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THE ANTILLEAN ELEUTHERODACTYLUS OF THE AURICULATUS GROUP

by

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DUNN (1926) first proposed that the multiplicity of Cuban species of *Eleutherodactylus* be separated into four groups. One of these, the *auriculatus* group, was characterized by him as having a granular belly, short (= patch-like) vomerine series, well developed digital discs, and an external vocal sac in the males. Such a diagnosis has proved increasingly valuable in arranging Cuban *Eleutherodactylus*, and has resulted (SCHWARTZ, 1965a) in a dendrogram showing the proposed relationships of the members of this assemblage in Cuba. As knowledge of the habits and calls of West Indian frogs has increased, it has become evident that the *auriculatus* group is widespread throughout both the Greater and Lesser Antilles; in addition to the structural features noted by DUNN, certain characteristics of habitat, habits, and voice show that there is a striking uniformity in these patterns as well. The purpose of the present paper is to summarize the current knowledge of the *auriculatus* group members in the West Indies.

Much of my work in Cuba was under the sponsorship of two National Science Foundation grants (G-3865 and G-6252), and for this financial assistance I am very grateful. Some of the details of calls and calling sites have been reported by my associates in the field: I wish to express my sincere gratitude for their assistance to Miss PATRICIA A. HEINLEIN and Messrs. RONALD F. KLINIKOWSKI, DAVID C. LEBER, and RICHARD THOMAS. Of the 37 species under discussion, I have heard calling and handled all but three in the field; such intimate association is invaluable with these frogs.

Before proceeding, it is necessary to clarify three nomenclatorial situations. SHREVE & WILLIAMS (1963), while discussing the amphibian fauna of southern

Hispaniola, included in the *auriculatus* group (which they termed the *varians* group), the species *inoptatus* Barbour; they also regarded *abbotti* Cochran and *audanti* Cochran as conspecific, and named *heminota* as a subspecies of *bakeri* Cochran. I have shown cause (SCHWARTZ, 1965b) whereby *inoptatus* should not be included in the *auriculatus* group, and (SCHWARTZ, 1966) that *abbotti* and *audanti* are distinct species which are in part sympatric. I have compared *heminota* and *bakeri* and find no valid reason for considering them subspecies; although their known distributions are allopatric, the frogs themselves are sufficiently distinctive (*bakeri* is large and robust, reaching a snout-vent length of 38 mm, *heminota* is small and delicate, with snout-vent lengths to 30 mm) that I consider them as separate species. Finally, SHREVE & WILLIAMS (1963: 324) used the combination *E. varians wetmorei*. In this usage they followed me (1960: 6). However, I have since collected *wetmorei* and consider that it is distinctive in voice, pattern and coloration; it should not be considered a subspecies of *E. varians*. This is a particular instance of two frogs which are structurally similar (sufficiently so as to convince the investigator of their conspecificity) which, upon familiarity in the field, demonstrate that they are very different vocally and chromatically. It is for this specific reason that I discuss with some reluctance in the present paper those few *auriculatus* group members with which I have had no field experience.

THE AURICULATUS GROUP MEMBERS

In addition to the characters pointed out above, two other features characterize the *auriculatus* group: 1) all are vocal and often surprisingly so for their relatively small size; 2) all call from objects above the ground (including trees, shrubs, herbs, grass, vines, and in two cases vertical boulder or rock faces). In adult size the species vary from small (16 mm) to rather large (58 mm), but most members are of moderate size (25 to 40 mm).

The following species are regarded as being members of the *auriculatus* group:

Cuba

varians Gundlach & Peters, (with its subspecies *olibrus* Schwartz
  ionthus Schwartz, and *staurometopon* Schwartz)
auriculatus Cope
eileenae Dunn
bartonsmithi Schwartz
ronaldi Schwartz
leberi Schwartz

Hispaniola

auriculatoides Noble
pituinus Schwartz
montanus Schmidt
patriciae Schwartz
bakeri Cochran
heminota Shreve & Williams
flavescens Noble
poolei Cochran
wetmorei Cochran
abbotti Cochran
audanti Cochran (with its subspecies *notidodes* Schwartz and *melatrigonum* Schwartz)
minutus Noble
haitianus Barbour
armstrongi Noble & Hassler

Puerto Rico (including the Virgin Islands)

portoricensis Schmidt
coqui Thomas
schwartzi Thomas
antillensis Reinhardt & Lütken
locustus Schmidt
eneidae Rivero
hedricki Rivero
cooki Grant
gryllus Schmidt
wightmanae Schmidt
brittoni Schmidt

Lesser Antilles

martinicensis Tschudi
urichi Boettger (with its subspecies *shrevei* Schwartz and *euphronides* Schwartz)
johnstonei Barbour
pinchoni Schwartz
barlagnei Lynch

Of the above forms, I have not collected only *poolei, bakeri, heminota,* and *hedricki.* Of these I have heard *hedricki* call and examined one freshly collected specimen, have handled many live and native-caught *heminota,* and have examined the holotype and paratypic series of *bakeri. E. poolei* is well illustrated by COCHRAN (1941: 40) and the illustration and description leave little doubt as to the affiliations of this species; I have also examined a series of this species in the American Museum of Natural History.

