THE RELATIONSHIPS OF AN ENSEMBLE OF GUATEMALAN AND MEXICAN FROGS (*ELEUTHERODACTYLUS*: LEPTODACTYLIDAE: AMPHIBIA)

por

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Resumen

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Se demostró que *Eleutherodactylus daryi* y *E. greggi* son especies del grupo de *Eleutherodactylus gollmeri,* el cual se encuentra definido por una sinapomorfía (fusión del sacro y una vértebra presacral). *Eleutherodactylus omiltemanus* es una especie de la serie *rhodopis* no de la serie *fitzingeri.* El grupo *Eleutherodactylus omiltemanus* desaperece al encontrarse todas sus especies incluidas en otros grupos. *Eleutherodactylus saltator* es un sinónimo de *E. mexicanus. Eleutherodactylus rhodopis sensu lato* consiste en dos especies, una más grande de las tierras altas (*E. rhodopis*), y *E. loki,* una especie más ampliamente distribuida en las tierras bajas.

La serie *rhodopis,* que incluye el grupo *rhodopis,* no se puede definir por que no hay sinapomorfias aparentes. Se asignan *E. occidentalis* y *E. omiltemanus* al grupo *rhodopis.* Dentro del "grupo" *rhodopis,* se encuentran tres agrupaciones: una que tiene el mesorquio negro (*E. hobartsmithi, E. mexicanus, E. pygmaeus,* y *E. sartori*), otra con el primer dedo pedial corto (*E. jota* y *E. podiciferus*), y una última que posee tubérculos subarticulares cónicos (*E. bransfordii, E. lauraster, E. loki, E. occidentalis, E. omiltemanus, E. rhodopis,* y *E. stejnegerianus*).

Sesenta de las ochenta y cuatro especies escencialmente mesoamericanas del subgénero *Craugastor* pertenecen a una entidad monofilética basada en la presencia de un dimorfismo sexual en el tamaño del tímpano. Esta entidad incluye las nueve especies del grupo *gollmeri,* las trece del grupo *rhodopis,* y 38 especies más (las tres del grupo *biporcatus,* 11 del grupo *milesi,* ocho del grupo *fitzingeri,* 15 del grupo *rugulosus,* e *E. uno*). Las 24 especies del subgénero *Craugastor* no incluidas en este clado son las 13 especies del grupo *alfredi* (incluyendo *E. bocourti*), las dos del grupo *augusti,* las

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dos del grupo *bufonifomis,* tres especies excluidas del grupo *fitzingeri* (*E. andi, E. cuaquero,* e *E. emcelae*), y cuatro especies sacadas del grupo *rugulosus* (*E. anatipes, E. anomalus, E. cheiroplethus,* e *E. zygodactylus*).

Palabras clave: *Eleutherodactylus,* Mesoamérica, Sistemática, Taxonomía

Abstract

Eleutherodactylus daryi and *E. greggi* are shown to be species of the *Eleutherodactylus gollmeri* group which is defined on the basis of having a synapomorphy (fusion of sacrum and presacral vertebrae). *Eleutherodactylus omiltemanus* is a species of the *rhodopis* Series rather than the *fitzingeri* Series. The *Eleutherodactylus omiltemanus* group disappears because all of its contained members are placed in other species groups. *Eleutherodactylus saltator* is a synonym of *E. mexicanus. Eleutherodactylus rhodopis sensu lato* contains two species, a larger upland *E. rhodopis* and the more widely distibuted lowland *E. loki.*

The *rhodopis* Series, containing the *rhodopis* group, is not definable because no synapomorphies are apparent. *Eleutherodactylus occidentalis* and *E. omiltemanus* are assigned to this "group." Within this "group" there is a cluster of species having black mesorchia (*E. hobartsmithi, E. mexicanus, E. pygmaeus,* and *E. sartori*), one having a shortened inner toe (*E. jota* and *E. podiciferus*), and one having conical subarticular tubercles (*E. bransfordii, E. lauraster, E. loki, E. occidentalis, E. omiltemanus, E. rhodopis,* and *E. stejnegerianus*).

Sixty of the 84 essentially Mesoamerican species of the subgenus *Craugastor* are placed in a monophyletic subunit based on the common presence of marked sexual dimorphism in tympanum size. The subunit includes the nine species of the *gollmeri* group, the thirteen species of the *rhodopis* group, and 38 additional species (the three species of the *biporcatus* group, the eleven species of the *milesi* group, eight species of the *fitzingeri* group, 15 species of the *rugulosus* group, and *E. uno*). The 24 species of *Craugastor* not included in that clade are the 13 species of the *alfredi* group (including *E. bocourti*), the two species of the *augusti* group, the two species of the *bufoniformis* group, three species removed from the *fitzingeri* group (*E. andi, E. cuaquero,* and *E. emcelae*), and four species removed from the *rugulosus* group (*E. anatipes, E. anomalus, E. cheiroplethus,* and *E. zygodactylus*).

Key words: *Eleutherodactylus,* Middle American, Systematics, Taxonomy

Introduction

The species group arrangement of Guatemalan and Mexican *Eleutherodactylus* largely dates from **Smith & Taylor's** (1948) summary account wherein they recognized four genera (*Eleutherodactylus, Microbatrachylus, Syrrhophus,* and *Tomodactylus*). **Lynch** (1965a, 1968) combined *Microbatrachylus* with *Eleutherodactylus* and proposed *Hylactophryne* for what Smith and Taylor had included in their *augusti* group. Although the current arrangement (**Lynch,** 1986; **Hedges,** 1989) includes all but one (*E. batrachylus* Taylor) of these frogs in two subgenera (*Craugastor* and *Syrrhophus*) of *Eleutherodactylus,* one small nuclear group has been the subject of several treatments (**Taylor,** 1941a; **Lynch,** 1970, 1976a; **Ford & Savage,** 1984; **Savage,** 1987) in which certain species are moved from group to group. The mobile taxa are included in the *gollmeri, mexicanus, omiltemanus,* and *rhodopis* groups as these supraspecific units were termed by Ford, Lynch, Savage, and Taylor. **Lynch & Duellman** (1997:45) mentioned that the 75 (actually 80) species of *Craugastor* were divided into eleven species groups and proposed one more (partitioning the *rugulosus* group into two groups with the proposal of an *anomalus* group) but in their Appendix I they anticipated some of the changes proposed here. Their species lists are complete except that they overlooked *E. pozo,* a species of the *rugulosus* group. The proposal by **De La Riva & Lynch** (1997) that two Bolivian species also are species of *Craugastor* is outside the scope of this paper.

Savage (1987:48), more than any other author, has attempted to formalize classification within *Craugastor* and recognized two Series, the *fitzingeri* Series (with seven

species groups) and the *rhodopis* Series (with a single species group), within what he called Section I. Although **Savage's** (1987) paper represents a considerable contribution to the study of the lineages within *Craugastor*, there is substantial reason to be skeptical of many of his claims.

Savage (1987:47) provided a cladogram of which part is reproduced here (Fig. 1A) wherein he recognized two lineages of [*Craugastor*] such that one was more closely related to *Hylactophryne* than the other. However, a cladogram (Fig. 1B) derived from his classification suggests that the *augusti* group [*Hylactophryne*] is not the sister group to Lineage 1 but rather only a part of Lineage 1. Elsewhere in his treatment of these frogs, he implies a very different derivative cladogram (Fig. 1C). The problem is that sometimes (e.g., **Savage**, 1987:48) the *fitzingeri* series includes seven groups and at other times (e.g., **Savage**, 1987:44) it includes no more than four. His classification (**Savage**, 1987:48) of Section I (= *Craugastor*) admits two Series (*fitzingeri* and *rhodopis*) but does not include the *E. biporcatus* group (or Series?) but that unit is listed as part of one major lineage (p. 44). **Savage** (1987:44) identified "six major lineages" defined by combinations of jaw musculature and karyology. Combination *a* included "*E. alfredi, E. biporcatus, E. fitingeri* series, and *E. omiltimanus* (sic) group" whereas combination *b* included the "*E. rhodopis series*". The use of series in these quotes suggests that three series are represented in Lineage 1 and that *Hylactophryne* is of coordinate rank to groups of series (= lineages). Nowhere does **Savage** (1987) indicate what evidence exists to support the node for Lineage 1 + *Hylactophryne*. The evidence must be in some feature of the *m. depressor mandibulae* (the dfsq, dfsqat, DFSQat, DFSQAT conditions) which **Lynch** (1993) showed were plesiomorphic.

Although the consensus diagram would represent the *rhodopis* series as the sister element to all other taxa included in the subgenus *Craugastor*, the only cladogram extractable from the evidence provided by **Savage** (1987) is one asserting that *Craugastor* is a monophyletic unit purported to include nine species groups (Fig. 1D). A variant consensus diagram (Fig. 1A) is supported only by the hypothesis that the karyotype of the *rhodopis* series is a derived karyotype (the only characters linking the elements of the other lineage are plesiomorphic). **Savage** (1987) was certainly convinced of the distinction between the two lineages because he opines (p. 48) the "If the relationships implied...[Fig. 1A] turn out to be correct, lineages 1 and 2 ultimately might be regarded as distinct genera. " **Savage's** (1987) Section I [= subgenus

Craugastor of **Hedges** (1989) and **Lynch** (1986)] was partitioned into two lineages based on a derived karyotype (diploid number 18) in Lineage 2 (= *rhodopis* Series) and a plesiomorphic karyotype (diploid number 22, occasionally 20) in Lineage 1. The *rhodopis* Series then contained ten species of which karyotypes were available for only
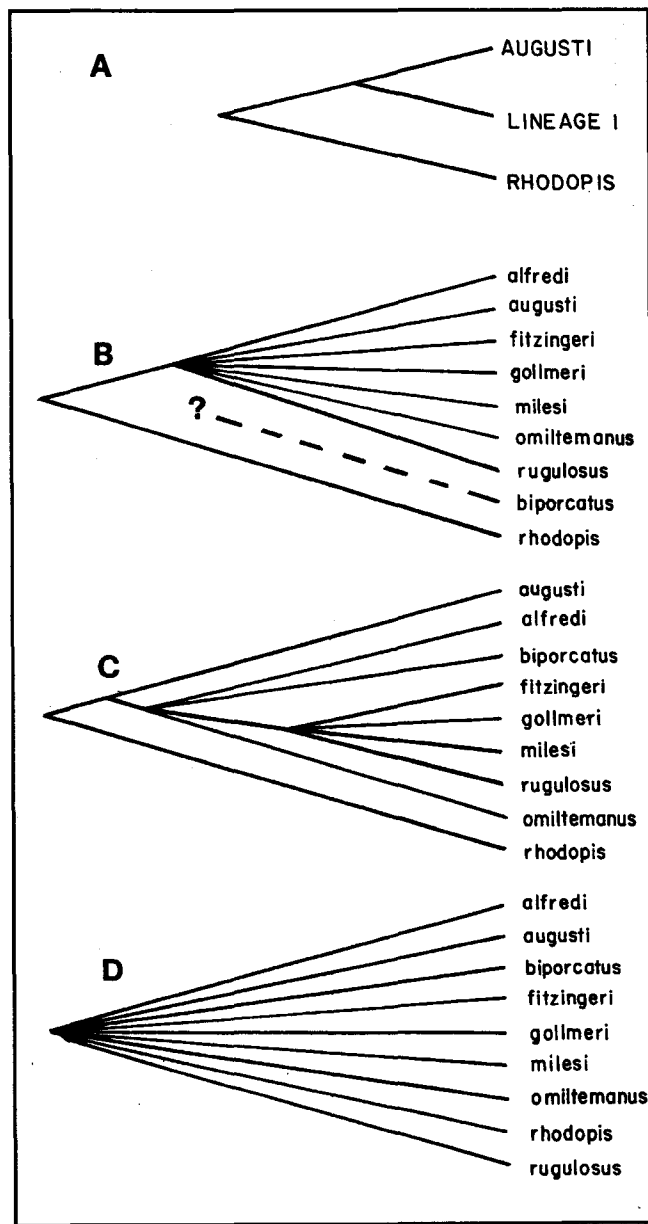

Figure 1. (A). Cladogram extracted from **Savage's** (1987:47) figure. (B) Derivative cladogram from **Savage's** (1987:48) classification. (C) Derivative cladogram from **Savage's** (1987:44) listing of contents of Lineages 1 and 2. (D) Cladogram based on evidence provided in **Savage** (1987).

three (*bransfordii, podiciferus,* and *rhodopis*) and species groups assignments are made on the same "superficial, key" characters employed by Taylor and Lynch. To the extent that **Savage** (1987) tried to define lineages and groups, his definitions conflate combinations of characters with derived characters. The former are not cladistic parameters in contrast to the latter.

The subgenus *Craugastor* contains 84 recognized species (not counting the two from Bolivia) partitioned into eleven (Savage did not separate the *anomalus* and *rugulosus* groups) species groups (only *E. uno* is not assigned), viz., *alfredi* group (12), *anomalus* group (4), *augusti* group (3), *biporcatus* group (3), *bufoniformis* group (2), *fitzingeri* group (12), *gollmeri* group (7), *milesi* group (11, with the addition of four species recognized by **McCranie & Wilson**, 1997), *omiltemanus* group (3), *rhodopis* group (11, with the addition of *E. lauraster*), and *rugulosus* group (15).

Savage (1987) included ten species in his *rhodopis* Series (*E. bransfordii, E. hobartsmithi, E. jota, E. mexicanus, E. podiciferus, E. pygmaeus, E. rhodopis, E. saltator, E. sartori,* and *E. stejnegerianus*). Subsequently, **Savage et al.** (1996) described *E. lauraster.* He, following **Ford & Savage** (1984), also recognized an *omiltemanus* group for three species (*E. daryi, E. greggi,* and *E. omiltemanus*), some of which had been considered previously (**Lynch**, 1970) as members of the *mexicanus* group (combined, in part, with the *rhodopis* group by **Lynch**, 1976a). **Savage's** (1987) focus was upon the species that he included in the *gollmeri* group and his attention to the *rhodopis* Series was exclusional rather than direct. The purpose of the present paper is two-fold: (1) to resolve certain taxonomic issues that continue to plague students of Mexican frogs and (2) to criticize some of the systematic conclusions arrived at by **Savage** (1987).

Two Mexican species of *Eleutherodactylus* [*E. mexicanus* (Brocchi) and *E. rhodopis* (Cope)] account for much of the taxonomic confusion that beset frogs of this genus in Mexico because each exhibits pattern polymorphism (**Lynch**, 1966). The pattern polymorphism, when coupled with sexual dimorphism in size, led to a plethora of names. Because the otherwise similar frogs did not assort ecologically or geographically, **Duellman** (1960, 1961) and **Stuart** (1963) argued that these were probably genetic variants of one another. At present, *E. mexicanus* includes three synonyms (*Microbatrachylus fuscatus* Davis and Dixon, *M. lineatissimus* Taylor, and *M. oaxacae* Taylor) whereas *E. rhodopis* includes nine (*Hylodes beatae* Boulenger, *Eleutherodactylus dorsoconcolor* Taylor, *E.*

dunnii Barbour, *E. loki* Shannon and Werler, *Syrrhophus mystaceus* Barbour, *Hylodes plicatus* Günther, *H. sallaei* Günther, *Eleutherodactylus sanmartinensis* Shannon and Werler, and *Hylodes venustus* Günther).

