographers are skilled at finding distribution patterns that seem to support their own ideas, while apparently ignoring distributions that are uncomfortably nonconcordant. Robust biogeographic theory rests not upon that sort of exercise but rather, as I have pointed out in my extensive statement of biogeographic principles (all 25 of them; Savage, 1983), on objectively evaluating the relationships of phylogenies to one another and to earth history.

In this regard a somewhat restated principle 24 seems most applicable: The preferred method of analysis involves construction of cladograms of area interrelationships from cladograms of phylogenetic relationships; a hypothesis is then developed that relates phylogeny to geography; major vicariance and dispersal events once identified from the hypothesis may be associated with known paleogeologic and/or paleoecologic events, or lead to novel predictions relating to earth history (geologic and climatic); the hypothesis is then tested by comparison of phylogenetic-area relationships for additional groups having similar geographic ranges.

The hypothesis generated for the *Eleutherodactylus gollmeri* group conforms to this principle, in being based upon the discoveries provided by the cladistic analysis which required no prior judgment of the former history of dispersals, vicariances, or geologic age of the distributional events. Its validity now rests upon additional phylogenetic analyses to verify if a general pattern is involved; the hypothesis already provides an explanation of the process by which the pattern evolved. The

challenge now to workers (including me) on the biota of Mexico and Central America is to undertake the task of rigorously testing the model presented here, for only in this manner can a scientific biogeography progress.

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It is a great pleasure to have this paper included in the series honoring Dr. Robert F. Inger of Field Museum of Natural History, who has made so many contributions to our knowledge of tropical frogs. Although the bulk of his studies on these animals has been devoted to Paleotropical forms, his innovative approaches to their systematics, life histories, and ecologies have served as a stimulus and inspiration to his colleagues studying throughout the tropics.

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