CHARACTERISTICS

As previously noted, the frogs listed above share in a community of morphological characteristics. Common features are the presence of an external vocal sac in males, a short patch-like tooth row, a granular belly, and prominent digital discs. Only two species are aberrant in some of these characters: *armstrongi* has a long vomerine tooth row and a smooth belly. This species has been placed in the *ricordi* group by SHREVE & WILLIAMS (1963: 328), but due to its enlarged discs, its loud voice (*ricordi* members have faint and insect-like irregular voices), and its arboreal calling sites, its affiliations are surely more with the *auriculatus* group than elsewhere. The second aberrant species is *E. coqui,* which has straight or slightly flexed, rather long vomerine series; *coqui* agrees with the balance of the assemblage in its other morphological characters.

SCHWARTZ (1960) and SHREVE & WILLIAMS (1963) have shown that inguinal glands are somewhat more widespread in West Indian *Eleutherodactylus* than had been previously supposed. Although these glands are not a widespread feature in the *auriculatus* group, they do occur in the following members: *varians, montanus, patriciae, wetmorei, armstrongi,* and *antillensis.* Although, of these members having glands, *montanus* and *patriciae,* and *varians* and *wetmorei* seem to be closely related pairs, I do not feel that the presence or absence of glands should be considered as unduly significant insofar as relationships are concerned. The six gland-bearing members do not appear to be more closely related to one another than to other non-gland-bearing members. Of the gland-bearing members, one is Cuban, four are Hispaniolan, and one is Puerto Rican.

GOIN (1954) has shown that in the *gossei* group of Jamaican *Eleutherodactylus* there is a community of patterns in the seven species included therein. Later (1960), GOIN discussed various dorsal patterns in *Eleutherodactylus* and listed species from both the Antilles and the mainland which had common pattern elements. In the *auriculatus* group, one pattern element occurs with remarkable frequency in many species and another occurs only in this group:

1) middorsal line, either hair-line or broad. This feature, either a fine pale hair-line or a broad dorsal midline on a dark dorsal ground color, occurs in 20 of the 37 species assigned to the *auriculatus* group (*auriculatus, eileenae, ronaldi; abbotti, audanti, montanus, patriciae, heminota, bakeri; portoricensis, coqui, antillensis, locustus, gryllus, brittoni, wightmanae; martinicensis, urichi, johnstonei, pinchoni*). The highest incidence of its occurrence is in Puerto Rico (seven of 11 species), its lowest in Hispaniola (six of 14 species). The middorsal line occurs as a pattern feature in 16 of 60 non-*auriculatus* group members in the Antilles (*alticola, cundalli, gossei, luteolus, junori, pantoni, nubicola* from Jamaica; *zugi, klinikowskii, dimidiatus, emiliae, cubanus, intermedius, varleyi* from Cuba; *jugans* and *parabates* from Hispaniola). The greater incidence (45%) of median dorsal lines in *auriculatus* group species compared with non-*auriculatus* group members (27%) is of interest.

2) Five *auriculatus* group members have as a regular pattern feature a broad creamy to silvery interocular bar involving the basal portion of the snout just before the eyes (*varians, wetmorei, auriculatoides, coqui, urichi*). As far as I know, this broad interocular bar occurs in no other West Indian species of *Eleutherodactylus*, and thus may be considered as restricted to the *auriculatus* group.

Of equal importance with morphology and pattern is the community of calling sites for the *auriculatus* members. Invariably these frogs call from above the ground surface (in contrast to, say, the *ricordi* group members which call from on or near the ground). The calling sites vary from the high forest canopy (*hedricki, varians, wetmorei*), low trees and shrubs (*eileenae, ronaldi, bartonsmithi, auriculatoides, armstrongi, portoricensis, coqui, cochranae, martinicensis, urichi*), herbaceous cover – including aroids and terrestrial bromeliads (*leberi, abbotti, audanti, pituinus, patriciae, flavescens, minutus, haitianus, antillensis, locustus, eneidae, brittoni, wightmanae, schwartzi, johnstonei, pinchoni*), or viny tangles (*auriculatus*). It should of course be understood that occasional individuals of several of these species at times are encountered in atypical situations. For instance, *varians* males have been collected from low bromeliads in low trees in Cuba and the Isla de Pinos, a single *pituinus* was taken calling on a bare rock, and *pinchoni* has been collected calling from dead leaves on the ground. *E. eneidae* calls with some degree of regularity from moss-covered cutbanks in Puerto Rico, as does *coqui* from exposed earthen banks, and *auriculatus* may be encountered in herbaceous, rather than viny, cover. *E. flavescens* likewise, although considered a caller from herbaceous cover, resorts often to viny tangles.