The first set (*E. mexicanus*) includes frogs that lack tarsal tubercles, have low supernumerary tubercles (if visible at all), have rounded (not projecting) subarticular tubercles, have narrow digits (= lack disks) and have the thumb slightly shorter than the second finger (Fig. 2), have black mesorchia (juvenile females have black mesovarial pigment), display sexual dimorphism in tympanum size (tympanum of male about seven-eighths eye length, that of females about three-fifths eye length), have poorly developed vomerine odontophores (frequently concealed in tissue of palate except in large females where the low odontophores are slanted), and lack ventral pads
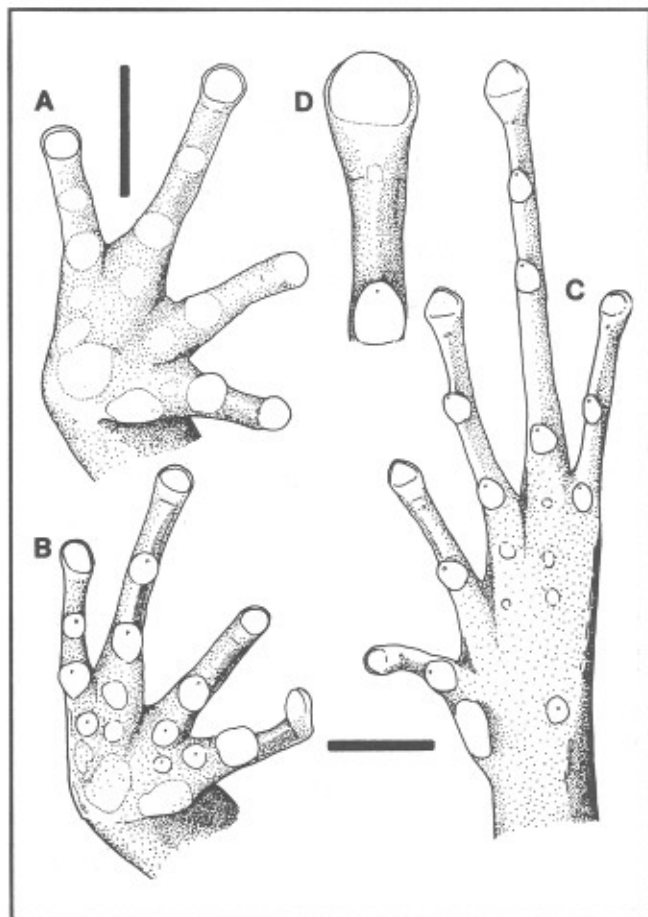

Figure 2. (A) Palmar view of hand of *Eleutherodactylus sartori* (UMMZ 88001). (B, C) Hand and foot of *Eleutherodactylus loki* (UMMZ 147197). (D) Enlarged view of fourth toe of UMMZ 147197. Scales equal 2 mm.

on the inner two fingers and innermost toe. These are moderate-sized animals, adult males are 17.6-28.1 ($\bar{x}$ = 23.5 ± 0.5, N = 50) mm SVL and adult females are 29.5-39.9 ($\bar{x}$ = 36.1 ± 0.6, N = 23) mm SVL. Females less than 25.5 mm SVL show no development of oviductal convolutions or thickening and females with some convolution (but small ovarian eggs) are 25.7-29.9 mm SVL.

Frogs of the second set (*E. rhodopis sensu lato*) have an inner tarsal tubercle (sometimes fold-like, but always with a median elevation), numerous small supernumerary plantar tubercles, elevated and projecting subarticular tubercles, have narrow digits and the thumb is slightly longer than the second finger (Fig. 2), have white mesorchia, display sexual dimorphism in tympanum size (that of males is 72-91% eye length whereas that of females is 50-66% eye length), and have well-developed vomerine odontophores. Frogs of the second set have a finely tuberculate texture above (smooth in *E. mexicanus*) and males have white nuptial pads (absent in *E. mexicanus*).

Savage (1987) correctly pointed out that all previous students of Mexican *Eleutherodactylus* had confused, either specifically or supraspecifically, species allied to *E. gollmeri* with those allied to *E. rhodopis*. That such confusion occurred suggests that group definitions are artifical and inadequate. Savage (1987) did not subdivide the *rhodopis* Series into species groups but the series was traditionally divided into three groups in Mexico, a *mexicanus* group (*mexicanus, saltator,* and *sartori*), a *pygmaeus* group (*hobartsmithi* and *pygmaeus*), and a *rhodopis* group (*rhodopis*). Taylor (1952) aligned morphs now placed in *bransfordii* and *stejnegerianus* with his genus *Microbatrachylus* (viewed by Lynch, 1970, as made up of some species of the *mexicanus* group and the species of the *pygmaeus* group) and emphasized the differences between *podiciferus* and *rhodopis* (presumably at the level of species groups). The two species of the *pygmaeus* group lack the outer (accessory) palmar tubercle and lack vomerine odontophores (but have the dentigerous process) in contrast to the other species. *Eleutherodactylus loki* (see Taxonomy) and *E. rhodopis* have an inner tarsal tubercle whereas the other species lack any tubercles or folds along the inner edge of the tarsus. The subarticular tubercles of *bransfordii, lauraster, loki, rhodopis,* and *stejnegerianus* are projecting in contrast to the rounded (or flattened) subarticular tubercles of the other taxa. *Eleutherodactylus jota* and *E. podiciferus* have a shortened first toe in contrast to the other species. The skin of the abdomen is coarsely granular in *E. bransfordii, E. lauraster,* and *E. stejnegerianus* but smooth in the remaining species. In the accounts below, I will use "cluster"

to refer to the phenetically similar species as grouped by earlier workers on the Mexican herpetofauna.

This paper concerns the systematic arrangement for several Guatemalan and Mexican frogs but part of the difficulty for previous arrangements was the incomplete or erroneous database. I have concluded that two taxonomic changes need to be made for these frogs [*Eleutherodactylus rhodopis* (Cope), *sensu* Savage (1987), is partitioned into two species: *E. loki* Shannon and Werler and *E. rhodopis* (Cope); and *E. saltator* Taylor is a synonym of *E. mexicanus* (Brocchi)].

Materials and methods

Measurements were taken to the nearest 0.1 mm using dial calipers and a dissecting microscope. Sex and maturity was determined by examining the gonads. Abbreviations used in the text are: E-N (distance from anterior edge of eye to nostril), HW (greatest width of head), IMT (length of inner metatarsal tubercle), IOD (interorbital distance), SVL (snout tip to anal opening). Means are reported ± one standard error of the mean. Cleared and stained skeletal preparations were made following Dingerkus & Uhler (1977). Specimens examined are listed in Apprendix 1.

Taxonomic issues (redescriptions and species diagnoses) are of some importance to the systematic discussion but focus on different characters. Some systematic ambiguity derives from inadequate descriptions but the descriptive data seem out of place in a paper concerned about relationships. In order to have ready access to the taxonomic data without disrupting the flow of arguments, I have allocated redescriptions and diagnoses to the taxonomy section (next).

Results (Taxonomy)

Eleutherodactylus mexicanus cluster.— At present, three species are recognized (*E. mexicanus, E. saltator,* and *E. sartori*). *Eleutherodactylus sartori* is a distinct species but requires redescription to correct errors in Taylor's (1942) original description that were repeated by Lynch (1965a, 1970) and to enable ready comparisons among species of the *rhodopis* series. *Eleutherodactylus saltator* is proposed herein to be a synonym of *E. mexicanus* for which a diagnosis is provided.

Eleutherodactylus mexicanus (Brocchi)

Leuiperus mexicanus Brocchi, 1877: 484. Type-locality: Mexico. Type apparently in Paris.

Eleutherodactylus mexicanus Kellogg, 1932:98-99, 108-112.

Microbatrachylus oaxacae Taylor, 1940: 504. [Holotype: CNHM 100001, Cerro San Felipe, Oaxaca, Mexico]. Synonymy by Lynch (1970).

Microbatrachylus lineatissimus Taylor, 1941a: 87. [Holotype: CNHM 100036, Cerro San Felipe, Oaxaca, Mexico, 7000-8000 ft. Elevation]. Synonymy by Lynch (1970).

Eleutherodactylus saltator Taylor, 1941a: 89. [Holotype: CNHM 100116, Omilteme, Guerrero, Mexico]. **New synonymy.**

Microbatrachylus fuscatus Davis & Dixon, 1957:146. [Holotype: TCWC 12171, 20 miles E. Tulancingo, Hidalgo, Mexico, 7300 ft.]. Synonymy by Lynch (1965a).

Eleutherodactylus lineatissimus: Lynch, 1965a:11.

Eleutherodactylus oaxacae: Lynch, 1965a:11.

This is an abundant terrestrial frog in the Oaxacan highlands but remained poorly-known during the Smith-Taylor exploration of Mexican herpetology because no precise type-locality was known that could be revisited and because Taylor recognized the genus *Microbatrachylus* for small species. Among the species that Taylor included in *Microbatrachylus* were two (*lineatissimus* and *oaxacae*) found at the same type-locality on the slopes of Cerro San Felipe in Oaxaca. Taylor also found what he called *E. mexicanus* at the same locality. It is my impression that Taylor restricted the name *mexicanus* to females and allocated most juvenile and male specimens to *Microbatrachylus.* Unlike *hobartsmithi* and *pygmaeus,* the Oaxacan frogs have an outer supernumerary palmar tubercle.

In describing *E. saltator,* **Taylor** (1941a) contrasted it not with *mexicanus* but rather with what he called *calcitrans* (= *omiltemanus*). He emphasized the presence of a black mesorchium in *saltator* as evidence that *saltator* provided a connection between *Eleutherodactylus* and *Microbatrachylus.* The nearest Taylor ever came to contrasting *mexicanus* and *saltator* is evident in his key (**Taylor,** 1941a). My reading of that couplet suggests that Taylor was contrasting a sample of one male and three females with another sample of females.

Although Taylor distinguished *mexicanus* and *saltator* because the former had shorter legs (measured by scoring the extent of heel overlap between the flexed hindlimbs), I find that variation in hindlimb length is more nearly continuous in *E. mexicanus.* The populations from Hidalgo,

Puebla, and Veracruz have the shortest hindlimbs (**Davis & Dixon,** 1957; **Lynch,** 1965a) whereas those from Guerrero are the longest but those from the Oaxacan highlands are intermediate [9 males have shank lengths 57.9-61.3 ($\bar{x}$ = 59.3 ± 0.3)% SVL and 11 females have values of 56.1-69.2 ($\bar{x}$ = 62.9 ± 1.5)% SVL]. Ten (CAS 143086-87, 143924-25, CNMH 100116, 10235, UIMNH 21437, USNM 47013-14, 304808) Guerreran females have shank/SVL ratios of 60.6-70.5 ($\bar{x}$ = 65.7 ± 1.0)%. Taylor also distinguished *mexicanus* and *saltator* on the basis of the sizes of the inner metatarsal tubercles ("less than three-fourths the length of the first toe " in *saltator* and "double the size of that in *saltator* " for *mexicanus*). Six females (CAS 143086-87, 143924-25, USNM 47013-14) from Guerrero, have IMT/first toe length ratios of 0.44-0.77 ($\bar{x}$ = 0.61 ± 0.03) and nine females from the vicinity of Oaxaca city (KU, USNM) have values of 0.52-0.72 ($\bar{x}$ = 0.62 ± 0.02). Six Oaxacan males (KU) have values of 0.56-0.72 ($\bar{x}$ = 0.62 ± 0.03). Taylor may well have used small specimens of *mexicanus* in making his contrasts, in which case, he would have perceived the inner metatarsal tubercle of *mexicanus* to be larger than that of *saltator.* Comparing adult females shows that there is no difference. The interpretation that Taylor was using animals of different sizes is consistent with his claim that the two species differ in expression of the vomerine dentition ("small or moderately distinct " in *saltator* vs "reduced or absent " in *mexicanus*). **Lynch** (1970) contributed to the confusion by reporting that the two differ because *mexicanus* has small outer tarsal tubercles and *saltator* does not. Very small tubercles can be seen in freshy preserved examples but these quickly fade and disappear. **Taylor** (1941) even recorded them as present in the freshy collected type-specimens of *saltator;* 50 yr later, they cannot be seen.

The only difference I have detected in contrasting specimens from the Oaxacan highlands with those from Guerrero is that the Guerrero populations are monomorphic and do not include the striped polymorph (*"lineatissimus"*), the white-lipped polymorph, or the uniform dorsum polymorph that are seen in the Oaxacan populations. Because the differences cited by **Taylor** (1941a) to distinguish *E. saltator* are not adequate to separate specimens from Guerrero (including the type-series) from those from Cerro San Felipe and Llano de las Flores in Oaxaca and I do not find other differences between frogs from these areas, I here place *Eleutherodactylus saltator* Taylor in the synonymy of *Eleutherodactylus mexicanus* (Brocchi). To facilitate comparisons among species, I provide a numbered diagnosis for *E. mexicanus.*

Diagnosis.— (1) skin of dorsum and limbs smooth with or without feeble longitudinal folds, usually including

one dorsolateral fold, that of flanks areolate, that of venter smooth; (2) tympanum prominent, sexually dimorphic, its length 84.0-90.6% eye length in males, 50.0-63.2% eye length in females; (3) snout rounded to subacuminate in dorsal view, truncate in lateral profile; canthus rostralis distinct, sinuous or weakly concave; (4) upper eyelid lacking tubercles, slightly narrow than to equal to IOD; (5) vomerine odontophores concealed in tissue of palate in small individuals, low and oblique in larger individuals; (6) males lacking vocal slits and nuptial pads; testes black; (7) first finger very slightly shorter than second; digit tips very slightly expanded, bearing ventral pads on outer fingers but not inner fingers; (8) fingers lacking lateral fringes or keels; (9) ulnar tubercles not developed or only feebly visible; (10) heel and tarsus lacking tubercles or folds; (11) two metatarsal tubercles, inner oval and not compressed, 4-5 times size of prominent rounded outer; supernumerary plantar tubercles absent or feebly developed; (12) toes lacking lateral fringes and webbing; toe disks narrow but larger than those of fingers; (13) dorsal pattern polymorphic (see **Lynch**, 1966); most common morph is brown above with slightly darker blotches; posterior surfaces of thighs cream with brown flecks or spots; venter cream; throat spotted and mottled with brown; (14) adults moderate-sized, males 17.6-28.1 ($\overline{X}$ = 23.5) mm, females 29.5-39.9 ($\overline{X}$ = 36.1) mm SVL.

Eleutherodactylus mexicanus is most similar to the smaller *E. sartori* (redescribed below). The two can be distinguished because the skin of the dorsum of *sartori* bears low tubercles and *sartori* has narrow lateral keels on the digits.

Description.— Descriptions of individuals are provided by **Davis & Dixon** (1957), as *Microbatrachylus fuscatus*, **Taylor** (1940), as *M. oaxacae*, and **Taylor** (1941a), as *Eleutherodactylus saltator* and as *M. lineatissimus*.

Distribution.— Intermediate to high elevations (1500-3420 m) in the highlands of Guerrero and Oaxaca as well as along the southeastern edge of the Mexican Plateau in Hidalgo, Puebla, and western Veracruz.

Eleutherodactylus sartori Lynch

Microbatrachylus montanus Taylor, 1942:67 [Holotype: USNM 115507, Mount Ovando, Chiapas, Mexico,1818 m].

Eleutherodactylus sartori Lynch, 1965a:10 (replacement name for *Microbatrachylus montanus*, Taylor, 1942, *nec Eleutherodactylus montanus* Schmidt, 1919).

Taylor (1942) named *Microbatrachylus montanus* from moderate to intermediate elevations in southeastern Chiapas, Mexico, based on four female individuals. The species has occasioned little comment and remains known only from Taylor's description. When **Lynch** (1965a) combined *Microbatrachylus* with *Eleutherodactylus,* it became necessary to replace Taylor's name owing to secondary homonymy with *Eleutherodactylus montanus* Schmidt, 1919. Since 1965, the Chiapan species has been called *E. sartori* Lynch. **Lynch** (1970) assigned *E. sartori* to the *mexicanus* group of **Taylor** (1941a) with *E. greggi* Bumzahem, *E. mexicanus* (Brocchi), *E. occidentalis* Taylor, *E. omiltemanus* (Günther), and *E. saltator* Taylor, but had no new information of *E. sartori*.

Subsequently, many changes have occurred in the supraspecific groupings of this small ensemble of frogs. **Lynch** (1976a) combined Taylor's *mexicanus, pygmaeus,* and *rhodopis* groups but assigned *E. greggi* and *E. omiltemanus* to a largely South American group (*unistrigatus* group), **Lynch** (1976b) removed *E. occidentalis* to the then-recognized genus *Hylactophryne* (now the *augusti* group of the subgenus *Craugastor*), **Ford & Savage** (1984) removed *E. greggi* and *E. omiltemanus* to a new species group with their new species, *E. daryi*, **Lynch** (1986) proposed recognizing the subgenus *Craugastor,* including all these species and nearly 70 others, and **Savage** (1987) recognized the *gollmeri* group, including some members earlier included in the *rhodopis* group (of Taylor and of Lynch), and the *rhodopis* series for 10 species, including *E. mexicanus, E. saltator,* and *E. sartori.*

Diagnosis.— (1) skin of dorsum bearing low tubercles, most distinct on lower back, that of venter smooth; (2) tympanum distinct, large and round in males, smaller in females; (3) snout subacuminate in dorsal view, rounded in profile; canthus rostralis distinct; (4) IOD broader than upper eyelid, flat; no enlarged tubercles on upper eyelid; (5) vomerine odontophores concealed in tissue of palate or, if visible, oblique, widely separated; (6) males lack vocal slits and nuptial pads; testes black; (7) first finger slightly shorter than second; narrow disks on outer fingers; inner fingers lack ventral pads; (8) fingers bearing narrow lateral keels; (9) no ulnar tubercles; (10) no heel or tarsal tubercles or folds; (11) two metatarsal tubercles, inner oval, about 1 1/2 times size of round outer; no supernumerary plantar tubercles; (12) toes with lateral keels, no webbing; toe disks narrow but larger than those of outer fingers; (13) dorsal pattern obsolete; posterior surfaces of thighs finely reticulated with brown; throat brown with cream spots; venter cream with faint brown reticulum; (14) adults small, males 14.5-18.7 ($\overline{X}$= 16.2 ± 0.3, n = 15) mm SVL, females 21.3-27.5 ($\overline{X}$= 24.0 ± 0.4, n = 20) mm SVL.

