FOUR OSTEOLOGICAL SYNAPOMORPHIES WITHIN *ELEUTHERODACTYLUS* (AMPHIBIA: LEPTODACTYLIDAE) AND THEIR BEARING ON SUBGENERIC CLASSIFICATIONS

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Resumen

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Con base en el estudio de los cráneos de 307 especies del género *Eleutherodactylus* y que representan todas las entidades subgenéricas, fueron evaluados cuatro caracteres en relación con la clasificación actual. Tres de tales caracteres ya eran conocidos; el cuarto fue nuevo. *Craugastor* y las *Eleutherodactylus conspicillatus, myersi,* y *sulcatus* son series plesiomorficas para cada carácter. Orejas epioticas se encuentran únicamente en 14 especies de las Antillas y su distribución taxonómica sugiere que ni *Euhyas* ni *Pelorius* son monofiléticos. La fusión del frontoparietal y proótico aparece en 60 especies cuya distribución taxonómica sugiere que ni *Eleutherodactylus* ni *Euhyas* son monofiléticos. Aunque hay problemas de homología, la fusión parece restringida a la serie de *Eleutherodactylus abbotti* y al grupo de *Eleutherodactylus martinicensis, Euhyas,* y *Syrrhophus.* Sin embargo, algunas especies de *Euhyas* muestran la condición plesiomorfica. La separación ancha de los vómeres es un carácter en general congruente con la fusión frontoparietal-proótico, pero está restringida al grupo de *abbotti-martinicensis-Euhyas-Syrrhophus.* El análisis de este carácter sugiere que la longitud de la serie de dientes del vomer necesita un estudio muy cuidadoso para separar condiciones no homologas y para considerar el subgénero *Euhyas* como monofilético. La muesca medial del vomer, un carácter nuevo, es compartida únicamente por la serie de *Eleutherodactylus binotatus* y por la mayoría de *Euhyas.* Sin embargo, los dos clados adquieren la muesca de manera diferente.

Palabras clave. Cráneos, *Eleutherodactylus,* ranas, sistemática

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Abstract

Based upon study of the skulls of 307 species of *Eleutherodactylus* representing all identified subunits, four characters are examined relative to the current classification. Three of these were identified previously but the fourth is a new one. *Craugastor* and the *Eleutherodactylus conspicillatus, myersi,* and *sulcatus* series are plesiomorphic for each character. Epiotic flanges are restricted to 14 Antillean species and the distribution suggests that neither *Euhyas* nor *Pelorius* is monophyletic. Fusion of the frontoparietal and prootic is reported for 60 species and the distribution suggests that neither *Eleutherodactylus* nor *Euhyas* is monophyletic. Although there are some problems with homology, the fusion appears restricted to the *Eleutherodactylus abbotti* series, the *Eleutherodactylus martinicensis* group, *Euhyas,* and *Syrrhophus.* However, some *Euhyas* exhibit the plesiomorphic condition. The wide separation of the vomers is a character largely congruent with frontoparietal-prootic fusion but is restricted to the *abbotti-martinicensis, Euhyas* and *Syrhhophus* unit. Restudy of this character suggests that vomerine tooth series length is in need of careful study to separate nonhomologous states and that *Euhyas* may be monophyletic. A new character, median notch of the vomer, is shared only by the *Eleutherodactylus binotatus* series and most *Euhyas* but the two clades acquire the notch in two different ways.

Key words: Frogs, *Eleutherodactylus*, skulls, systematics

Introduction

The genus *Eleutherodactylus* consists of, at present (**Lynch & Duellman**, 1997, and recent descriptions) no fewer than 600 species distributed from the southern United States through the Antilles and Middle America to northern Argentina with notably high species densities in northwestern South America (Colombia and Ecuador) and the island of Hispaniola. One-third of the species are known from Colombia.

Few authors (**Hedges**, 1989; **Lynch**, 1971, 1976, 1986, 1993; **Lynch & Duellman**, 1997; **Savage**, 1987) have attempted to view the genus as a whole and to search for general patterns. For most of the past 20 yr, I have focused on species-level cladograms, largely in Colombia and Ecuador, the area of greatest species diversity. The *status quo* consists of the proposals of **Hedges** (1989) and **Lynch & Duellman** (1997) wherein five subgenera are recognized: the nearly Middle American *Craugastor* (now about 100 species), the Antillean and South American *Eleutherodactylus* (now about 400 species), the Antillean *Euhyas* (about 85 species), the Hispaniolan *Pelorius* (six species), and the nearly Mexican *Syrrhophus* (24 species).

Lynch & Duellman (1997) divided the subgenus *Eleutherodactylus* into six series: the *abbotti* series (13 species, West Indies), the *binotatus* series (25 species, coastal forests of Brasil), the *conspicillatus* series (about 100 species, northern and western South America), the *martinicensis* series (about 200 species, Antilles and northern and western South America), the *myersi* series (nine species, northwestern South America), and the *sulcatus* series (eight species, western South America) but deferred assigning subgeneric names.