The only major exception to the arboreal rule for calling sites in the group are *E. cooki* and *E. barlagnei*. *E. cooki* vocalizes from the vertical faces of huge boulders, in the fissures of which it spends the day. The transition from an arboreal to a petricolous calling site would not seem particularly difficult; both are (or can be) more or less vertical surfaces, and doubtless *cooki* (which is restricted to the boulder-strewn slopes of the Sierranía de Panduras in southeastern Puerto Rico), once becoming an inhabitant of this rather specialized habitat, has adopted the boulder faces as a secondary and economical substitute for the trunks of trees. *E. barlagnei* also resorts to vertical boulder and rock faces in mountain torrents, but males vocalize from rocks in slack water along the margins of the streams rather than from boulders wetted by the dashing torrents themselves. As in the case of *cooki*, *barlagnei* seems to be an *auriculatus* group member which has become secondarily petricolous, and its calling sites are related to its rock-inhabiting proclivities.

Although it would be expected that, because of their arboreal tendencies, members of the *auriculatus* group would be the dominant forest frogs of the Antilles, such is not the case. Although the broad-leaf forests of Cuba (*varians, eileenae, bartonsmithi*), Hispaniola (*wetmorei, auriculatoides, minutus, armstrongi*), and Puerto Rico (*portoricensis, coqui, eneidae, gryllus, wightmanae, hedricki*) have representatives of the group, there is a distinct tendency for members to be associated with other habitats. For instance, *ronaldi* (although an arboreal caller) vocalizes from trees in open areas, such as pastures. The species *leberi, abbotti, audanti, montanus, brittoni, locustus, schwartzi, martinicensis, johnstonei* and *urichi* are all more abundant in open areas either in or adjacent to forest. The species *haitianus, patriciae,* and *pituinus* are clearly associated with upland pine forests above 4000 feet in Hispaniola. *E. flavescens, auriculatus,* and *antillensis* are denizens of open areas, such as abandoned pastures or rather mesic savannas. Of the group members, only *cochranae* inhabits (in part of its range) the xeric forests of

Puerto Rico; in the Virgin Islands, however, it occurs in shaded and moderately mesic woods. Once more it should be pointed out that the above categories are not absolute. They do serve to show the variety of ecological situations which members of the group occupy through the Antilles, and to point out that all species are not inhabitants of mesic broad-leaf forest. Altitudinally the species range from sea level to over 8000 feet in the Cordillera Central of Hispaniola.

VOICE

Vocally, the members of the *auriculatus* group fall rather neatly into several categories; geographically remote species often have calls which are remarkably similar, and the same style of voice occurs in widely separated members of the assemblage. A discussion of anuran calling is hampered from the outset by the difficulty of rendering the sounds made by these amphibians into some simple syllabic symbols; admittedly audiospectrograms facilitate the visualization of such calls, but in many cases I have not been able to record the respective voices of these species. The calls of the members of the group may be categorized as follows:

I. The common names of *E. eileenae* in Cuba, where it is called "colín" and of *E. coqui* in Puerto Rico, where it is called "coquí" give a concise rendition of the calls of members of this assemblage (see THOMAS, 1966, for audiospectrograms of three included species). Included species are:

eileenae
wetmorei
flavescens
portoricensis
coqui
schwartzi
antillensis
johnstonei
urichi

In these frogs, the call is composed of two notes, the second note higher than the first and accented. The renditions "co-quí" and "co-lín" (or perhaps less appropriately but equally correct "boop-beep") show the form of the call. Of these first group members, *flavescens* repeats the two-note call continuously, without distinct breaks between the groups, and *urichi* emphasizes the second syllable, the first being rather weak. Finally, *antillensis* utters both a "co-quí" call and a 5- or 6-times repeated "ic...ic...ic..." call, which is reminiscent of the calls of the next group.