Description.— Head as wide as body, about as wide as long; HW in males 37.0-42.2 ($\bar{X} = 39.8 \pm 0.5$, n = 13)% SVL, in females 38.1-43.8 ($\bar{X} = 40.5 \pm 0.4$, n = 21)%; snout subacuminate in dorsal view, rounded in lateral profile; snout short, E-N in males 66.7-81.0 ($\bar{X} = 73.9 \pm 1.4$, n = 13)% eye length, in females 68.6-89.7 ($\bar{X} = 78.5 \pm 1.2$, n = 21)%; nostrils directed dorsolateral, not protuberant; canthus rostralis relatively well-marked, its edge rounded, weakly convex; loreal region weakly concave, sloping abruptly to lips; lips not flared; interorbital space flat; upper eyelid width in males 65.2-100.0 ($\bar{X} = 82.6 \pm 3.8$, n = 12)% IOD, in females 57.1-100.0 ($\bar{X} = 78.8 \pm 3.0$, n = 20)%; upper eyelid with several non-conical warts; supratympanic fold well-defined, obscuring upper edge of tympanic annulus, continuing posteriorly as short dorsolateral fold; tympanum round in males, annulus narrowly separated from eye, nearly touching edge of upper jaw, its length 75.6-97.6 ($\bar{X} = 86.0 \pm 1.7$, n = 12)% eye length, in females, higher than long, annulus distinct, separated from eye by distance less than tympanum diameter, its horizontal length 45.2-65.5 ($\bar{X} = 54.0 \pm 0.9$, n = 21)% eye length; postrictal tubercles subconical, fused, forming short ridge (most obvious in larger females); in larger females, choanae small, round, not concealed by palatal shelf of maxillary arch; in males and smaller females, choanae larger, partially concealed by palatal shelf of maxillary arch; in larger females, vomerine odontophores median and posterior to choanae, oblique, separated on midline by distance 3X odontophore width, bearing 2-3 teeth, each twice size of a choana; in males, vomerine odontophores usually absent, if present, concealed in tissue of palate (as in immature females); tongue slightly longer than wide, not notched posteriorly, posterior 1/5 not adherent to floor of mouth; males lack vocal slits.

Dorsolateral folds not extending posterior to arms; thin sagittal ridge on dorsum; dorsum bearing low tubercles, those above ilia larger, forming rows; skin of upper surfaces of limbs feebly tuberculate; skin of flanks smoother than dorsum; skin of ventral surfaces smooth; discoidal folds prominent anteriorly, obsolete posteriorly (apparently just anterior to groin); no anal sheath; skin below vent (and extending onto undersides of thighs) areolate; inguinal "gland" diffuse, not evident externally, evident only as thin glandular area on inner surface of skin of groin); no ulnar tubercles; palmar tubercle bifid (outer lobe smaller), much larger than oval thenar tubercle; supernumerary palmar tubercles protuberant, smaller than subarticular tubercles which are elevated, subconical, round; fingers bear lateral keels; no expansion of digit tips I-II, slight expansion of III-IV; ventral pads (and circumferential grooves) on III-IV but not I-II; when

fingers adpressed equally, I slightly shorter than II (Fig. 2); males lack nuptial pads on thumbs.

No heel or tarsal tubercles; inner metatarsal tubercle 1 1/2 times as long as wide, outer metatarsal tubercle 2/3 size of inner, round; no supernumerary plantar tubercles; subarticular tubercles elevated, round, conical; toe disks larger than those of outer fingers; disk of Toe V smaller than those of toes III-IV; when toes III and V adpressed against Toe IV, Toe III longer than Toe V; toes bearing lateral keels, no webbing; ventral pads present on toes II-V, not on inner toe; heels overlapping when flexed hind limbs held perpendicular to sagittal plane; shank in males 49.7-59.5 ($\bar{X} = 54.5 \pm 0.8$, n = 13)% SVL, in females 49.3-60.6 ($\bar{X} = 54.8 \pm 0.7$, n = 21)%.

Males have small, round, black testes.

Coloration.— Pale brown above with scattered brown flecks; dark brown anal triangle; canthal-supratympanic stripe dark brown; side of head and anterior flanks brown; labial bars indistinct, usually evident only as one band below eye and another half-moon along lip half way to tip of snout; limb bars distinct, slightly narrower than interspaces; posterior surfaces of thighs finely marbled or reticulated with brown; throat pale brown with small cream spots; chest and venter cream with indistinct brown reticulum (most noticeable on chest).

Distribution.— At moderate to intermediate elevations (1200-1900 m) on the Sierra Madre of Chiapas, Mexico.

Relationships.—*Eleutherodactylus sartori* has been included in the *pygmaeus, mexicanus,* and, finally, *rhodopis* groups of *Eleutherodactylus*. The transfers reflected successively more inclusive groupings rather than differences of opinions although **Savage** (1975:270) expressed doubts about **Lynch's** (1965a, 1970) association of *E. greggi* and *E. sartori* because the former has well-developed vomerine odontophores and they were reported as lacking in the latter. Now that more material is known and the skeletal features of *E. sartori* are known, it is clear that Taylor and Lynch erred in reporting that the species lacks vomerine teeth because teeth and odontophores are present but sometimes buried in the tissue of the palate. The throat of male *E. sartori* is darker than the venter and might be described as darkened in freshly-collected material. Phenetically, *E. sartori* is most similar to *E. mexicanus* but none of the shared traits can be considered a synapomorphy at present.

Eleutherodactylus omiltemanus (Günther)

Syrrhophus omiltemanus Günther, 1900:216 [Syntypes: BM 1901.12.19.7-8, Omilteme, Guerrero, Mexico, 2400 m].

Hylodes calcitrans Günther, 1900:230 [Syntypes: BM 1901.12.19.25-43, Omilteme, Guerrero, Mexico, 2400 m].

Eleutherodactylus calcitrans: Taylor, 1941a:91-93.

Eleutherodactylus omiltemanus: Lynch, 1970:175-176.

During the Smith-Taylor era of Mexican herpetology and continuing until 1970, this species was known as *E. calcitrans* (Günther), under which it accumulated most of its literature.

Diagnosis.— (1) skin of dorsum shagreen, bearing larger warts on lower back, that of venter areolate; (2) tympanum distinct, large and round in males, smaller in females; (3) snout subacuminate in dorsal view, rounded in lateral profile; canthus rostralis distinct; (4) IOD broader than upper eyelid in females, as wide as in males; low tubercles on upper eyelids; (5) vomerine odontophores concealed in small individuals, oval and narrowly separated in large females; (6) males lack vocal slits and nuptial pads; testes white; (7) first finger as long as second; fingers lacking expanded disks, pads on outer fingers; subarticular tubercles of fingers conical; (8) fingers lacking lateral keels; (9) no ulnar tubercles; (10) no heel or tarsal tubercles or folds; (11) two metatarsal tubercles, inner oval, large, not compressed, 3-5 times size of subconical outer; few supernumerary plantar tubercles; (12) toes lacking lateral fringes or webbing; toe disks narrow but larger than those of outer fingers; fifth toe shorter than third; (13) brown above with little indication of pattern except limb bars; throat brown with cream spots; venter cream; posterior surfaces of thighs dull yellow with brown spots or mottling; (14) adults small, males 21.2-26.9 ($\overline{x} = 24.0 \pm 0.7$, N = 8) mm, four females 32.3-36.5 ($\overline{x} = 34.1$) mm SVL.

Eleutherodactylus omiltemanus most closely resembles *E. bransfordii*, *E. lauraster*, and *E. stejnegerianus* because each has the inner two fingers about the same length, short limbs, and areolate skin on the venter. The inner metatarsal tubercle (Fig. 3) of *E. omiltemanus* is much larger than those of *E. bransfordii*, *E. lauraster*, and *E. stejnegerianus*, *E. bransfordii*, *E. lauraster*, and *E. stejnegerianus* have numerous small supernumerary plantar tubercles, and *E. omiltemanus* is a larger frog. These four species share conical subarticular tubercles with *E. loki* and *E. rhodopis* but these last two species have inner tarsal tubercles, a thumb that is clearly longer than the second finger, and smooth skin on the venter. **Savage et al.** (1996) regarded *E. lauraster* as very distinctive in part because it has basal webbing of the toes

and the first finger shorter than the second. I do not see much evidence of either character in their illustrations but agree that *E. lauraster* is distinctive and probably most closely related to *E. bransfordii* and *E. stejnegerianus*.

Description.—Head broader than long, as wide as body in males, narrower than body in gravid females; HW 40.7-45.1 ($\overline{x} = 43.2 \pm 0.4$, N = 8)% SVL in males, 39.3-44.8 ($\overline{x} = 42.2 \pm 0.5$, N = 13)% in females; snout subacuminate in dorsal view, rounded in lateral profile; nostrils very slightly protuberant, directed dorsolaterally; E-N 73.3-90.3 ($\overline{x} = 81.5 \pm 2.1$, N = 8)% eye length in males, 76.7-86.8 ($\overline{x} = 82.8 \pm 1.2$, N = 13)% in females; canthus rostralis sharp, weakly concave; loreal region concave, sloping abruptly to lips; lips slightly flared in larger females; a few slightly elevated warts on upper eyelid; upper eyelid width 95.0-100.0 ($\overline{x} = 99.3 \pm 0.7$, N = 7)% IOD in males, 75.0-100.0 ($\overline{x} = 87.6 \pm 2.6$, N = 12)% IOD in females; temporal region vertical; tympanum of males round, large, its length 85.2-119.4 ($\overline{x} = 100.8 \pm 3.8$, N = 8)% eye length, of females higher than long, smaller, its length 54.8-69.4 ($\overline{x} = 60.2 \pm 1.3$, N = 13)% eye length; postrictal tubercles
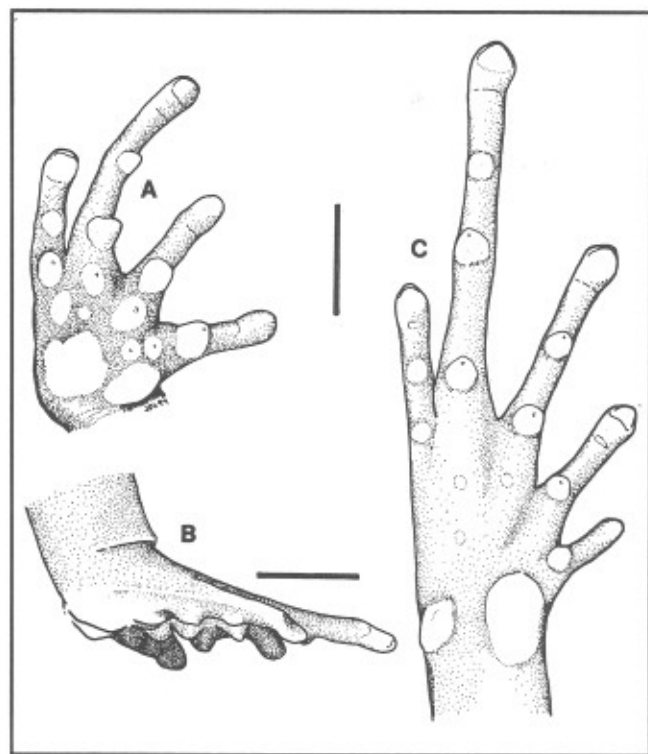

Figure 3. *Eleutherodactylus omiltemanus.* (A) Palmar view of hand. (B) Lateral view of hand. (C) Plantar view of foot. Based on USNM 304807. Scales equal 2 mm.

nonconical; supratympanic fold distinct, ending posterior to tympanum; short "dorsolateral" fold extending posteriorly from supratympanic fold to a point level with arm insertion; choanae small, round to wider than long, not concealed by palatal shelf of maxiallary arch; vomerine odontophores sometimes poorly defined (small and buried in tissue of palate) but relatively large (twice size of a choana), oval, separated medially by distance nearly equal to odontophore width, bearing 4-7 teeth in a slanted row; tongue wider than long, not notched posteriorly, posterior 2/5 not adherent to floor of mouth; males lacking vocal slits and vocal sac.

Skin of dorsum shagreen (larger flattened warts visible on lower back), that of flanks, venter, and undersides of thighs areolate; skin of throat smooth; discoidal folds not apparent; no ulnar tubercles; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles large, nonconical; subarticular tubercles conical, small, simple (Fig. 3); fingers lacking lateral keels; fingers lacking discs, tips somewhat bulbous, outer fingers have terminal groves (Fig. 3); first and second fingers of equal length; males lack nuptial pads on thumbs.

No tubercles or folds on heel or tarsus; inner metatarsal tubercle large, its length not quite twice its width, not laterally compressed, slightly shorter than length of first toe; outer metatrsal tubercle subconical, one-third to one-fifth size of inner; 0-3 supernumerary plantar tubercles; subarticular tubercles small, conical, simple; toes lacking lateral keels; toe tips bulbous, lacking disks but bearing terminal groves except on Toe I (Fig. 3); first toe not short, tip of Toe I reaching to distal edge of subarticular tubercle of Toe II; Toe V shorter than Toe III; shank of males 46.6-51.9 ($\overline{X}$ = 48.5 ± 0.6, N = 8)% SVL, of females 47.3-54.4 ($\overline{X}$ = 50.8 ± 0.7, N = 15)%.

The testes are white; however, TCWC 10095 has testes lightly stippled with brown and TCWC 10092 has one white and one lightly dusted testis. The testes are reticulate in MZFC 2988.

Dorsum usually uniform dark brown in alcohol (occasional specimens have black or dark brown blotches on dorsum); sides of head and anterior flanks darker than dorsum; limb bands well-defined; throat and chest brown, usually with scattered cream spots, venter cream; posterior surfaces of thighs dull yellow with brown mottling.

Distribution.— Intermediate elevations (1818-2500 m) in central Guerrero, Mexico.

Remarks. Above, I compared *E. omiltemanus* only with species of the *rhodopis* series and not with the other two

species assigned to the *omiltemanus* group by **Ford & Savage** (1984). I am convinced of two things (developed in the Results section of this paper) – that *E. omiltemanus* is actually a member of the *rhodopis* group (or series) and that *E. daryi* and *E. greggi* are species of the *gollmeri* group, distantly related to *E. omiltemanus.*

The *Eleutherodactylus rhodopis cluster.* **Smith & Taylor** (1948) recognized five species and **Shannon & Werler** (1955) described two more. By the early 1960s, all seven were viewed as probably genetic variants of the same species and the "group" collapsed to its current state except for the confusion of some species of the *gollmeri* group with *E. rhodopis.* In the mid-1970s, following study of material at the University of Michigan, I came to the conclusion that two species were included in what was then known as *E. rhodopis.* My undocumented opinion was used by **Lee** (1980) in his study of the herpetofauna of the Yucatan Peninsula (because each of us then thought I would publish my findings promptly). The account below is intended to document my opinion that both *E. loki* Shannon & Werler and *E. rhodopis* (Cope) should be recognized.

Most of the nominate species of the *rhodopis* group were described on the basis of specimens collected on the mountain slopes of central Veracruz, Mexico (*beatae*, La Perla, near Orizaba, 6000 ft.; *dorsoconcolor*, Tequeyutepec; *dunnii* and *mystaceus*, Cerro de los Estropajos, west of Jalapa; *plicatus*, Jalapa; *rhodopis*, Orizaba and Cordoba, *sallaei*, "Mexico", and *venustus*, Jalapa). The other two names (*loki* and *sanmartinensis*) were based on specimens from Volcán San Martín.

Savage (1987:27) provided a reasonably complete definition for *E. rhodopis* (*sensu lato*) but overlooked variation in size (Table 1) at maturity (and some minor, but correlated, differences). He reported that adult males reach 30 mm and adult females reach 40 mm [SVL], which is true for only a few population systems (Table 1). In order to evaluate variation in body size, I divided the distribution of the *rhodopis* cluster into a series of population systems, relying primarily upon material examined from the collections of KU, MZFC, and UMMZ. Adult males from Hidalgo, most of Puebla, and western Veracruz are large animals, often exceeding 25.0 mm SVL and adult females from these same populations achieve the sizes mentioned by **Savage** (1987), 34-44 mm SVL. The holotypes of three names (*beatae, mystaceus,* and *plicatus*) are males and are 25.0, 26.0, and 19.5 mm SVL, respectively. The holotypes of four names (*dorsoconcolor, dunnii, rhodopis,* and *venustus*) are adult females and are 39.2, 35.0, 40.2, and 35.0 mm SVL, respectively. The holotype of *sallaei* is a juvenile female 28.0 mm SVL. In

contrast, frogs from Volcán San Martín are markedly smaller. Twenty-two males are 16.4-22.7 mm SVL and females are 23.0-34.0 mm SVL, about the size of males of the larger form found on the Sierra Madre (23-29 mm SVL). The holotypes of *loki* and *sanmartinensis* are adult females 32.1 and 29.6 mm SVL.