When I was much younger (**Lynch**, 1971), I proposed dividing *Eleutherodactylus* into two divisions whose contents (updated to present taxonomy) are as follows: ALPHA (Antillean *Eleutherodactylus abbotti* and *martinicensis* series, *Euhyas, Pelorius,* and *Syrrhophus* plus "some" Andean *Eleutherodactylus*) and BETA (*Craugastor, Eleutherodactylus binotatus, conspicillatus,* mainland *martinicensis,* and *sulcatus* series). During the past 17 yr, I have been gathering osteological on the genus in an attempt to identify clades and to test the several proposals available. In 1983, I began a systematic survey of skeletons of *Eleutherodactylus* and now have studied those of about one-half (307) of the species of the genus. In the present paper, I intend to explore four potential synapomorphies – (1) the epiotic flange mentioned by **Lynch** (1996), (2) the fusion of the frontoparietal and prootic mentioned by **Lynch** (1971), (3) wide separation of the vomers, mentioned by **Lynch** (1971), and (4) a median notch of the vomer, not mentioned to date. In each case, strict outgroup comparison (**Lynch**, 1997) reveals that the cited feature is derived.

The minimum number of supraspecific taxa of immediate concern is eleven: *Craugastor* (**Lynch**, 1986, proposed one synapomorphy), *Euhyas* (no synapomorphy, as crafted by **Lynch & Duellman**, 1997, supported by a plesiomorphy), *Pelorius* (no synapomorphy, see **Lynch**, 1996), *Syrrhophus* (no synapomorphy but distinctive among Middle American *Eleutherodactylus* owing to frontoparietal-prootic fusion and the absence of vomerine teeth), and at least seven presumed clades now submerged in the subgenus *Eleutherodactylus*) – the *abbotti* series, the *binotatus* series (each exhibiting an ungual notch [**Lynch**, 1976], not to be confused with emargination of the disks as implied by **Savage** [1987]), the *conspicillatus* series, the Antillean *martinicensis* series (about 40 species, Antilles, sharing a synapomorphy of toes lengths with the mainland species, *fide* **Lynch & Duellman**, 1997), the mainland *martinicensis* series (more than 200 species, Nicaragua to Bolivia and the mouth of the Amazon), the *myersi* series, and the *sulcatus* series.

Materials & Methods

Skulls or singly or doubly cleared and stained skeletons were prepared for between one and 30 specimens of more than 280 species of frogs and I examined skeletons of some 20 additional species prepared by other investigators (see Appendix 1) representing approximately half of the current diversity of *Eleutherodactylus*.

THE EPIOTIC FLANGE

The derived condition (illustrated by **Lynch**, 1996) has been found in only 14 Antillean species of the 307 species sampled. **Lynch** (1996) cited this feature as potentially uniting the *inoptatus* group of *Pelorius* and *Euhyas* but deferred generating an explicit hypothesis because too few *Euhyas* had been studied (but cited **Flores**, 1984, for data on Jamaican species). I have now examined 41 species of *Euhyas* and the feature is evident in ten (*brevirostris, dimidiatus, glandulifer, jugans, leoncei, nubicola, richmondi, symingtoni, ventrilineatus,* and *zeus*) as well as in the three species of the *inoptatus* group of *Pelorius*. Of greater curiosity is the observation that the feature also occurs in *E. bakeri*, a species **Lynch & Duellman** (1997) assigned to the *martinicensis* group but that **Hedges** (1989) considered a *Euhyas*.

The character suggests that neither *Euhyas* nor *Pelorius* is monophyletic. Within *Euhyas*, the *nubicola* and *ricordii* groups are cleaved by the character but both species of the *symingtoni* group exhibit the feature. The species of *Euhyas* exhibiting the character represent an odd assortment of species.

FRONTOPARIETAL-PROOTIC FUSION

The dataset for frontoparietal-prootic fusion consists of **Lynch** (1971) reporting fusion in 32 West Indian species and nine Mexican species, **Flores** (1984) reporting data for 21 Antillean species, 14 with fusion (nine species also examined by Lynch but they disagree on *furcyensis* and *orcutti*), **Joglar** (1989) reporting fusion in 56 Antillean species and seven Mexican species (his reports differ from **Lynch**, 1971, for six species because he denies fusion in *atkinsi, auriculatoides, coqui, jugans, limbatus,* and *ricordii*; they differ from Flores for three species but agreeing with Lynch for *furcyensis* and *orcutti*) and **Lynch** (1996) reporting non-fusion for all six species of *Pelorius*.

My studies (1983-1999) result in data for 307 species wherein I found fusion in 13 Mexican species, 39 Antillean species, and eight South American species. Joglar and I disagree for one *Syrrhophus* (*teretistes*), ten *Euhyas* (*atkinsi, brevirostris, dimidiatus, glandulifer, jugans, limbatus, pinarensis, ricordii, schmidti,* and *ventrilineatus*) and for two *Eleutherodactylus* (*auriculatoides* and *coqui*) – in each case I see the fusion and he denies it.