In addition to the difference in size (Table 1), frogs from the Caribbean slopes of Hidalgo, Puebla, and Veracruz have uniformly white throats (no dark stippling) and lack small tubercles along the other edge of the tarsus and heel whereas those from the los Tuxtlas have dark stippling on the throats and anterior chest, have small tubercles along the outer edge of the tarsus, and have a cluster of small tubercles on the heel. Additionally, the frogs from the Caribbean slopes lack a ventral pad on the innermost toe and the innermost fingers whereas those from the Tuxtlas have circumferential grooves (pads) on all digits.

The larger frog having a white throat and lacking outer tarsal tubercles is found in Chiapas (Cintalapa, Tuxtla Gutierrez), Hidalgo (near Tenango de Doria), Puebla (Huachinango), and Veracruz (above Acultzingo, Banderilla, Jalapa, Orizaba). The Chiapas localities are relatively low (545-667 m) in contrast to those from Hidalgo, Puebla, and Veracruz (1500-2100 m). Samples from the Huatusco region of Veracruz suggest that either the two forms are sympatric or that they hybridize. UMMZ 119909 (7.5 km SW Huatusco) consists of eight individuals. These correspond to *rhodopis* in terms of throat color and size but have outer tarsal tubercles. UMMZ 119613 (3.2 km S Huatusco, 1330 m) consists of nine adult males (20.1-24.6 mm SVL, a juvenile female 28.9 mm SVL, and three adult females 37.8-38.8 mm SVL). In color and tarsal features they are *E. rhodopis*. UMMZ 117045 (3.2 km SW Huatusco, 1303 m), collected either at the same site or very nearby contains two specimens, a male 22.3 mm SVL and a gravid female 28.0 mm SVL, here assigned to *E. loki*. UMMZ 118193 (3.2 km SW Huatusco, 1303 m) contains four gravid females 33.6-35.7 mm SVL. They lack the outer tarsal tubercles but have a light dusting of brown on their throats. Collections from the Vista Hermosa area (population 7) of northern Oaxaca (1500-1600 m) contain relatively large frogs (assigned here to *E. loki*) having outer tarsal tubercles and darkened throats. The sample also includes a juvenile female 25.2 mm SVL.

Collections from Volcán San Martín range in altitude from 455 m to 1200 m but all individuals correspond to the smaller frog as do frogs from the lowlands of northern Oaxaca, northern Chiapas, Tabasco, and the Pacific versant of Chiapas, Guatemala, and El Salvador (Table 1). These data might be interpreted as reflecting an inverse rela-tionship between body size and altitude except for the frogs from central Chiapas (large size, relatively low elevation). The Vista Hermosa (Oaxaca) frogs are from higher elevations than the remaining dark-throated frogs with outer tarsal tubercles and are nearly as large as those from west-central Veracruz and adjacent Hidalgo and Puebla. The collections from the Huatusco region are from localities of intermediate elevations (ca 1300 m) and contain frogs exhibiting a mixture of character states but some of each extreme combination).

I do not have evidence of sympatry at present, but the available data are tantilizing, suggesting that sympatry will be observed with further collecting (MZFC 1226-28, from 3 km N Jalapa, road to Naolinco, are *E. loki*, from an area otherwise populated by the larger *E. rhodopis*, population system 2). If size were the only feature separating the two groups, I would interpret the data most parsimoniously as an altitude effect. The other differences cannot be so interpreted and, in spite of the apparent merging of the two forms in the Huatusco region (which I interpret as evidence of hybridization), I recommend recognizing two species in what has been called *Eleutherodactylus rhodopis* (Cope). One, found at moderate elevations in Hidalgo, Puebla, western Veracruz, and at low elevations in central Chiapas, is the larger *E. rhodopis* which has seven synonyms (*Hylodes beatae* Boulenger, *Eleutherodactylus dorsoconcolor* Taylor, *E. dunnii* Barbour, *Syrrhophus mystaceus* Barbour, *Hylodes plicatus* Günther, *H. sallaei* Günther, and *H. venustus* Günther). The other smaller species, found mostly at lower elevations (San Luis Potosi to northwestern Honduras along the Atlantic versant and from the Isthmus of Tehuantepec to El Salvador along the Pacific versant), is *E. loki* Shannon & Werler. It has a single synonym (*E. sanmartinensis* Shannon & Werler).

Eleutherodactylus rhodopis (Cope)

Lithodytes rhodopis Cope, 1867: 323 (Lectotype: USNM 16558, Orizaba and Córdoba, Veracruz, Mexico).

Hylodes sallaei Günther, 1869: 487 (Holotype: BMNH 57.7.31.27, "Mexico").

Hylodes plicatus Günther, 1900: 228 (Holotype: BMNH 1901.12.19.38, Jalapa, Veracruz, Mexico).

Hylodes venustus Günther, 1900: 234 (Holotype: BMNH 1901.12.19.37, Jalapa, Veracruz, Mexico).

Hylodes beatae Boulenger, 1903: 552 (Syntypes: BMNH 1903.9.30.236-237, La Perla, near Orizaba, Veracruz, Mexico).

Table 1. Variation in sizes at maturity in *Eleutherodactylus loki* and *E. rhodopis*. Populations are identified by number and are localized on the distribution map (Fig. 4). Values are reported for adults as the range (followed by mean, in boldface, ± 1 Standard error of the mean and sample size). If no sample size is indicated, there is a single observation or two (when a range is provided).

Pop.	ID	Adult males	Juv females	Yg females	Adult females
1	R	22.8-28.5 (**25.5**, 6)	24.6-31.5(3)	31.3-32.3	37.6-45.7 (**42.2**±1.3, 7)
2	R	18.1-26.6 (**23.5**±0.4, 30)	23.1-27.7(7)	34.9-38.3	36.1-43.9 (**39.4**±0.6, 17)
3	R	23.2-26.5 (**24.8**±0.3, 12)			36.1-41.2 (**38.5**±0.6, 9)
4A	R	17.5-24.6 (**22.3**±0.4, 21)	13.0-32.0(9)		33.6-38.8 (**36.1**±0.6, 10)
4B	L	22.3			28.0
5	L	14.9-22.8 (**18.8**±0.4, 24)	20.2-23.7(5)	25.5	23.0-34.3 (**27.9**±0.4, 50)
6	L	21.2-24.2 (**22.6**, 6)			28.6-34.0 (**31.6**, 5)
7	L	17.8-25.6 (**21.4**±0.4, 21)	15.0-25.2(6)	27.6	29.5-37.6 (**33.7**±0.4, 21)
8	L	17.1-23.0 (**20.5**±0.3, 29)		23.4	25.0-31.7 (**28.5**±0.4, 25)
9	L	18.3-23.0 (**20.7**±0.4, 11)	17.5-25.1(3)	23.9	26.3-30.9 (**28.8**±0.4, 12)
10	L	20.1-23.7 (**21.4**, 4)	20.2		30.8
11	R	23.5	30.0	31.5-33.1(3)	
12	R	24.2-24.3	27.4	36.1	37.1
13	L	19.1-23.4 (**20.8**, 5)	25.7-26.4(3)		29.2-34.6 (**31.2**±0.4, 13)
14	L	16.8-20.6 (**18.6**±0.2, 20)	13.6-15.2(5)		21.5-28.9 (**25.9**±0.6, 12)
15A	L	15.9-22.0 (**19.4**±0.2, 49)	24.6-25.2(6)	24.7-28.2	24.5-31.6 (**28.5**±0.3, 43)
15B	L	22.9			27.5-32.4 (**30.5**, 4)
16	L	22.6-23.9	24.8(2)		34.1-36.0
17	L	18.6-24.6 (**21.6**±0.3, 25)	27.7-30.0		27.7-35.0 (**30.9**±0.4, 19)
18	L	19.6-21.9 (**20.8**, 5)		25.0-28.4	28.7-34.0 (**31.3**±0.6, 8)
19	L		25.5		

Eleutherodactylus rhodopis: Kellogg, 1932:97-98.

Eleutherodactylus dunni Barbour, 1922: 111 (Holotype: MCZ 8242, Cerro de Los Estropajos, W of Jalapa, Veracruz, Mexico).

Syrrhophus mystaceus Barbour, 1922: 112 (Holotype: MCZ 8241, Cerro de Los Estropajos, W of Jalapa, Veracruz, Mexico).

Eleutherodactylus dorsoconcolor Taylor, 1941b: 152 (Holotype: USNM 110619, Tequeyutepec, Veracruz, Mexico).

Diagnosis. (1) Skin of dorsum finely tuberculate, bearing system of thin folds in many polymorphs, that of venter smooth; (2) tympanum distinct, large and round in males, smaller and oval in females; (3) snout acuminate to subacuminate in dorsal view, rounded in profile; canthus rostralis sharp, concave to straight, (4) IOD narrower than upper eyelid width; no cranial crests; upper eyelid not bearing pungent tubercles; (5) vomerine odontophores prominent, triangular in outline, closely juxtaposed, between and behind choanae; (6) males lack vocal slits; nuptial pad present on thumb; testes white; (7) first finger slightly longer than second, narrow disks on fingers; innermost fingers, at least thumb, lack ventral pads; subarticular tubercles large, conical; (8) no lateral keels on fingers; (9) no ulnar tubercles; (10) inner edge of tarsus bearing inner tarsal tubercle, sometimes set on vague fold; no outer tarsal tubercles; heel lacking cluster of small tubercles; (11) two metatarsal tubercles, inner elongate, 3-4 times size of subconical outer; numerous small supernumerary plantar tubercles; (12) toes bearing nearly cuspidate disks on Toes III-IV; innermost toe lacks ventral pad; toes lack lateral fringes, keels, and webbing; Toe III longer than Toe V when each are apressed to Toe IV; (13) color pattern extremely variable and polymorphic; dorsum usually gray to dark brown with brown to black blotches, spots, or stripes; posterior surfaces of thighs brown; lips and limbs banded; throat and venter white; (14) adults moderate-sized, males 17.5-28.5 (rarely less than 20.0) mm SVL, females 33.6-45.7 (rarely less than 35.0) mm SVL.

Descriptions. The descriptions of most synonyms are brief and emphasize what is now viewed as pattern polymorphism (**Barbour**, 1922, **Boulenger**, 1903, **Kellogg**, 1932, and **Taylor** 1941b).

Distribution. Largely restricted to western Veracruz and adjacent Hidalgo and Puebla (Fig. 4) between 1200 and 2100 m elevation. There is also an apparently disjunct population in central and southeastern Chiapas (and adjacent Oaxaca).

Remarks. The issue, of whether there are two species of the *rhodopis* cluster in Mexico, Belize, El Salvador, Guatemala, and Honduras remains to be tested critically. **Savage's** (1987) failure to consider adult size (other than maximun size) in carrying out taxonomic decisions, allowed him to repeat an earlier error (**Savage & Emerson**, 1970) wherein he failed to detect *E. stejnegerianus* among his samples of *E. bransfordi*, clouding an otherwise marvelous analysis of polymorphic variation. Those two taxa were first recognized on the basis of molecular evidence (**Miyamoto**, 1983) but turned out to be distinguishable by size and secondary sex characters as well (personal observation, 1984).

The critical areas lie in Puebla, Veracruz, eastern Oaxaca, and in central Chiapas where *E. loki* appears to be replaced at higher elevations by *E. rhodopis*. My limited samples suggest sympatry (or near sympatry) in the Huatusco and Jalapa regions of western Veracruz but those samples are nowhere sufficient to resolve the issue. Unfortunately, habitat destruction may have rendered the question moot.
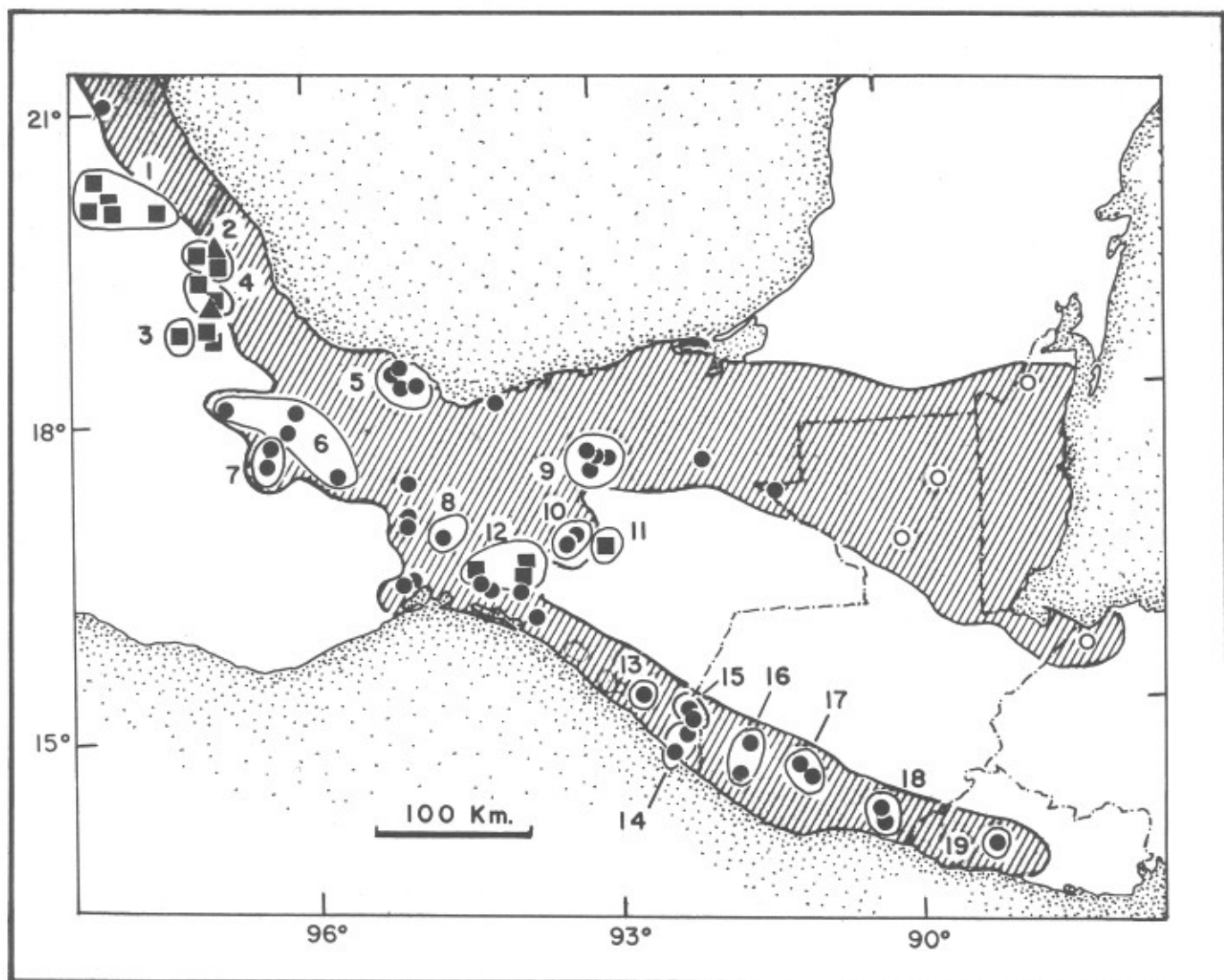

Figure 4. Map of the known distributions of *E. loki* (circles) and *E. rhodopis* (squares). Localities of near sympatry are represented by trangles. Open symbols represent literature records. Population systems are identified by number (see Table 1).

Eleutherodactylus loki Shannon & Werler

Eleutherodactylus loki Shannon & Werler, 1955: 368. (Holotype: Formerly FAS 4748, Volcán San Martín, Veracruz, Mexico, 1060 m. Deposited in UIMNH).

Eleutherodactylus sanmartinensis Shannon & Werler, 1955: 375. (Holotype: Formerly FAS 4750, Volcán San Martín, Veracruz, Mexico, 1060 m. Deposited in UIMNH). **New synonymy**.