I re-examined some of the specimens studied by **Joglar** (1989) because I was concerned that we might be scoring specimens differently (he treated the character as frontoparietal-otoccipital fusion). In the cases of *atkinsi, auriculatoides, coqui, dimidiatus, jugans, pinarensis, ricordii, teretistes,* and *ventrilineatus,* he could see a suture between the frontoparietal and exoccipital in each of these taxa and concluded that there was no frontoparietal-prootic fusion. My restudy of these specimens reveals the suture between the frontoparietal and exoccipital but no suture between the frontoparietal and prootic.

Considering all reports (**Lynch**, 1971, 1996, **Flores**, 1984, **Joglar**, 1989, **Wiens & Coloma**, 1992, and here), data are available for 343 species of *Eleutherodactylus* (Table 1). The two Middle American clades (*Craugastor* and *Syrrhophus*) differ in that the latter exhibits the fusion and the former is plesiomorphic. For the South American complement of the genus, only nine taxa (*E. bicumulus, E. danae, E. douglasi, E. gracilis, E. nicefori, E. platydactylus, E. simonbolivari, E. vicarius,* and *E. vidua*) seem to exhibit the fusion (of five species of the *binotatus* series, 69 species of the *conspicillatus* series, 100 species of the mainland *martinicensis* series, five of the *myersi* series, and nine of the *sulcatus* series).

Four clades are recognized here for the West Indies and one is completely sampled (*Pelorius*). *Pelorius* is distinctive in that all six species exhibit the plesiomorphic condition. By way of contrast, four species of the *abbotti* series exhibit the fusion as do 23 of 24 species of the Antillean *martinicensis* series. For *Euhyas*, 43 of 55 species exhibit the fusion. Sampling densities are acceptable (100%, 30%, 63%, and 65% respectively).

The biases are such that I suspect that **Joglar** (1989) erred in reporting that *E. urichi* (*martinicensis* group) lacks fusion and I question my own results to the effect that nine of 188 species from South America exhibit the fusion. There is2 no question that *Euhyas* is polymorphic for this character (the only presumed clade to be so). As constituted here (identical to **Lynch & Duellman**, 1997), *Euhyas* is diagnosed using a plesiomorphic character (toe 5 shorter than toe 3, except in *E. zeus*) and hence very suspect as a clade.

Hedges (1989), and perhaps **Joglar** (1989), argued that frontoparietal-prootic fusion is sufficient to link *Euhyas* + *Syrrhophus*. If so, given my doubts about *E. urichi* and nine South American taxa, the synapomorphy is more powerful than that because it also sweeps up the *E. abbotti* series (West Indies) + the *E. martinicensis* group (West Indies), a slightly modified Alpha Division of the genus. However, no special relationship may be called for between *Euhyas* and *Syrrhophus*, given the available data, as **Hedges** (1989) has done and **Joglar** (1989) has implied because one could argue with equal force for a relationship between the *abbotti* series and either of the above.

There is some reason to be cautious with this character. **Flores** (1984) reported that small juveniles of *E. nubicola* did not exhibit the fusion but that larger individuals did. He also reported that when he prepared skeletons of juvenile *E. cundalli*, all exhibited the fusion. **Flores** (1984) illustrated *E. griphus* and *E. sisyphodemus* as having short sutures evident just medial to the anterior epiotic eminence. His drawings of *E. grabhami* and *E. orcutti* show much more extensive sutures. However, **Joglar** (1989) reports fusion for each of these species and my specimens of *E. orcutti* do not demonstrate sutures. Too few species have been studied using an ontogenetic series but what little data are available suggest that there is an ontogenetic fusion being confused with a non-ontogenetic fusion. At least several *Euhyas* (*greyi, richmondi, sierramaestrae,*[2] *symingtoni,* and *zeus*) exhibit complete sutures along the borders of the frontoparietal such as one sees in *Craugastor, Pelorius,* or mainland *Eleutherodactylus.* For seven species, there are disagreements (among **Flores**, 1984, **Joglar**, 1989, and **Lynch**, 1971 and here) as to whether fusion occurs or not (*furcyensis, glandulifer, glaphycompus, grabhami, orcutti, richmondi,* and *schmidti*). This character suggests that the subgenera *Eleutherodactylus* and *Euhyas* are not monophyletic.

Table 1. Frontoparietal-prootic fusion data for eleven presumed clades of *Eleutherodactylus.*

	Fusion	No fusion
MIDDLE AMERICA		
Craugastor	0	53
Syrrhophus	13	0
ANTILLES		
Euhyas	43	12
Pelorius	0	6
abbotti series	4	0
martinicensis series[3]	23	1
SOUTH AMERICA		
binotatus series	0	5
conspicillatus series	5	64
martinicensis series	4	96
myersi series	0	5
sulcatus series	0	9

VOMER

The vomer of *Eleutherodactylus* exhibits many variations. Heretofore, attention has been paid to four features of the vomer: (1) the width ("length" *aucctorum*) of the vomerine tooth series (many authors), (2) the relationship of the vomerine tooth series, between or posterior, to the choanae (**Lynch**, 1989), (3) the presence of a vomerine tooth series (many authors), and (4) median separation of the vomers (**Lynch**, 1971). In my view, we have not figured out the states of (1). Species such as *E. dimidiatus* (**Lynch**, 1996) are very distinctive for the width of the vomerine tooth series and worlds apart from species such as many *Syrrhophus.* **Joglar** (1989) used little more than long vomerine tooth series to distinguish between his *ricordii* group (core of *Euhyas*) and what he termed the *unistrigatus* group.

There seems to be (to me, at least) few problems as concerns (2) – the *discoidalis* group (**Lynch**, 1989) contains the only species exhibiting the plesiomorphic condition. However, I can't decide what to do with species having "lost" the dentigerous process and teeth (as in several *Syrrhophus*). Species which lack the dentigerous process cannot have a width of their odontophore. Although we can detect the presence of vomerine teeth (using cleared and stained specimens), an odontophore requires some additional structure.

The vomers are paired dermal bones supporting the anterior palate and associated intimately with the choanae.

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[2] That *E. cuneatus* exhibits fusion and *E. sierramaestrae* does not (**Joglar**, 1989, and confirmed here) suggests that **Estrada & Hedges** (1998) erred in treating them as synonyms.

[3] Most of these species were not studied here and represent the reports of **Joglar** (1989) and **Lynch** (1971).

Trueb (1993) recognized four parts. In its most extensive expression in eleutherodactylines, one can recognize a prechoanal ramus, a postchoanal ramus, and anterior ramus, a dentigerous process (bearing or not the odontophore and teeth), and a palatine shelf.

Odontophore shape has been used as a character for hylid frogs (**Duellman**, 1970; **Goin**, 1961) and indirectly for eleutherodactylines (expressed as "length" of the odontophore, in the argot of the specialist, as short, long, very long). Among the five subgenera of *Eleutherodactylus* as currently recognized, the vomerine tooth length data are (for *Euhyas*, data from **Joglar**, 1989):

Craugastor	short (51), absent (2).
Syrrhophus	absent (13)
Pelorius	medium long (6)
Euhyas	absent (1), short, medium long (17), long (19), very long (32)
Eleutherodactylus	short (180), medium long (8)

It has always been assumed (**Hedges**, 1989, **Joglar**, 1989, **Lynch & Duellman**, 1997) that long (or very long) odontophores were derived and that loss of odontophores and teeth was also derived. Using the distal edge of the odontophore relative to the margins of the choana (**Dunn**, 1926, **Schwartz**, 1958) seems clear enough but supposes that all compared species have their odontophores (and choanae) in the same places (and, see below).

For *Craugastor*, the only two species (*E. hobartsmithi, E. pygmaeus*) having lost their odontophores exhibit a long dentigerous process (consistent with a loss argument). The same may be said for *Euhyas* where the only species (*E. limbatus*) lacking odontophores has a long dentigerous ramus (**Lynch**, 1971). In the case of *Syrrhophus*, the situation is more complex. Some species (*E. leprus, E. longipes*) have long dentigerous processes, others have short dentigerous processes (*dixoni, grandis, marnockii, rufescens, teretistes*), and a few have no dentigerous processes (*angustidigitorum, dennisi, nitidus, pipilans, saxatilis*). *Eleutherodactylus* and *Pelorius* do not exhibit vomer reduction.

MEDIAN NOTCH OF THE VOMER

This character has never been mentioned although **Lynch** (1996) illustrated it (while illustrating a different character, the epiotic flange). At the time, I had not examined an adequate sample of *Euhyas* to see the character. It was not noted by **Flores** (1984) because all his taxa exhibited it nor did **Joglar** (1986, 1989) note the feature. I only noted it casually during my survey (1993-1997) of *Euhyas*. The palatine shelf exhibits some interesting variation where the shelf can be detected (absent in *Syrrhophus* [but see below] and at least one *Euhyas*). In the species of *Craugastor, Pelorius,* and the *abbotti, conspicillatus, martinicensis, myersi,* and *sulcatus* series, the palatine has the same morphology as in ceratophryine, hylodine, leptodactyline, and most telmatobiine vomers, i.e., the shelf extends medially in a convex manner, sometimes reaching the vomer opposite.