Diagnosis. (1) Skin of dorsum finely tuberculate, bearing system of thin folds in many polymorphs, that of venter smooth; (2) tympanum distinct, large and round in males, smaller and oval in females; (3) snout acuminate to subacuminate in dorsal view, rounded in profile; canthus rostralis sharp, concave to straight, (4) IOD narrower than upper eyelid width; no cranial crests; upper eyelid not bearing pungent tubercles; (5) vomerine odontophores prominent, triangular in outline, closely juxtaposed, between and behind choanae; (6) males lack vocal slits; nuptial pad present on thumb; testes white; (7) first finger slightly longer than second, narrow disks on fingers; all fingers bearing ventral pads; subarticular tubercles large, conical; (8) no lateral keels on fingers; (9) no ulnar tubercles; (10) inner edge of tarsus bearing inner tarsal tubercle, sometimes set on vague fold; series of small tubercles along outer edge of tarsus; cluster of small tubercles on heel; (11) two metatarsal tubercles, inner elongate, 3-4 times size of subconical outer; numerous small supernumerary plantar tubercles; (12) toes bearing nearly cuspidate disks on Toes III-IV; all toes bearing ventral pads; toes lack lateral fringes, keels, and webbing; Toe III longer than Toe V when each are apressed to Toe IV; (13) color pattern extremely variable and polymorphic; dorsum usually gray to dark brown with brown to black blotches, spots, or stripes; posterior surfaces of thighs brown; lips and limbs banded; venter white but throat and chest heavily stippled with brown; (14) adults small, males 14.9-25.6 (rarely more than 24.0) mm SVL, females 21.5-37.6 (rarely more than 34.0) mm SVL.

Descriptions. The original descriptions of *E. loki* and *E. sanmartinensis* (each of adult females) are available in **Shannon & Werler** (1955).

Distribution. Mostly in low elevation sites but from sealevel to 2100 m from San Luis Potosí along the Caribbean lowlands to Belize and northwestern Honduras; crossing the Isthmus of Tehuantepec and thence southeast along the Chiapas and Guatemalan versant to El Salvador (Fig. 4).

Remarks. There is clearly an altitude effect on size, individuals from higher elevations are slightly larger than those from the lowlands (Table 1, population systems 14,

15A, and 15B represent progressively higher samples along the slopes of Volcán Tacaná and mean sizes increase; population system 16 is from generally higher collecting sites than 17-18, in southern Guatemala; and population system 7 on the Sierra Juárez of northern Oaxaca is from 1500 to 2100 m).

Results (Systematics)

Apparent Synapomorphies Within Craugastor

Lynch (1986) argued that *Craugastor* was diagnosed by the E condition of the adductor muscles of the jaw (and trigeminal nerve). However, no other proposed synapomorphies are available for this clade. In order to examine Savage's hypothesis critically, additional synapomorphies are needed. I suggest that the following four characters are synapomorphies and that they call for a very different hypothesis concerning the relationships of frogs of the subgenus *Craugastor*.

(A) *Strong Sexual Dimorphism in Tympanum Size*. Many authors have noted the pronounced difference in tympanum size in adult males and females of many species of *Craugastor* (Fig. 5). In addition, many species do not exhibit sexual dimorphism in tympanum size (e.g., *E. augusti*, **Zweifel**, 1956). In other species of *Eleutherodactylus* (outside of the subgenus *Craugastor*), tympanum size either shows no variation among sexes or males have only slightly larger tympani than do females. The two conditions seen in species of *Craugastor* (dimorphic, not dimorphic) are contrasted with a single condition in other *Eleutherodactylus* (not dimorphic), enabling us to conclude that the not dimorphic condition is plesiomorphic and the dimorphic condition is apomorphic. Furthermore, ontogenetic observations (of species within *Craugastor*) reveal that the dimorphic condition is derived because young males have tympani the same size as females (**Lynch**, 1965b).

Strong sexual dimorphism is seen in all species assigned to the *biporcatus*, *gollmeri*, *milesi*, *omiltemanus*, and *rhodopis* groups. Although frogs of the *alfredi* group vary in tympanum size (**Campbell & Hillis**, 1989), no species appears to exhibit marked sexual dimorphism. No dimorphism is apparent in the two species of the *bufoniformis* group nor in the two species of the *augusti* group studied by **Zweifel** (1956). *Eleutherodactylus occidentalis*, assigned to the *augusti* group by **Lynch** (1976b), does exhibit pronounced dimorphism. Four species (*anatipes*, *anomalus*, *cheiroplethus*, and *zygodactylus*), sometimes assigned to the *rugulosus* group (**Savage et al.**, 1988), differ from the other 15 species in lack-

ing dimorphism in tympanum size. Four species (*andi, bocourti, cuaquero,* and *emcelae*) previously assigned to the *fitzingeri* group (**Savage**, 1987) differ from the remaining eight species in lacking dimorphism as well.

(B) *Fusion of the eighth and sacral vertebrae*. Nine species of *Craugastor* exhibit fusion of the sacrum and first presacral vertebrae. Seven of these were assigned to the *gollmeri* group by **Savage** (1987). *Eleutherodactylus daryi* and *E. greggi* were assigned to the *omiltemanus* group by **Ford & Savage** (1984). No other *Craugastor* (including *E. omiltemanus*) exhibit this fusion. Comparable fusions are seen in two species of the *galdi* group of the subgenus *Eleutherodactylus* (**Lynch**, 1996) and in some species of the *ricordii* group of the subgenus *Euhyas* (**Joglar**, 1986). This sort of fusion also is known for the *Rana palmipes* group (**Lynch**, 1965c) and a small clade of African ranids (**Clarke**, 1981). For at least *E. gollmeri* and *E. noblei*, ontogenetic changes reveal that fusion is derived. The most parsimonious solution is to view fusion (apomorphic) as derived independently at least five times.

(C) *Fifth toe longer than the third*. **Lynch & Duellman** (1997) argued that the state of a fifth toe shorter than the third is plesiomorphic (that condition occurs in 61 species of *Craugastor*). The species of the *alfredi* group and *E. bocourti* are peculiar in having the fifth toe longer than the third. This character is complicated because there is a third state (also derived) that **Lynch & Duellman** (1997) argued had evolved only once in contrast to no fewer than five independent acquisitions of the state exhibited by the *E. alfredi* group.

(D) *Heavy cranial crests borne laterally on frontoparietal bones*. Only three species of *Craugastor* have elevated cranial crests (*biporcatus* group). Although comparable crests occur as well in some members of the subgenus *Eleutherodactylus*, the condition seen in the *biporcatus* group is viewed as derived relative to the absence of cranial crests.

If each of these four apomorphies is argued to have evolved once in frogs of the subgenus *Craugastor*, then some of the species groups recognized by **Savage** (1987) will require dismemberment, specifically the *augusti* group (removing *E. occidentalis*), the *fitzingeri* group (removing *E. bocourti* to the *alfredi* group and removing *E. andi, E. cuaquero,* and *E. emcelae*), the *omiltemanus* group (removing *E. daryi* and *E. greggi* to the *gollmeri* group), and the *rugulosus* group (removing *E. anatipes, E. anomalus, E. cheiroplethus,* and *E. zygodactylus*).

Monophyly of Gollmeri, Omiltemanus, and Rhodopis Groups

As mentioned above, there is no character known to link the *gollmeri* and *omiltemanus* groups as being more closely related to one another than is either to the *rhodopis* group. At present, including the changes advocated above, the *Eleutherodactylus gollmeri* group contains seven species (*E. chac, E. gollmeri, E. laticeps, E. lineatus, E. mimus, E. noblei,* and *E. rostralis*), the *Eleutherodactylus omiltemanus* group contains three species (*E. daryi, E. greggi,* and *E. omiltemanus*), and the *Eleutherodactylus*
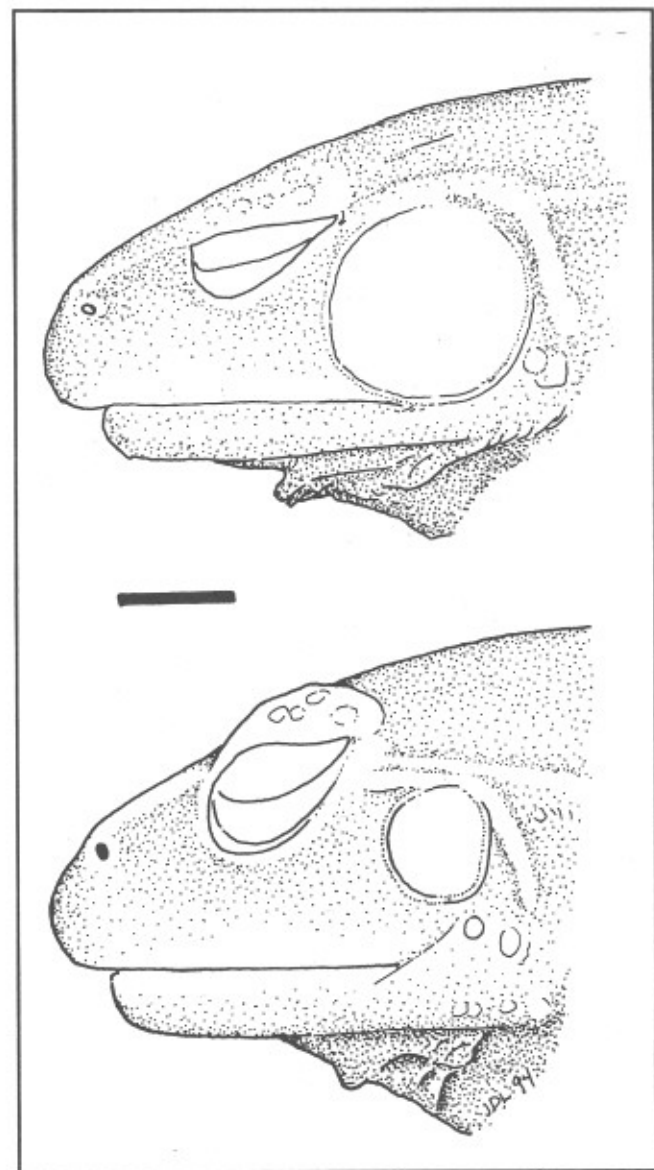

Figure 5. Sexual dimorphism in tympanum size in *Eleutherodactylus omiltemanus*. (Top) Male, USNM 304807. (Bottom) Female, CNHM 124684. Scale equals 2 mm.

rhodopis group contains eleven species (*E. bransfordii, E. hobartsmithi, E. jota, E. lauraster, E. loki, E. mexicanus, E. podiciferus, E. pygmaeus, E. rhodopis, E. sartori,* and *E. stejnegerianus*).

These three groups as well as the *fitzingeri* group were defined by **Ford & Savage** (1984) and **Savage** (1987) using twenty characteristics (one karyological, two myological, and seventeen features of external anatomy). Karyological data are available for few species, making the characteristic difficult to evaluate. One of the myological features is of no use within *Craugastor* because it is a synapomorphy of *Craugastor* (**Lynch**, 1986); I have argued that the other myological feature was overinterpreted by Savage and his coworkers (**Lynch**, 1993). The features of external anatomy include two of head shape (chunky vs slender, narrow vs broad), cranial crests, vomerine odontophores, vocal slits in males, nuptial pads in males, tympanum (prominent vs concealed), inguinal glands, disks of fingers and toes (expanded or not, some or all digits, sizes of outer disks relative to those of inner digits, emargination and shape), lengths of inner two fingers, subarticular tubercles (rounded vs projecting), supernumerary tubercles of foot, supernumerary tubercles of hand, tarsus (fold, tubercle, or no ornamentation), toe webbing (none vs basal vs extensive), and texture of venter (smooth vs granular). One characteristic involving the head (chunky vs slender) appears descriptive and too subjective to use. Another characteristic mentioned for the *gollmeri* group ("elegant ") suffers from the same difficulty.

Errors in group assignments made on the basis of such a list of characteristics results from failure to distinguish between primitive and derived states and/or incorrect polarizing of characteristics. **Savage's** (1987) account does not contain an explicit explanation of polarization although he does refer to primitive and derived conditions and does identity one outgroup. I am not able to agree that Savage has correctly polarized the characteristics he used and am thus unable to agree that his assertions of monophyly for several groups are objective.

The Eleutherodactylus omiltemanus Group. This species group was crafted by **Ford & Savage** (1984) to accomodate two species from the highlands of Chiapas and Guatemala and one species from central Guerrero. Although *E. greggi* and *E. omiltemanus* were long considered species of the *mexicanus* group, **Lynch** (1976a) assigned them to his *unistrigatus* group based on finger lengths and the texture of the venter. This created a biogeographic enigma, as noted by **Ford & Savage** (1984) who pointed out that the *daryi-greggi-omiltemanus* group

was separated by 600 km from the nearest locality for any species of the *unistrigatus* group (but they neglected to point to the 800 km gap internal to their species group). Of greater significance, they pointed out that these three species share the "E" condition of the *m. adductor mandibulae* in contrast to the "S" condition seen in frogs of the *unistrigatus* group.

Lynch (1986) agreed and extended the argument by asserting that the "E" condition is a synapomorphy linking these three species with more than 70 others in the subgenus *Craugastor.* **Ford & Savage** (1984) used the "E" condition of the *m. adductor mandibulae,* the "DFSQAT" condition of the *m. depressor mandibulae,* and the observation that *E. greggi* has a karyotype of 2N = 22 (and N.F. = 40) to argue "that the *daryi-greggi-omiltemanus* group forms a natural unit.... "

However, taken individually or collectively, these three characters are either plesiomorphic within *Craugastor* or represent characters for which polarities remain to be established (**Lynch**, 1986, 1993). Therefore, they cannot serve as sufficient evidence to assert that the *omiltemanus* group is a natural unit.

The "evidence" that these three species form a natural unit must be the "trivial features of morphology that are subject to many convergences in the genus" (quoted from **Ford & Savage**, 1984:5) so rounded criticized by **Savage & DeWeese** (1979, 1981). **Ford & Savage** (1984:5) characterized the three frogs as having "narrow nonemarginate finger and toe disks, no tarsal fold or tubercle, no toe webbing, finger I shorter than finger II, a strongly granulate (areolate) venter, a distinct sub-integumentary inguinal gland, and no vocal slits in adult males."

If these seven characteristics are treated as a combination and that combination is viewed as a feature, then the *omiltemanus* group can be diagnosed. The grouping of *E. omiltemanus* with *E. daryi* and *E. greggi* is a consequence of confusing combinations with characters and evidence.

Savage (1987) contrasted frogs of the *gollmeri* group with those of the *rhodopis* Series, in part, on the grounds that the former were "long-legged" frogs and the latter have "short legs." But, as shown by **Savage** (1987), *E. laticeps* varies ontogenetically in leg length. Even ignoring that species, the shanks of *gollmeri, lineatus, mimus,* and *noblei* are 54.8-72.6% SVL. *Eleutherodactylus daryi* and *E. greggi* have comparably long hindlegs (shank 61-71% SVL) but *E. omiltemanus* has markedly shorter legs (shank 47-54% SVL) as noted by **Günther** (1900) and **Taylor** (1941a). *Eleutherodactylus mexicanus, E. loki,* and

E. rhodopis have hindlegs that are comparable in length (shank 49.1-72.8% SVL) to those of the "long-legged " members of the *gollmeri* group (when expressed as shank/ SVL). The "shortness " of the legs of some of these frogs is evident when adpressing the hindlimb against the body and must reflect either differences in thigh length or the length of the trunk. *Eleutherodactylus sartori* has shorter legs than *E. mexicanus* but they are not so short as the hindlimbs of *E. omiltemanus.*

Eleutherodactylus daryi and *E. greggi* have a habitus more consistent with the stockier members of the *gollmeri* group (e.g., *E. chac* and *E. lineatus*) than with that of *E. omiltemanus* whose chunky body and head appear more like members of the *rhodopis* Series.

Savage (1987) distinguished the *gollmeri, omiltemanus,* and *rhodopis* groups using non-karyological characteristics as well (so that species lacking karyologic data could be assigned to groups and Series). Comparing the definitions he provides, the *gollmeri* group is distinguished because its members possess "one or more disc cover pointed " and "some disc pads swollen to cuspidate ". His claim that these are synapomorphies of the *gollmeri* group is true only in a restricted and contingent sense where he uses the *fitzingeri* group as the ancestor for the *gollmeri* group and in so doing ignores the *rhodopis* group.

However, pointed digital disk covers occur in frogs of the *diastema* group (which also have swollen to cuspidate disc pads). Of greater concern is that such features are sometimes apparent in *E. loki* (Fig. 2C-D) and *E. rhodopis*, species long-associated (**Smith & Taylor**, 1948) with frogs now assigned to the *gollmeri* group. Even the projecting subarticular tubercles of the *gollmeri* group appear as well in *E. rhodopis* (**Taylor**, 1952). In general, the species assigned by **Savage** (1987) to the *gollmeri* group have larger disks (greater expansion of the digit tip) than do the frogs of the *rhodopis* Series but considerable variation is evident.