By way of contrast, there is a concavity medially of the palatine shelf of the vomer in 32 (but not all) *Euhyas*: *alcoae, armstrongi, atkinsi, cundalli, cuneatus, dimidiatus, etheridgei, furcyensis, glandulifer, glaphycompus, gossesi, greyi, heminota, klinikowskii, lentus, leoncei, monensis, nubicola, orcutti, oxyrynchus, pezopetrus, pictissimus, pinarensis, planirostris, ricordii, rufifemoralis, schmidti, sierramaestrae, symingtoni, thomasi, weinlandi,* and *zeus*. In addition,

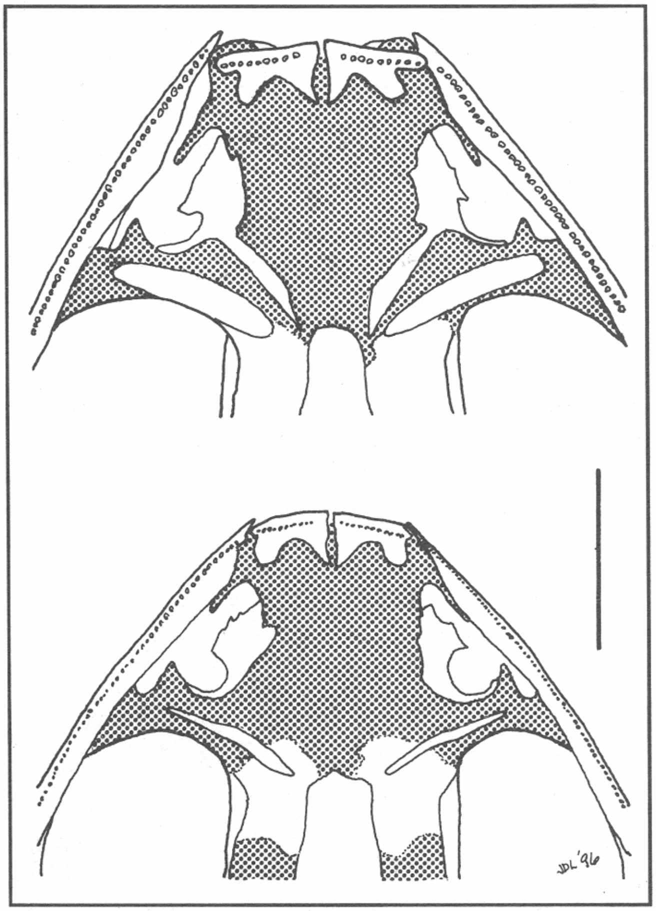

Figura 1. Palates of *Syrrhophus leprus* (KU 35963, top) and *S. cystignathoides* (KU 105500, bottom). Cartilage is in stipple. Scale equals 2 mm.

based on the illustrations in **Flores** (1984), the feature is seen as well in *alticola, andrewsi, cavernicola, fuscus, grabhami, griphus, jamaicensis, junori, luteolus, pantoni,* and *sisyphodemus.* The following eight species of *Euhyas* do not exhibit the concavity: *brevirostris, jugans, karlschmidti, minutus, richmondi, semipalmatus, varleyi,* and *ventrilineatus.* The case for *limbatus* is debatable due to the reduction of the vomer. In the cases of *E. leprus* and *E. longipes* (*Syrrhophus*), one can see a medial emargination of the vomer (Fig. 1) but no imagination can record the feature for the other eleven *Syrrhophus* (whose vomers are so reduced).

The data presented here, added to those of **Flores** (1984), reveal that a derived condition is seen in 43 species now assigned to *Euhyas,* but not in eight others. Furthermore, the plesiomorphic condition is seen in 51 of 53 *Craugastor* (two species cannot be scored), the six *Pelorius,* the 183 species of the mainland *conspicillatus, martinicensis, myersi,* and *sulcatus* series, and the four species of the *abbotti* series and at least a dozen species of the Antillean *martinicensis* series. The only species outside of *Euhyas* to exhibit the feature are all six species examined of the *binotatus* series (*binotatus, guentheri, nigriventris, octavioi, parvus,* and *venancioi*) and perhaps two species of *Syrrhophus* (Fig. 2).

This character suggests that the subgenera *Eleutherodactylus* and *Euhyas* are not monophyletic. It also implies a novel Mexican-Antillean-Brasil connection (but, see below).

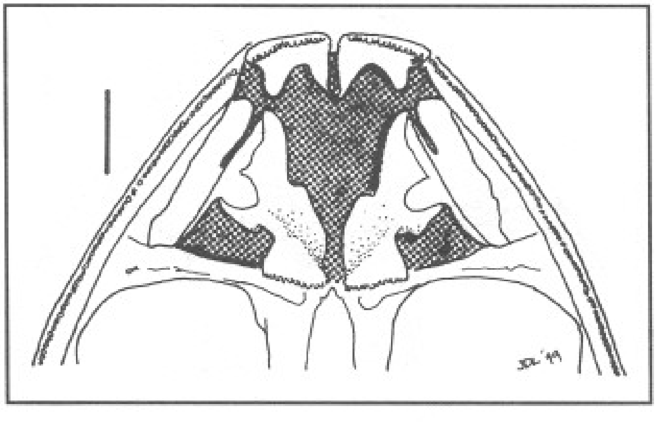

Figura 2. Palates of *Eleutherodactylus binotataus* (KU 74199) showing one expression of the median notch of the vomer. Cartilage is in stipple. Scale equals 2 mm.