Cranial Morphology and Osteology

Eleutherodactylus sartori.— Each specimen dissected exhibits bilaterally the E condition of the adductor muscles (the mandibular ramus of the trigeminal nerve passes medial to the most external adductor). Each exhibits a condition of the *m. depressor mandibulae* in which the fibers originating on the squamosal do not extend medial to the crest of the otic ramus of the squamosal (lack the "flap" condition) and in which approximately 20% of the fibers originate on the dorsal fascia and 80% originate on the squamosal (and possibly on the posterior wall of the tympanic annulus). Such a condition is termed DFSQAT. The trigeminal nerve character is what is to be expected for a species of the *rhodopis* series (**Lynch**, 1986; **Savage**, 1987). The depressor muscle character is what is expected for **Savage** (1987) but not for **Lynch** (1993) who found a dorsal flap in other species of this series.

The skull is broader than long and moderately acuminate. The maxillary arch is complete. The nasals are large, with rounded medial borders, and are separated medially (Fig. 6B). The nasals are separated widely from the frontoparietals, exposing the sphenethmoid. The anterior border of the frontoparietals is convex so that the most medial portions extend farther anteriorly than do the lateral portions. The frontoparietals closely approach one another and essentially cover the fontanelle. The frontoparietals do not bear crests and are not fused to the prootics or exoccipitals. The epiotic eminences are low, barely reaching above the surface of the relatively short crista parotica.

The palatal shelf of the premaxilla is dissected deeply. That of the maxilla is less broad. The vomers are widely separated and tri-radiate. The dentigerous process is not reduced in size and bears a low odontophore on its posterior extent (Fig. 7B). The odontophore bears a clump of teeth. The neopalatines are large bones that extend medially to lie just posterolateral to the most posterior portion of the vomer. The cultriform process of the parasphenoid is blunt anteriorly, does not reach to the vomers, and does not taper. The alary processes of the parasphenoid are long and slightly deflected posteriorly. The occipital condyles are widely separated and not stalked. The median rami of the pterygoids are long and extend medially to overlap the lateral extent of the parasphenoid. The anterior and posterior rami of the pterygoids are not angled relative to one another.

In lateral view, the alary processes of the premaxillae are oriented vertically. The nasals cover much of the nasal capsule laterally but do not reach the *pars facialis* of the maxilla. The quadratojugal is long and slender and broadly overlapped by the posterior end of the maxilla. The zygomatic ramus of the squamosal is deep and only about two-thirds the length of the otic ramus (Fig. 8B).

Eight procoelus vertebrae lie anterior to the sacrum. Each of the nine vertebrae is independent (no fusion).

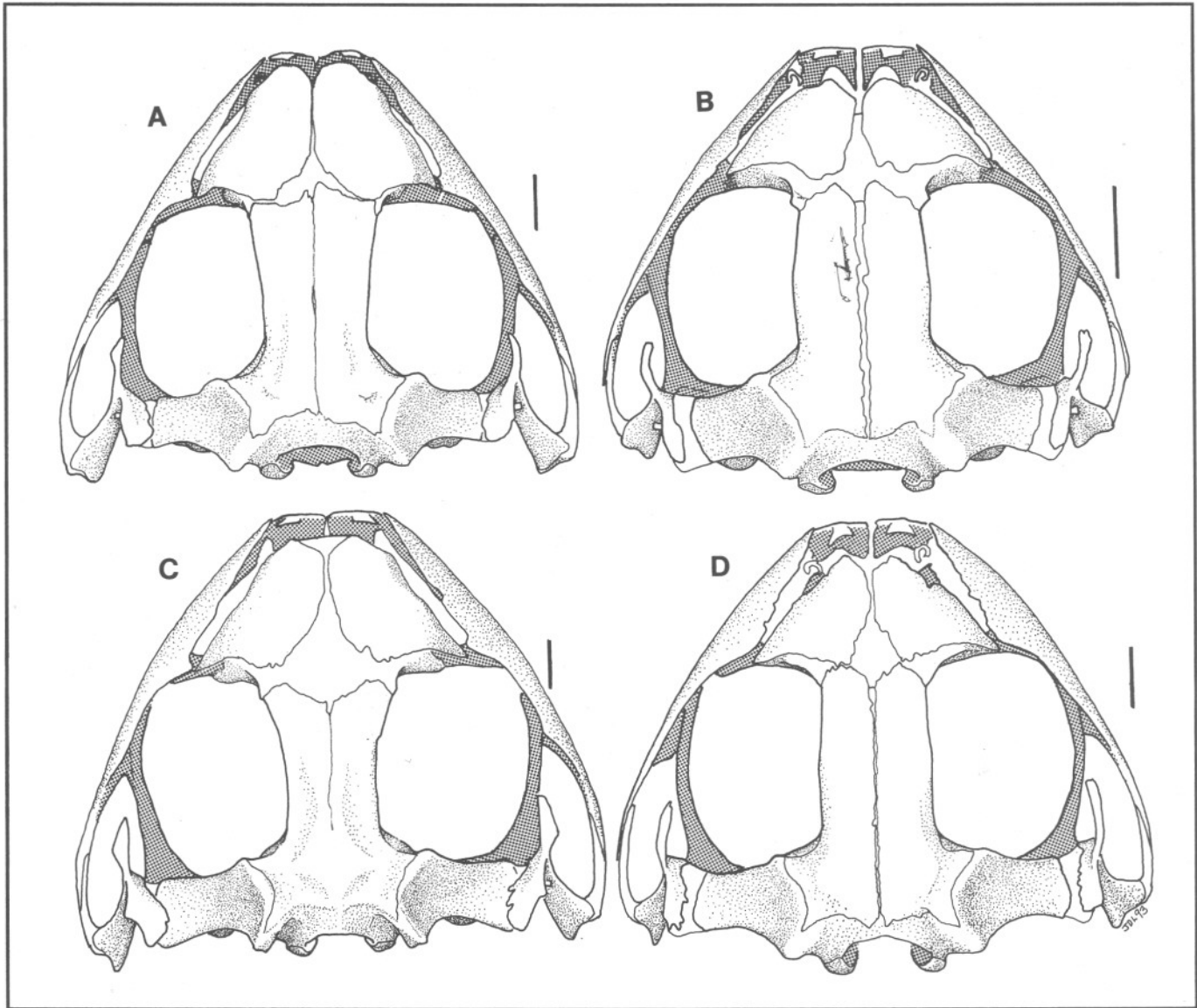*Species of the Rhodopis Series.*— I examined crania of seven species of the *rhodopis* group (*bransfordii,*

Figure 6. Dorsal views of crania of four species of the subgenus *Craugastor.* (A) *E. rhodopis*, KU 54072, (B) *E. sartori*, UMMZ 88366, (C) *E. rostralis*, KU 209112, (D) *E. greggi*, UMMZ 88007. Scales equal 2 mm.

mexicanus, podiciferus, pygmaeus, rhodopis, sartori, and *stejnegerianus).* In most of these, the nasals are large, broadly in contact medially, and cover most of the dorsal aspect of the nasal capsules and sphenethmoid as in *E. rhodopis* (Fig. 6A). *Eleutherodactylus mexicanus, E. pygmaeus,* and *E. sartori* have smaller nasals not extending so far posteriorly or medially and having a lesser median contact (if any). The anterior edges of the frontoparietals are transverse with a suggestion of a convex border medially (Fig. 6A) in all of these except *E.*

mexicanus although the slight separation of the frontoparietals obscures the prominence of the medial extension of the frontoparietal in *E. sartori.* In *E. mexicanus,* the anterior border of the frontoparietals is transverse without a convex border. The frontoparietals occlude the frontoparietal fontanelle, have nearly parallel lateral borders, lack cranial crests, and are not fused to the prootics. The otic shelf of the squamosal is narrow in *E. mexicanus, E. pygmaeus,* and *E. sartori* (Fig. 6B) but is broader in the other taxa (Fig. 6A).
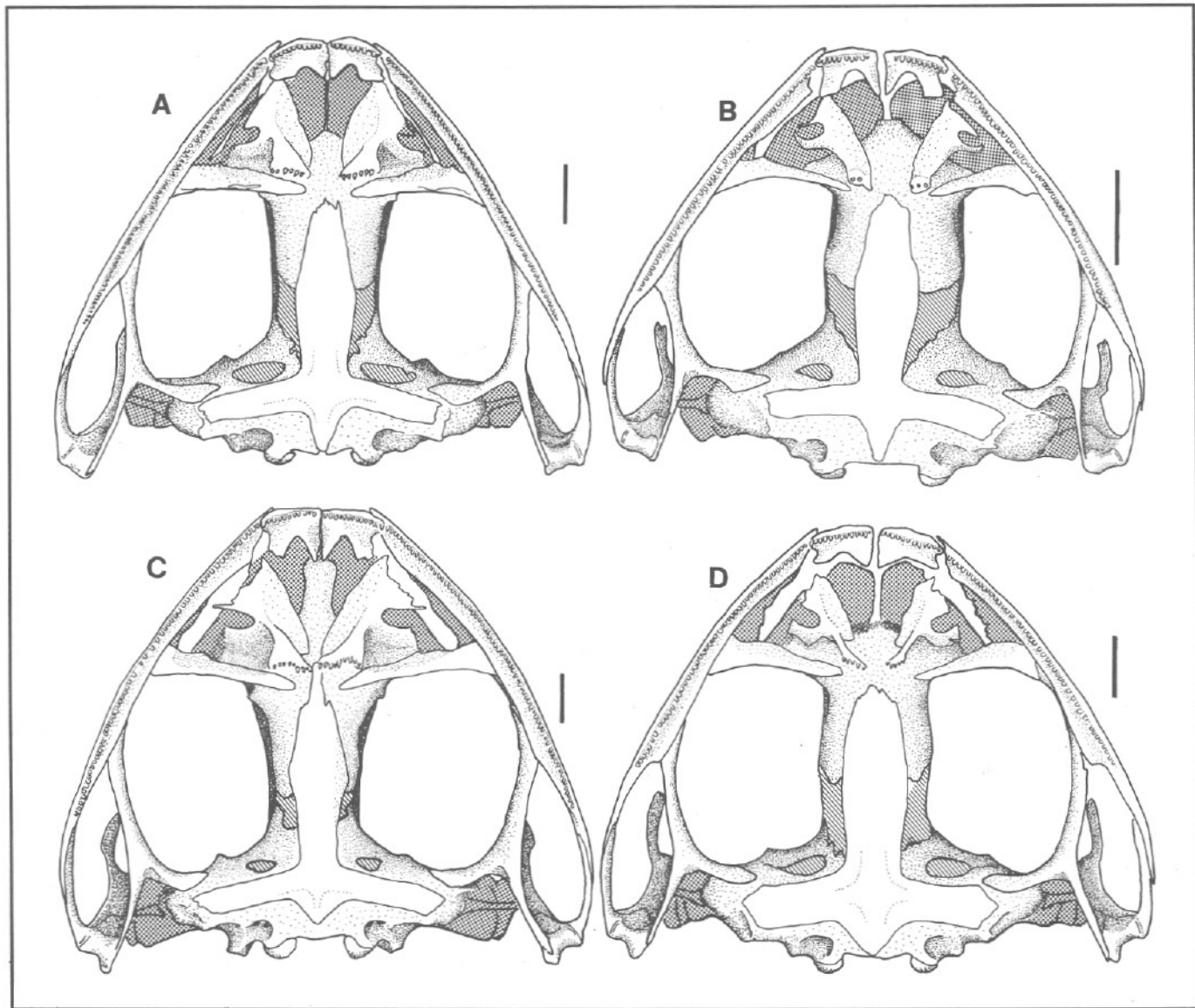
Figure 7. Ventral views of crania of four species of the subgenus *Craugastor*. (A) *E. rhodopis*, KU 54072, (B) *E. sartori*, UMMZ 88366, (C) *E. rostralis*, KU 209112, (D) *E. greggi*, UMMZ 88007. Scales equal 2 mm.

The alary processes of the premaxillae are vertical in all taxa and most have a deep *pars facialis* of the maxilla (like that of *E. sartori*, Fig. 8B). The zygomatic ramus of the squamosal is shorter than the otic ramus and is pointed in most taxa (*E. sartori* differs in having a blunt zygomatic ramus). The palatal shelf is dissected deeply (Fig. 7) in most taxa (less deeply in *E. bransfordii* and *E. rhodopis*, Fig. 7A). The vomers are large and widely separated with relatively massive triangular odontophores in *E. bransfordii*, *E. podiciferus*, *E. rhodopis* (Fig. 7A) but have smaller odontophores and narrower dentigerous processes in *E. mexicanus* and *E. sartori* (Fig. 7B). *Eleutherodactylus pygmaeus* lacks odontophores and teeth and has a long thin bony projection (dentigerous process) extending posteromedially to a point just medial to the neopalatines. The cultriform process of the parasphenoid is pointed and extends to the level of the neopalatines in *E. bransfordii*, is somewhat blunter and slightly shorter in *E. rhodopis* (Fig. 7A) and *E. sartori* (Fig. 7B), and more obviously blunt and shorter in the other taxa. The alary processes of

the parasphenoid are deflected slightly posteriorly and the posterior process of the parasphenoid extends nearly to the foramen magnum in all taxa. The pterygoids are well ossified and the anterior ramus extends halfway up the orbit in all taxa. The median ramus is shorter in *E. mexicanus* and *E. pygmaeus* (not reaching medially as far as the lateralmost level of the parasphenoid ala) whereas in the other taxa the median ramus reaches a level that overlaps the lateralmost level of the ala (the two elements do not meet). Each of the ten species examined has eight articulating procoelous presacral vertebrae.

A Synapomorphy for the Gollmeri Group.— In his account of West Indian *Eleutherodactylus,* **Joglar** (1986) included the first report of fusion of the sacrum and the adjacent presacral vertebra in two species of the *gollmeri* group (the record is buried in a lengthy table and easily overlooked). After verifying that Joglar's five specimens exhibited the fusion, I surveyed additional material of all seven species of the *gollmeri* group. Dissections of three to seven specimens of each species (N = 29) demonstrated that all exhibit fusion of the eighth and sacral vertebrae. In the case of *E. gollmeri,* I examined 14 specimens of various sizes. Those less than 19 mm SVL (N = 4) do not exhibit the fusion but the ten specimens 20-50 mm SVL do exhibit the fusion. I assume that in all seven species, fusion occurs after hatching but before the animal is mature. Such a feature appears to be an unequivocal synapomorphy linking the seven species of the *gollmeri* group as recognized by **Savage** (1987).

When I surveyed the remaining species of *Craugastor,* I found only the condition of eight presacral vertebrae except for two species. Both *E. daryi* and *E. greggi* have the sacrum fused to the last presacral vertebrae whereas *E. omiltemanus* exhibits the plesiomorphic condition. The most parsimonious explanation of these data is that *E. daryi* and *E. greggi* are members of the *gollmeri* group whereas *E. omiltemanus* is not.