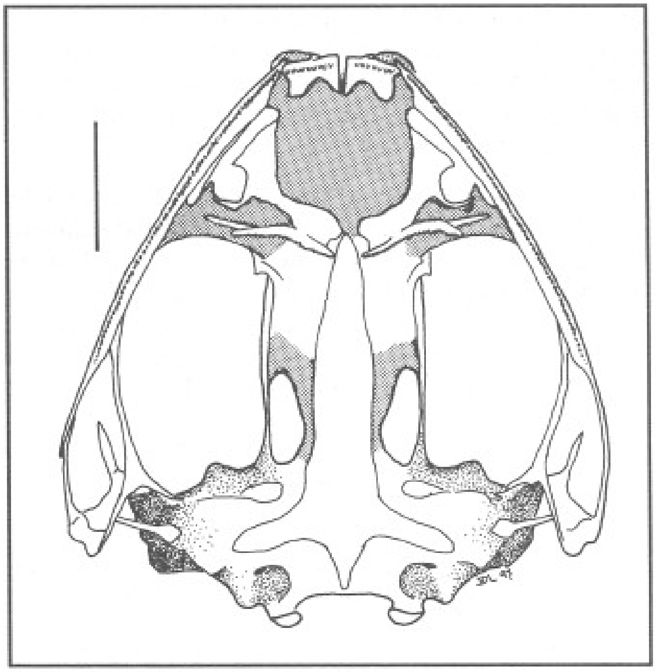

Figura 3. Ventral view of cranium of *Euhyas etheridgei* (MCZ 37338) showing a second expression of the median notch of the vomer. Cartilage is in stipple. Scale equals 2 mm.

I have decided that **Dunn**'s (1926) method (also used by **Schwartz,** 1958, and **Joglar**, 1989) of deciding if the odontophores was long or short confused more than it illuminated. *Eleutherodactylus etheridgei* is a good case in point (Fig. 3). By Dunn's method, it has "short" odontophores but they are short only in terms of their lateral terminis relative to the choanae. It is a long odontophore apparently displaced medially and should not be confused with the state exhibited by *E. cochranae* (**Lynch**, 1971:49). I have not yet decided how to quantify this feature but if I am correct in my assessment then "short odontophore" has at least three meanings (most Mainland frogs, *martinicensis* group, and many other West Indian taxa). **Schwartz** (1965:506) anticipated this position when he noted that frogs now placed in *Pelorius* do not have short vomerine tooth series "...these series in both species are rather long, and hardly patch-like."

SEPARATION OF THE VOMERS

I propose to revive an old hypothesis as concerns the vomers of *Eleutherodactylus.* As I see the situation now, there were two modes, one of largish vomers, narrowly separated medially (mainland, perhaps *Pelorius* and a few other Antillean taxa), and one of small widely separated vomers (Antilles and Mexico) shortly after the genesis of what we now term *Eleutherodactylus.* I am still inclined to view the former as primitive because it seems to be more general in occurrence among leptodactylids. **Lynch**

(1971) used vomer separation as one of the characters for his Alpha division of *Eleutherodactylus* but subsequently largely abandoned the proposal. The improved database and a re-interpretation of what constitutes short or long odontophores enable a more mature possibility of evaluating the character.

If the primitive condition for the vomers in an Antillean-Mexican clade includes the short odontophores such as are seen in the *martinicensis* group, then many *Euhyas* have modified the posterior part of their vomers by moving the odontophore medially (sometimes with growth of the odontophore laterally as well, masking the evidence of medial movement). Such a movement may well have the effect of producing a bend or kink in the palatine shelf and generating what I termed above the median notch. Because some species lack the median notch but have what I interpret to be medially displaced odontophores, there are two characters here.

If the median notch (in *Euhyas*) is a consequence of medial movement of the odontophore, then the presence of a median notch in the *E. binotatus* series must be the result of some other morphogenetic transformation (because there is no evidence of medial translation in mainland *Eleutherodactylus*). Accordingly, although each condition is here termed a median notch, the conditions are nonhomologous.

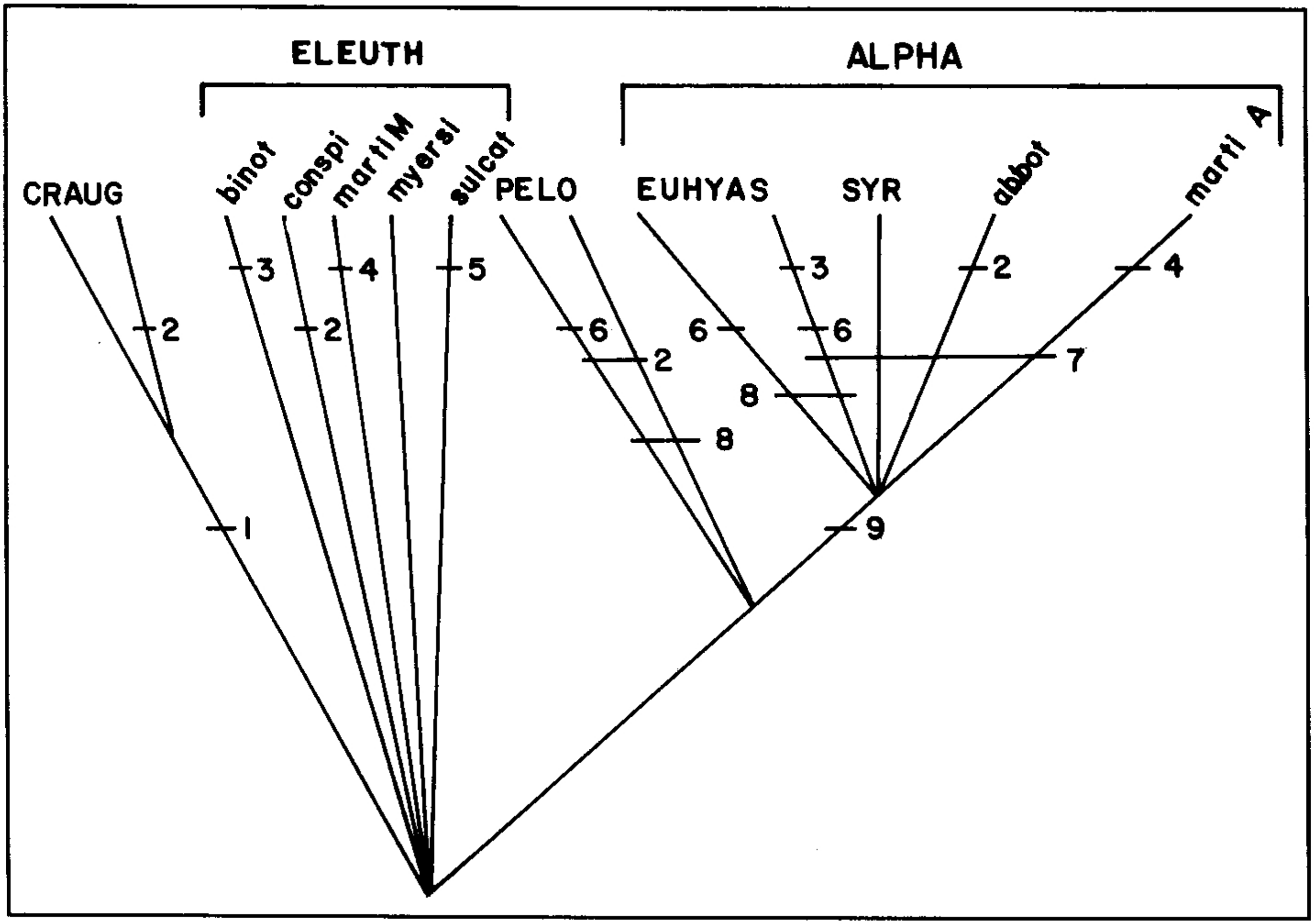

Figura 4. Working hypothesis of relationships within the genus *Eleutherodactylus*. Derived characters are indicated by numbers. 1: E condition of the adductor muscles. 2: Toe V slightly longer than toe III. 3: Median notch on vomer. 4: Toe V much longer than Toe III. 5: Posterior part of maxilla deep. 6: Epiotic flange. 7: Fusion of frontoparietal and prootic. 8: Medial movement of vomerine odontophore. 9: Vomers small, widely separated. Abbreviations: CRAUG (subgenus *Craugastor*), ELEUTH (subgenus *Eleutherodactylus*), PELO (subgenus *Pelorius*), SYR (subgenus *Syrrhophus*), abbot (*abbotti* series), binot (*binotatus* series), conspi (*conspicillatus* series), marti A (*martinicensis* series Antilles), marti M (*martinicensis* series Mainland), sulcat (*sulcatus* series).

Discussion

The four (or five) characters are not compatible but the incompatability derives from problems in the identification of homology. The epiotic flange character is not consistent with current classification (contra *Eleutherodactylus, Euhyas,* and *Pelorius*) nor is the frontoparietal fusion character (contra *Eleutherodactylus* and *Euhyas*) nor is the vomer character (contra *Eleutherodactylus* and *Euhyas*). However, the distributions of these characters cannot be described as chaotic but rather suggest particular zoogeographic units are identified with each. The epiotic flange is a feature of some Greater Antillean taxa. The fusion character groups Mexico plus the Antilles as does the vomer separation character. The developments of a median notch of the vomer (two ways) have occurred in a subset of Antillean taxa (the Mexican species cannot be scored with confidence) and in one clade of South American *Eleutherodactylus*).

Partially incongruent with the median notch (Antillean) clade is the fusion of the frontoparietal and prootic. However, before we place great weight on this fusion character, a good deal of additional work is needed to sort out the species exhibiting non-ontogenetic fusion from those exhibiting ontogenetic fusion. At least three states occur among the species currently assigned to *Euhyas* (no fusion, ontogenetic fusion, and non-ontogenetic fusion) and the dataset needs to be enlarged before one engages in *ad hoc* hypotheses concerning reversions. My working hypothesis (Fig. 4) for *Eleutherodactylus* recalls my position of 30 yr ago (**Lynch**, 1971) and agrees with one of **Joglar**'s (1989) cladograms and partially with that of **Hedges** (1989) but is completely antithetical to that of **Savage** (1987) and suggests that **Lynch & Duellman** (1997) are incorrect in their assertion that a very long fifth toe is a synapomorphy for the *E. martinicensis* series.