Assigning these two Guatemalan species to the *gollmeri* group challenges the characteristics advanced by **Ford & Savage** (1984) and by **Savage** (1987) as sufficient to define (in the sense of diagnose) the *gollmeri* and *omiltemanus* groups of *Eleutherodactylus.* **Savage** (1987:49) specifically identified four derived characteristics of the *gollmeri* group: swollen or cuspidate pads, projecting subarticular tubercles,
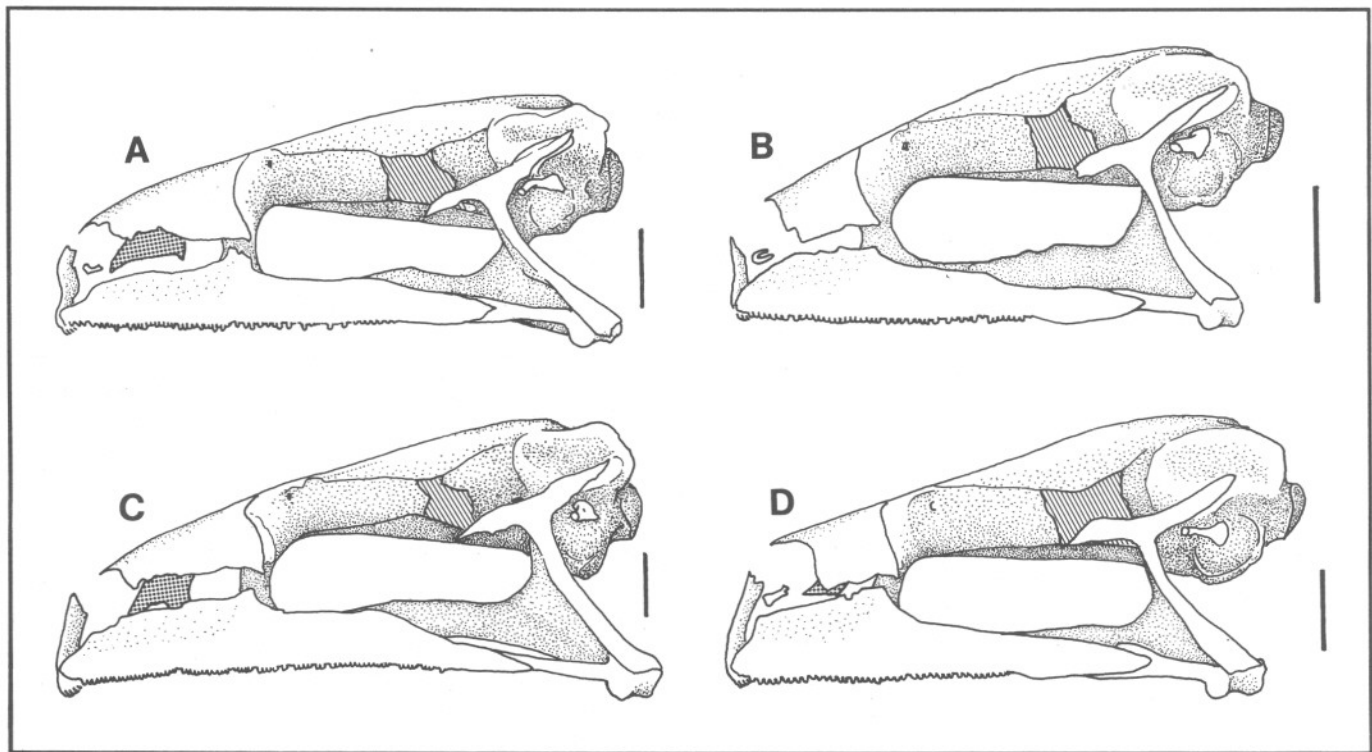

Figure 8. Lateral views of the crania of four species of the subgenus *Craugastor.* (A) *E. rhodopis,* KU 54072, (B) *E. sartori,* UMMZ 88366, (C) *E. rostralis,* KU 209112, (D) *E. greggi,* UMMZ 88007. Scales equal 2 mm.

no vocal slits, and no nuptial pads. These conditions are true for the seven species he included in the *gollmeri* group but are not unique, except as a combination, to those seven species. Neither *E. daryi* nor *E. greggi* has swollen digital pads or projecting subarticular tubercles but each lacks vocal slits and only *E. daryi* has nuptial pads. These two species are dissimilar to the remaining seven because neither has a tarsal fold and because each could be described as lacking toe webbing although there is some basal webbing in *E. greggi.*

Savage's decision as to what was derived for the *gollmeri* group depends primarily upon his assignment of the *fitzingeri* group as the sister group for the *gollmeri* group [**Savage** (1987:50) stated "only the *Eleutherodactylus fitzingeri* group, as reconstructed in the present paper, seems close to *E. gollmeri* and its allies. "]. Taking the characteristics that he viewed as primitive for the *gollmeri* group, there is no argument presented as to why he selected the *fitzingeri* group as the sister group when many members of his *rugulosus* group have the same character-states (but a dissimilar physiognomy). Savage appears to have judged the *fitzingeri* group as the surrogate ancestor of other species groups of *Craugastor* as well (**Savage**, p. 49, viewed "unexpanded disks, no toe webs, and no tarsal fold " as derived states for the *rhodopis* Series). The absence of a tarsal fold in frogs of the *rhodopis* Series may be derived but the ontogenetic transformation documented in *E. lineatus* by **Savage** (1987:33) and my own experience with *E. raniformis* and *E. rugulosus* would suggest that the presence of the fold is a derived condition.

Using an objective out-group approach would result in most of the external characteristics being viewed as equivocal in terms of polarization. Even an in-group approach results in more ambiguity than **Savage** (1987) admits.

The skulls of *E. gollmeri, E. laticeps, E. noblei,* and *E. rostralis* are very similar in having large nasals in anteromedial contact and which approach (or touch) the anterolateral processes of the frontoparietals (Fig. 6C). The anterior border of the frontoparietals is concave and the frontoparietals are broader anteriorly than posteriorly. The otic shelf is broad and overlaps the lateral portion of the crista parotica. The zygomatic ramus of the squamosal is pointed and about the same length as the otic ramus. The vomers are large, well separated, and bear large triangular odontophores. The cultriform process of the parasphenoid is long and slender, extending between the neopalatines (Fig. 7C) and contacting (or approaching, *E. noblei*) the dentigerous process of the vomer.

In *E. lineatus,* the nasals are somewhat smaller and do not approach the frontoparietals. The cultriform process

is shorter (reaching the posterior level of the neopalatines). In *E. daryi* and *E. greggi,* the nasals are smaller still and in only tenuous median contact. The anterior edge of the frontoparietals is either transverse (*E. daryi*) or difficult to classify (*E. greggi,* Fig. 6D). The frontoparietals have parallel lateral edges. The otic shelf is narrow and the otic ramus is slightly longer than the zygomatic ramus. The vomers are smaller bones having more modest and narrower odontophores. The cultriform process is short (not reaching the level of the neopalatines).

The osteological heterogeneity of the *gollmeri* group (*lineatus* as contrasted with *gollmeri, laticeps, noblei,* and *rostralis*) constrasts with the external homogeneity emphasized by **Savage** (1987) and is extended by the inclusion of *E. daryi* and *E. greggi.* However, **Savage** (1987) argued that the *gollmeri* group included a northern and a southern subgroup (I agree with the geographical description but find the biogeographic narrative uninformative) eventhough such a division is not compatible with his cladogram. Most of the osteological features mentioned here are too poorly understood to argue polarities but the distribution of states appears to be consistent with a very different cladogram for the *gollmeri* group. As mentioned above, Savage's cladogram is contingent upon his correct identification of the *fitzingeri* group as the ancestor of the *gollmeri* group but that identification is independent of any evidence.

On the strength of my identification of a vertebral fusion as a synapomorphy, I here transfer *E. daryi* Ford & Savage and *E. greggi* Bumzahem to the *Eleutherodactylus gollmeri* group. Nothing is gained by preserving the *Eleutherodactylus omiltemanus* group for a single species when it is so similar to some frogs of the *rhodopis* Series (see Discussion). It is here assigned to the *rhodopis* Series eventhough there are no unequivocal synapomorphies for that group. Like other species of the *rhodopis* group, *E. omiltemanus* has narrow digits, lacks an inner tarsal fold, and lacks toe webbing (derived features, *fide* **Savage**, 1987:49) but these features are not sufficient to assert that the *rhodopis* Series, with or without *E. omiltemanus,* is monophyletic.

Discussion

With the elimination of the *omiltemanus* group, five species of broad-head animals (*biporcatus* and *bufoniformis* groups), 63 species of the *fitzingeri* series (*alfredi, anomalus, fitzingeri, gollmeri, milesi,* and *rugulosus* groups), three species of the *augusti* group, thirteen species of the *rhodopis* Series, and the enigmatic

E. uno are recognized in the subgenus *Craugastor* (not including the two Bolivian species identified by **De La Riva & Lynch**, 1997). Although **Savage** (1987) arranged these into three or four Series, the only evidence he offered for the proposal was that the *rhodopis* Series has a derived karyotype (assuming that the polarity is established).

Because I have been working on South American *Eleutherodactylus* for most of the past twenty years, when I returned to examine this particular problem, I was struck by an apparent character widely evident among species of *Craugastor* — the strong sexual dimorphism in tympanum size (Fig. 5). The dimorphism in *E. omiltemanus* is especially distinctive but most *Craugastor* exhibit a dimorphism where the tympanum of the male is about twice the size of that of the female. Although the tympanum is "concealed" (absent in the terminology of **Lynch & Duellman**, 1997) in some species (e.g., the *milesi* group), the strong dimorphism is evident upon dissection. Such strong dimorphism is unknown in the Antillean or South American *Eleutherodactylus* and is not uniform within *Craugastor.*

Outgroup comparison reveals that the strong sexual dimorphism in tympanum size is confined to *Craugastor* whereas the absence of dimorphism occurs in some *Craugastor* as well as in other subgroups of the genus *Eleutherodactylus* and is taken here as a synapomorphy. The systematic result is to cleave the *augusti* group (removing *occidentalis* from it), the *fitzingeri* group (removing *andi, bocourti, cuaquero,* and *emcelae* from it), and the *rugulosus* group (removing *anatipes, anomalus, cheiroplethus,* and *zygodactylus* from it). Strong dimorphism in tympanum size diagnoses a unit composed of 59 species including three from the *biporcatus* "Series", 43 from the *fitzingeri* "Series", 12 from the *rhodopis* "Series", and *E. occidentalis. Eleutherodactylus uno* is known only from females but it is assigned here as well.

The resulting cladogram (Fig. 9) does not recommend recognition of Series at this juncture, certainly not the series mentioned by **Savage** (1987). Because only three (*alfredi, biporcatus,* and *gollmeri*) of the species groups is presently diagnosable on outgroup grounds, treating *biporcatus* and *rhodopis* as separate series from the remaining groups emerging from a common node in the cladogram and grouping the remaining lineages as a series overstates the database (Fig. 1D *versus* Fig. 9).

Based on the available evidence, it seems most appropriate to recognize eleven species groups for the nearly Middle American clade *Craugastor.* The contents are

changed for the *alfredi* (adding *E. bocourti*), *augusti* (removing *E. occidentalis*), *fitzingeri* (removing *E. bocourti* and the *E. andi* group), *gollmeri* (adding *E. daryi* and *E. greggi*), *rhodopis* (adding *E. occidentalis* and *E. omiltemanus*). A new species group is proposed for three species previously placed in the *fitzingeri* group but lacking the synapomorphy (pronounced sexual dimorphism in tympanum size) of most *Craugastor.* Lastly, the *E. omiltemanus* group disappears because all of its members are assigned elsewhere (*gollmeri* and *rhodopis* groups). The eleven species groups (and their contents) are: ALFREDI (*alfredi, bocourti, decoratus, glaucus, guerreroensis, megalotympanum, polymniae, silvicola, spatulatus, stuarti, taylori, xucanebi, yucatanensis*), ANDI (*andi, cuaquero, emcelae*), ANOMALUS (*anatipes, anomalus, cheiroplethus, zygodactylus*), AUGUSTI (*augusti, tarahumarensis*), BIPORCATUS (*aphanus, biporcatus, maussi*), BUFONIFORMIS (*bufoniformis, necerus*), FITZINGERI (*crassidigitus, fitzingeri, longirostris, melanostictus, monnichorum, raniformis, rayo, talamancae*), GOLLMERI (*chac, daryi, gollmeri, greggi, laticeps, lineatus, mimus, noblei, rostralis*), MILESI (*adamastus, chrysozetetes, cruzi, epochthidius, fecundus, matudai, milesi, omoaensis, saltuarius, stadelmani, trachydermus*), RHODOPIS (*bransfordii, hobartsmithi, jota, lauraster, loki, mexicanus, occidentalis, omiltemanus, podiciferus, pygmaeus, rhodopis, sartori, stejnegerianus*), RUGULOSUS (*anciano, angelicus, aurilegulus, azueroensis, berkenbuschii, brocchi, escoces, fleischmanni, merendonensis, pozo, psephosypharus, punctariolus, rugulosus, taurus, vocalis*), and NOT ASSIGNED (*uno*). I must add that these represent phenetic groups, lacking synapomorphies, except in the cases of the *alfredi, biporcatus,* and *gollmeri* groups.

Within the *rhodopis* group, six species have conical or projecting subarticular tubercles (*E. bransfordii, E. lauraster, E. loki, E. omiltemanus, E. rhodopis,* and *E. stejnegerianus*). The other species have rounded tubercles (Fig. 2). Within the *rhodopis* group, males of only three species have nuptial pads (*E. bransfordii, E. loki,* and *E. rhodopis*). Vocal slits are found in only *E. podiciferus* but *E. jota* probably has vocal slits as well (males are not known). Occasional males of *E. bransfordii* from Panama also have vocal slits. Phenetically, *E. loki* and *E. rhodopis* seem most closely allied to *E. bransfordii, E. lauraster,* and *E. stejnegerianus. Eleutherodactylus podiciferus* and *E. jota* are probably sister species (each has the first toe shortened) and these seven species may form a subgroup within the *rhodopis* group but this claim is not yet supported by evidence. The remaining species (Mexican) form a second phenetic subgroup. All have black mesorchia whereas all other species of the group
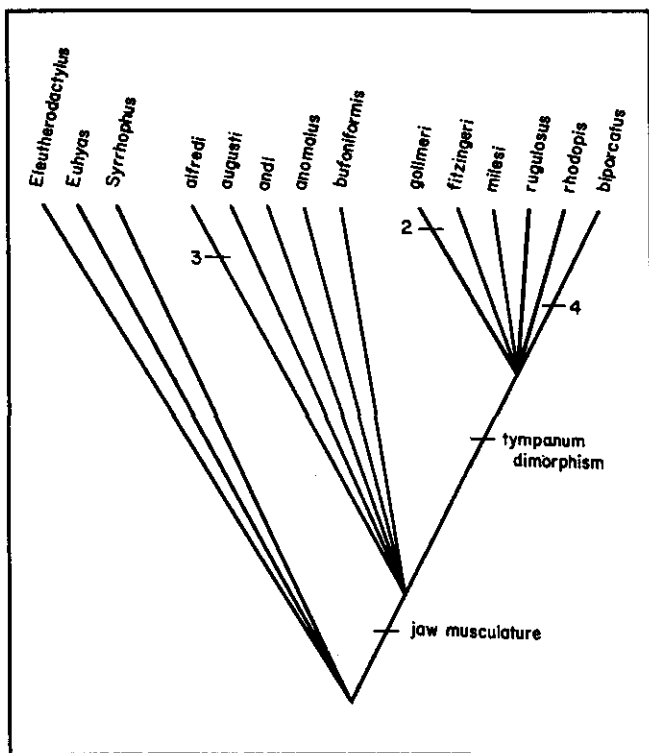
Figure 9. The hypothesis of relationships among Mesoamerican *Craugastor* most consistent with available evidence. Some synapomorphies are numbered: (2) sacral fusion, (3) fifth toe longer than third, (4) massive crests borne on lateral edges of frontoparietals.

have colorless ("white ") mesorchia. The vomerine dentitions (absent in *E. hobartsmithi* and *E. pygmaeus,* small, reduced odontophores in *E. mexicanus* and *E. sartori*) may provide an additional synapomorphy linking these taxa.

All of this labor was directed towards resolving the relationships among a handful of Guatemalan and Mexican frogs. The relationships among the taxa of the particular ensemble that is the subject of this paper are only partially resolved (Fig. 10). To this ensemble, I also assign *E. occidentalis* in light of the cladistic cleaving of the *augusti* group. As mentioned above, no characters are available to support the hypothesis that the *rhodopis* Series (or group) is monophyletic and the six putative synapomorphies depicted on the cladogram are of various qualities. Conical subarticular tubercles link seven of the thirteen species but such tubercles occur as well in the *gollmeri* group and in the *augusti* group of *Craugastor,* suggesting some confusion about homologies. Four species are linked by the possession of a black mesorchium but some males of *E. omiltemanus* have pigmented (lightly) mesentaries over the testes. In addition, black mesorchia appear repeatedly

among *Eleutherodactylus* and are surely not uniquely evolved. Two species are linked by postulated losses (of the outer palmar tubercle and the vomerine teeth). Such loss characters are at best weak evidence of relationship and are paralleled repeatedly elsewhere in *Eleutherodactylus.* The short first toe of *E. jota* and *E. podiciferus* appears to be a secure synapomorphy but links only two of thirteen taxa. The inner tarsal tubercles of *E. loki* and *E. rhodopis* are distinctive within *Craugastor* but such tubercles are relatively common and sporadic features elsewhere in the genus.