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APPENDIX 1

This appendix provides a list of the taxa examined, arranged according to the classification proposed by Lynch & Duellman (1997).

CRAUGASTOR (*anatipes, angelicus, andi, anomalus,augusti, azueroensis, berkenbuschii, biporcatus, bocourti, bransfordii, brocchi, bufoniformis,cheiroplethus, crassidigitus, daryi, decoratus, emcelae, escoces, fitzingeri, fleischmanni, gollmeri, greggi, hobartsmithi, laticeps, lineatus, loki, longirostris, maussi, matudai, melanogaster, merendonensis, mexicanus, milesi, necerus, noblei, occidentalis, omiltemanus, podiciferus, punctariolus, pygmaeus, raniformis, rhodopis, rostralis, rugulosus, sartori, spatulatus, stejnegerianus, talamancae, taurus, uno, vocalis, xucanebi, zygodactylus*).

ELEUTHERODACTYLUS

abbotti **series** (*haitianus*)

binotatus **series** (*binotatus, guentheri, nigriventris, octavioi, parvus, venancioi*).

conspicillatus **series** (*acatallelus, achatinus, actites,acutirostris, appendiculatus, babax, bicumulus, boconoensis, buckleyi, caprifer, carmelitae, carranguerorum, cerasinus, condor, conspicillatus, crenunguis, cristinae, cruralis, cryophilius, curtipes, danae, delicatus, devillei, discoidalis, dolops, douglasi, duellmani, elassodiscus, erythropleura, fenestratus, fraudator, gaigeae, galdi, gentryi, ginesi, insignitus,jaimei, johannesdei, labiosus, lancinii, lanthanites, latens, loustes, lymani, mantipus, medemi, megalops, nigrovittatus, orestes, orpacobates, pluvicanorus, quinquagesimus, rhabdolaemus, rubicundus, ruedai, ruthveni, sanctaemartae, satagius, silverstonei, stenodiscus, surdus, tenebrionis, toftae, terraebolivaris, thectopternus, vertebralis, vicarius, vidua, vilarsi, viridicans, w-nigrum*).

martinicensis **series** Antilles (*auriculatoides, bakeri, coqui, eileenae, pinchoni*).

martinicensis **series** Mainland (*acerus, acuminatus, alalacophus, altae, altamazonicus, anolirex, anotis, atratus, bacchus, baryecuus, bellona, bicolor, bogotensis, boulengeri, brevifrons, bromeliaceus, cacao, cajamarcensis, calcarulatus, carvalhoi, caryophyllaceus, celator, chalceus, chloronotus, colodactylus, cremnobates, croceoinguinis, crucifer, cruentus, cryptomelas, deinops, diadematus, diaphonus, diastema, dorsopictus, elegans, glandulosus, gracilis, imitatrix, incanus, incomptus, lacrimosus, leptolophus, leucopus, lichenoides, luteolateralis, lynchi, martiae, modipeplus, nervicus, nicefori, nyctophylax, obmutescens, ockendeni, orcesi, ornatissimus, pardalis, parvillus, peraticus, permixtus, philipi, phoxocephalus, piceus, platychilus, platydactylus, prolatus, prolixodiscus, proserpens, pseudoacuminatus, pugnax, pycnodermis, quaquaversus, racemus, restrepoi, ridens, riveti, roseus, ruidus, simoteriscus, simoterus, spilogaster, spinosus, supernatis, taeniatus, tamsitti, tayrona, thymalopsoides, thymelensis, torrenticola, trachyblepharis, unistrigatus, uranobates, variabilis, ventrimarmoratus, versicolor, viridis, walkeri*).

myersi **series** (*hectus, leoni, myersi, ocreatus, repens, trepidotus*).

sulcatus **series** (*cadenai, cerastes, cornutus, ingeri, laticorpus, necopinus, ruizi, sulcatus*).

EUHYAS (*alcoae, armstrongi, atkinsi, brevirostris, cundalli, cuneatus, dimidiatus, etheridgei, furcyensis, glandulifer, glaphycompus, gossei, greyi, heminota, jugans, karlschmidti, klinikowskii, lentus, leoncei, limbatus, minutus, monensis, nubicola, orcutti, oxyrynchus, pezopetrus, pictissimus, pinarensis, planirostris, richmondi, ricordii, rufifemoralis, schmidti,* *semipalmatus, sierramaestrae, symingtoni, thomasi, varleyi, ventrilineatus, weinlandi, zeus*).

PELORIUS (*chlorophenax, hypostenor, inoptatus, nortoni, parapelates, ruthae*).

SYRRHOPHUS (*angustidigitorum, cystignathoides, dennisi, dixoni, grandis, leprus, longipes, marnockii, nitidus, pipilans, rufescens, saxatilis, teretistes*).