The resulting polytomous cladogram is suggestive of two possibilities – (1) I lack sufficient competence to analyze the relationships among these frogs or (2) the *rhodopis* group is a non-monophyletic assemblage of taxa. It may well be that the *gollmeri* group (monophyletic) is more closely related to some or all of the seven species of the *rhodopis* group having conical subarticular tubercles than to any other subset of *Craugastor.* If so, **Savage's** (1987) cladogram would take on a very different form as nearly every character reversed its polarity.
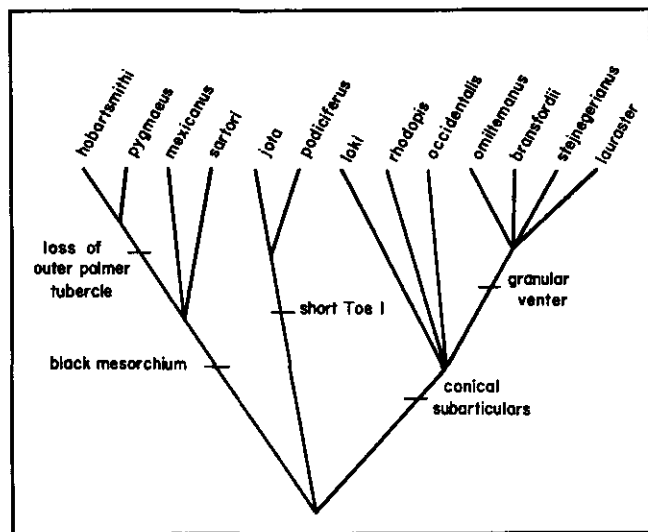
Figure 10. Hypothesis of relationships among the species of the *Eleutherodactylus rhodopis* group.

maturing of my views. In a much-modified way, this paper represents partial publication of my Masters' Thesis, completed under the direction of H. M. Smith (but about which, I have worried for a quarter-century). I must also acknowledge my colleague, Jay M. Savage, with whom I have differed for so many years – his criticisms, seldom accepted, but always appreciated, were fundamental in shaping my views – *¡Jota, muchissimas gracias!*

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A special thanks to several curators (Jonathan Campbell, William E. Duellman, Arnold G. Kluge, and Hobart M. Smith) who permitted me to prepare often-rare animals as cleared and stained skeletons as well as to make liberal dissections of materials under their care and to several collection managers (José Rosado, Greg Schneider, especially John Simmons, and Jens Vindum) who always responded promptly to yet another inquiry.

Lastly, in large measure, the delays in bringing this manuscript to print can be attributed to my romance with the Colombian frog fauna. Every time I came close to finishing the manuscript, another Colombian collection could always distract me. I thank Bob Powell for his badgering, which finally succeeded.

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APPENDIX I (Specimens examined)

This study has stretched across 35 years and I have taken data on many occasions during the interval. Given the long duration of data collection and the interruptions that occurred, I am sure that my lists of specimens examined are incomplete for many species. I made extensive use of the collection at UIMNH (1963-1965), KU (1965-1969, and as Visiting Curator in 1984 when many pertinent data were acquired), and UMMZ (as Visiting Curator in 1976 when many of my impressions about Mexican *Eleutherodactylus* were changed by seeing critical material for the first time).

In the following lists, the materials of *E. loki* and *E. rhodopis* are organized into the population systems identified in Figure 4 and table 1 with other localities appended. Only locality records (not museum numbers) are provided for *E. mexicanus*.

Eleutherodactylus chac. Dissections (KU 55921, 55924, 186245).

Eleutherodactylus daryi. Dissection (UTA), CS (UTA 6181).

Eleutherodactylus gollmeri. Dissections (KU 33129, 41035, 79962, 79964, 79968, 108595-99; subsequently, all the above less 33129 and 41035 were prepared as doubly stained skeletons). Cleared and stained skeletons (previous list plus KU 79961, 108582). Dry skeletons (KU 41036-37).

Eleutherodactylus greggi. Dissection (UMMZ 88007), CS (UMMZ 88007).

Eleutherodactylus laticeps. Dissections (KU 66024-26, 156334, 189846, 189862, 209039). CS head (KU 189846).

Eleutherodactylus lineatus. Dissections (KU 103132-33, 186176, 189651-52, 189656). CS (KU 189678).

Eleutherodactylus loki.

Population system 4B. Veracruz: 2 mi SW Huatusco, 4300´, UMMZ 117045(2).

Population system 5. Veracruz: Las Tuxtlas, Coyame, 1500´, UMMZ 11479(3); 0.5 mi N Coyame, Lago Catamaco, 1600´, MZFC 4726, UMMZ 115483; 1 mi N Coyame, UMMZ 111482; 1 mi E Coyame, 1500-1900´, UMMZ 111480-81; 1 mi NW Coyame, 1700´, UMMZ 111483; San Andres Tuxtla, Ebitrolotu, MZFC 1195, 1198-99, 1229-34, 4686, Jicacal, MZFC 1492, Alrededores Hotel Playa Azul, MZFC 1494; 8 km N San Andres Tuxtla, UMMZ 128336; 4 mi S San Andres Tuxtla, at Rio Bravo, UMMZ 113832-33; Sontecompan, UMMZ 128335; S slope Volcán San Martín, 2800-3800´, KU 58632-72, UMMZ 115479-82 (87), 118191-92, 1005-1500 m, UMMZ 128337-44, 4000´, UMMZ 122088-89; 2.4 mi NNW Tapalapan, Rio Tecolapán, 900´, UMMZ 115489.

Population system 6. Oaxaca: Mcpio. San José Tenango, MZFC (7). Mcpio. San Juan de la Lana, Jalahui, 200 m, MZFC 6641; 3 mi N Sarabia, Rio Sarabia, 250´, UMMZ 115492; 0.5 mi S Tolosita, 250´, UMMZ 115491; Tuxtepec, UMMZ 122091. Mpio. Valle Nacional: Km. 51, carr. Tuxtepec-Oaxaca, MZFC 4553(5); San Mateo Yetla, MZFC 4561; 5.2 mi S Valle Nacional, 1100´, UMMZ 115490; 2 km W Valle Nacional, MZFC 4545.

Population system 7. Oaxaca: Mcpio. Santiago Comaltepec, La Esperanza, MZFC 4558(7), 4562, 4570, 4587, 7309(3); La Quebradora, Km. 71.7, MZFC 4567; Metates, Km 65, MZFC 4549; Vista Hermosa, 1500 m, UMMZ 119615(14), 1500-1600 m, KU 58673, 58680-82, 58684, 65987-88, 71086, 71088-89, 86795-96, 86802, 86804-09, 86811, 86813.

Population system 8. Oaxaca: Chalchijapa, 105 km W Matias Romero, MZFC (135).

Population system 9. Chiapas: Juárez, 7 km E Estación Juárez, MZFC 2102-05, 4400-02; 4.5 km S Pichucalco, KU 93996-97. Tabasco: Teapa, UMMZ 113834(5); 4.5 mi N Teapa, UMMZ 119242; 1 mi E Teapa, UMMZ 119907(8); 8.4 mi W Teapa, UMMZ 120275(5).

Population system 10. Chiapas: 12 km NW Berriozabal, MZFC 4137; Ozocozuautla: Km 21.5 de Ozocozuautla, MZFC 1239; Parque Reserva, Laguna Bélgica, MZFC 1122, 1150-53.

Population system 13. Chiapas: Acapetagua, La Concepción, MZFC 1158-60; Cruz da Piedra, 2 km W Acocoyagua, UMMZ 87962, 88263(10); 6 km NE Escuintla, UMMZ 87925-30, 87932-35, 87936(6), 87937-51, 87964, 88263, 88279(3), 88325; 30 km NE Escuintla, UMMZ 87952-61, 88224; Mt. Ovando, UMMZ 87967, 87984-89.

Population system 14. Chiapas: 1 mi SE Puerto Madero, KU 41962; 7 mi ENE Tapachula, KU 41926-61

Population system 15A. Chiapas: San Geronimo, 760 m, MVZ (101).

Population system 15B. Chiapas: Colonia Talquian, 1650 m, MVZ (1); Finca Monte Perla, 960 m, MVZ (3); Upper Unión Juárez, 1300 m, MVZ (1).

Population system 16. GUATEMALA, Depto. Retalhuhen: Hac. Casa Blanca, UMMZ 107778-79. Depto. San Marcos: KU 58628-31. Finca La Paz, 1025-1660 m, UMMZ 98271(2), 98272, 98273(4), 98274(2), 98275, 107780(7), 107781(3), 107782, 107783(8), 107784(9), 107785(2), 107786(2), 109675.

Population system 17. GUATEMALA, Depto. Chimaltenango: 1-2 km SE Yepocapa, 1500 m, UMMZ 107775(3), 7 km S Yepocapa, 1350 m, UMMZ 107774. Depto. Solola: Finca Santo Thomas, 200-400 m, UMMZ 107762(2), 107763

Population system 18. GUATEMALA, Depto. Jutiapa: Finca La Trinidad, UMMZ 107776-77. Depto. Santa Rosa: Finca La Gloria, 450-1160 m, UMMZ 107764-69, 107770(2), 107771(2), 107772, 107773(3).

Population system 19. EL SALVADOR. San Salvador: 2.4 km SE Ilopango, KU 184415.

Other records: Chiapas: 6.5 km SW Palenque, MZFC 4185. Tonolá: Juárez, MZFC 1285, 1287. Oaxaca: Mpio. San Juan de Lalana: 2-4 km NW Jalahui, MZFC 5855(9), 5856(3), 5859, 1.5 km SW Jalahui, MZFC 5857. Puebla: Cuetzalán, Sima de Cruz Verde, KU 191896-97; 5 km SW Cuetzalán, Grutas de Atepolihuit, KU 173101. San Luis Postosi: Hoya de las Guaguas, KU 193270. Tabasco: La Venta, USNM 117556. Veracruz: Jesus Carranza, KU 24327-28; Sierra Santa Martha, Arroyo Chivo, Rancho La Ceiba, 530 m, MZFC 7387. Veracruz, 9 mi SW Fortín, UMMZ 95127; Jalapa, 3 km sobre la carretera a Naolinco, MZFC 1226-28. GUATEMALA, Piedras Negras, UIMNH 14585-653; Santa Cruz, 6 mi E Yaxha, UMMZ 75378. Dept. Santa Rosa, Finca Santa Isabel, 13 km SW Pueblo Nuevo Vinas, 3500´, UMMZ 107082.

Eleutherodactylus mexicanus.—All MEXICO. Guerrero: Atoyac de Alvarez, El Iris; Chilpancingo, vic. Omiltemi; between Puerto Chico and Asoleadero, 2550-2600 m; Tlacuapa, al NE de Tlacuapa. Hidalgo: Cerro de Tutotepec, 1660 m; Metepec, Aserradero Apulco, carr. a Huayacocotla; Metzquititlan, Carpinteros, camino a La Mojonera; Tenango de Doria, El Potrero, 1500-2100 m, 3.5 km N Palo Gacho, ca 2000 m, Temapa, 3 km SW Tenango de Doria, 4 km SW Tenango de Doria; 32 km E Tulancingo, 2250 m; Zacualtipan, La Mojonera, 2000 m.

Oaxaca: Cerro Machin; Cerro Madrena Lachivia, 2100 m; Cerro de Oro (cerca Tuxtepec); Cerro Peña La Troje, ca. 10 km SW El Tejocote; Cerro San Felipe;10 mi S Juchatengo, 5350´;Peña Verde (30 km W San Juan Bautista Cuicatlan); Puerto Soledad, 20 km W Teotitlan del Camino; Putla de Guerrero, Llano de Guadalupe, Reyez Llano Grande, Peñas Negras; San Agustin Loxicha, a Soledad Buenavista, carr. Oaxaca-Pochutla, El Soledad, Km 178 carr. Oaxaca-Pochutla, km 3 al Jalateco, Tierra Blanca; 30 and 33 km N San Gabriel Mixtepec, 1530-1675 m; San Juan Bautista Atatlahuca, 2015-2100 m; Santiago Comaltepec, Brecha, 8.1 and 11.4 km NE cima de Cerro Pelón, Metates, desviación a San Isidro, 2010 m, San Isidro Yolox, Km. 88 and Km 104 carretera Tuxtepec a Oaxaca, Vista Hermosa and 4.2 km S; Santo Tomas Teipam; Sierra de Juárez, Llano de las Flores. Puebla: Honey, 2000 m; Huachinango; 3 km W Huachinango, 1970 m; Lago Tejocotal, 11 km E Acaxochitlán, 2250 m; Veracruz: 6 km SSE Altotonga; Huayococotla, ejido El Lechales; 3 km E Las Vigas.

Eleutherodactylus mimus. Dissections (KU 37126-27, 157736).

Eleutherodactylus noblei. Dissections (KU 28172, 34115, 34118-19), CS (KU 30877, 36947, 108575).

Eleutherodactylus omiltemanus.— Guerrero: 8 km SW Chilpancingo, 1818 m, TCWC 10093; 6.4 km W Mazatlan, 2242-2485 m, TCWC 10092, 10095; Omiltemi, 2040 m, CNMH 104673, 124677-85, 173681, KU 129160, UIMNH 15836, 15838-41, USNM 116481; Omiltemi, camino al Cedral, MZFC 2982; Omiltemi, trail to La Joya, Omiltemi State Park, 2200-2500 m, MZFC 2988, 4422, USNM 304807; 2 km N Omiltemi, cañada de La Perra, MZFC 2984; 2.6 km N Omiltemi, camino a Trincherillas, MZFC 4427; 2.6 km NE Omiltemi, cañada de Potrerillos, MZFC 2980, 2986-87, 2989, 4428; 0.3 km E Omiltemi, MZFC 2981; 1 km S Omiltemi, camino a Agua Fria, MZFC 2979, 2983, 2985; 1.6 km W Omiltemi, 2424 m, TCWC 10091.

Eleutherodactylus rhodopis.

Population system 1. Hidalgo: Tenango de Doria, Colonia 5 de mayo, 1460-2100 m, MZFC 7662-63; near Tenango de Doria, 6000´, UMMZ 95239; El Potrero, 3 km S Tenango de de Doria, MZFC 6116-17, 7665, 7672, 7686; 10 km delante de Tlalchinol, MZFC 1510. Puebla: Huachinango, UMMZ 69518; 3 km W Huachinango, 1970 m, KU 54070, 54072-73, 54075-76, 54079, 54100-01; 5.7 mi SW Huachinango, UMMZ 121584(3).

Population system 2. Veracruz: Banderilla, 5300´, UMMZ 115484(30); 15 mi N Jalapa, UMMZ 89410(6); 3

mi W Jalapa, Cerro de Los Estropajos, UMMZ 105386; 7 mi above (= W?) Jalapa, 5000´, UMMZ 89399(2), 89400(3), 89401(8), 89402(3), 89403(3), 89404(9), 89405, 89406(7), 89407(7), 89458(4), 90316; 7.2 mi W Jalapa, 5000´, UMMZ 99511-12.

Population system 3. Veracruz: above Acultzingo, UMMZ 89409(76), 90317(4), 90318(2), 90319.

Population system 4 A. Veracruz: Coscomatepec, 5000´, KU 26805; Huatusco, 5000´, KU 26081-82, 26093-95, 26792, 26795, 27077, 126079; 2 mi S Huatusco, 1330 m, UMMZ 119613(13); 2 mi SW Huatusco, 4300´, UMMZ 118193(6); 3 km SW Huatusco, 1325 m, KU 54102-03; 2.2 mi SW Huatusco, 4300´, UMMZ 119243; 4.7 mi SW Huatusco, UMMZ 119909; 10 mi S Jalapa, road to Xico, UMMZ 122090.

Population system 10. Chiapas: Tuxtla Gutierrez, 1800´, UMMZ 115495(4), Cerro Hueco, El Zapotal, MZFC 1515.

Population system 12. Chiapas: 5.1 mi SW Cintalapa, 2200´, UMMZ 115496; 20.8 km SW Las Cruces, KU 41963. Oaxaca: Sierra Madre, 16 km N Jicaro a colonia Rudolfo Figueroa, cerca Cerro Baul, 1577 m, MZFC 7249; Zanatepec, aprox. 7 km N Zanatepec, MZFC 6558(3)

Other records: Veracruz, 2 km N Paraje Nuevo, KU 24425, 26096-98.

Eleutherodactylus rostralis. Dissections (KU 209110-11, 209113), CS (KU 209112).

Eleutherodactylus sartori.— All from Chiapas, Mexico. Municipio La Concordia, Predio Bélgica and Reserva El Triunfo, 1680 m, MZFC 7897, 7899-7900, 7902. Municipio Villaflores, La Sepultura, Ejido Tres Picos, 1380 m, MZFC 7896, 7898, 7901. Depto. Libertad: San Bartolome, Monte Cristo, UMMZ 135348, 135479; Depto. Soconusco: vicinity Escuintla, UMMZ 117037, 133272; La Esperanza (vicinity of Escuintla), USNM 115701; Cerro Ovando, 1200 m, UMMZ 87968, 1200-1400 m, UMMZ 87992-93, 1600 m, UMMZ 87970-81, 88221 (5), 1700 m, UMMZ 88367, 1800 m, UMMZ 87996-06 (88000 cleared and doubly stained skeleton), 88368 (6), 1818 m, USNM 115507 (holotype), 1900 m, UMMZ 88366 (3, one cleared and doubly stained skeleton), Las Nubes (Cerro Ovando), USNM 115702. Cerro Tres Picos, 2182 m, CAS 170008-12, 170014-15, 170040, 170045, 170049-50, 170052-53, 170055-56, 170058, 170060, 170062-65, 170067.