II. The second category of calls is that of a repeated flat telegraphic clicking; this group is composed of

auriculatus
ronaldi
bartonsmithi
haitianus
pituinus
brittoni
gryllus
audanti
(*abbotti*)
and possibly *cooki*

As I have recently shown (1965a), the Cuban members of this call group may be grouped into *auriculatus* and *ronaldi*, the first with a continuous flat metallic clicking (see Bogert, 1960: 161, for a visual rendition) and *ronaldi* with a slow rapping, and *bartonsmithi* with a non-metallic 4 or 5 note clicking. *E. haitianus* has a descending scale of staccato notes, and *pituinus* has 7 to 8 staccato, slightly rising notes, the individual notes in both cases sounding much like "wheep" or "breep". *E. gryllus* has a rapid telegraphic clicking and *brittoni* an insect-like repeated, "tic...tic...tic..." To this group likely also belongs *E. cooki*, whose voice was reported by Grant (1932) as a melodious, whistled "pe...pe...pe..." Although I have heard *cooki* call in its native haunts, the call was much obscured by other calling frogs, and my impression is not the same as that of Grant.

Schwartz (1966) pointed out that *E. audanti* and *E. abbotti* from Hispaniola had calls which were similar, except that that of *abbotti* was lower in pitch. Even this statement is not correct; additional evidence indicates that the call of *audanti* is a series of flat telegraphic clicks, whereas that of *abbotti* is as described above (Schwartz, 1966: 372) – a series of "tuck-wheep" 's interspersed with some flat "tuck" 's. The call of *audanti* is thus clearly like those of the other members of the call group, and I interpret the *abbotti* call as a derivative of it.

III. Another section of the group has penetrating metallic calls. These species are

leberi
varians
auriculatoides
armstrongi
hedricki
(and *montanus*)

Within this assemblage, the call varies from a single metallic note (*leberi, armstrongi*) to a series of notes on the same pitch (*varians* and *hedricki* with 2 or 3 notes, *auriculatoides* with a continuous metallic pinging). *E. varians* and *hedricki* have loud calls, and the metallic timbre of the call coupled with the groupings of the notes give the distinct impression of hammering on an anvil. Since both these species call from the canopy, the calls resound throughout the forest in a remarkable manner, and the individual males are regularly difficult to collect. I group *montanus* with these metallic callers only provisionally, rather than separating it into another group; the call of *montanus* is a repetitive single isolated note (rendered in the field as "breep") and not particularly metallic in quality.

IV. Of three Puerto Rican and one Lesser Antillean species,

locustus
eneidae
wightmanae
martinicensis

the first two have similar calls consisting of an initial whistle (very clear and penetrating and reminding me in quality of the Antillean members of the avian genus *Myadestes*), followed by a series of flat raps or clicks. The call of *wightmanae* lacks the preliminary whistle, and the call is limited to a series of 5 to 7 whistled notes, which in chorus sound like the crescendo and diminuendo tinkling of bells. I associate *wightmanae* with *locustus* and *eneidae* only provisionally; the calls of the three can be associated if the *wightmanae* call is interpreted as a *locustus-eneidae* call which has been modified by the loss of the initial whistle and a modification of the following flat notes into a series of whistles.

There is a possibility that the calls of *eneidae* and *locustus* have been derived from a call like that of *abbotti* (or vice versa); the first pair of species has a preliminary whistle followed by a series of flat rappings, whereas *abbotti* has (in effect) a series of flat notes followed by (in effect) a whistle. Conceivably, a constant repetition of either sort of call might result in the transposition of the whistle from the end to the beginning of the series.

I have associated *martinicensis* with this call group tentatively. The call of this Lesser Antillean species is a short single rising note, alternating with a 5-note rapid clicking. The voice and call pattern of *martinicensis* is much like that of *antillensis* of Puerto Rico, although the latter species has a 2-note call, which alternates with a 5- or 6-note clicking. In associating *martinicensis* with *locustus-eneidae*, I have placed emphasis on the initial whistle or single note rather than on the clicked series; possibly the other choice would have been preferable, and *martinicensis* might better be associated with the *eileenae-wetmorei* series via *antillensis*.

V. This group consists of

minutus
patriciae
cochranae

In these three species the call is a single whistled note, rising in *minutus* and *cochranae*, falling in *patriciae*. (It is possible that, of these three species, *cochranae*, which is closely related to *locustus*, should perhaps better be associated with the *locustus-eneidae* group, its call being interpreted as a *locustus-eneidae* call which has retained the initial whistle and lost the following series of flat notes).

VI. The single remaining species

barlagnei

cannot be associated vocally with any other group. The call is made up of a four or more unit trill which falls in pitch as the call progresses. No other *auriculatus* group frog has a call or call fragment which is a trill. It seems possible that the peculiar (for *auriculatus* group) call of *E. barlagnei* may somehow be associated with the torrential streams which it inhabits – i.e., the noise of the stream has brought about an evolutionary attempt to develop a call which will resound above the noise of the cataracts. Since presumably *E. barlagnei* has developed from some herb- or shrub-inhabiting (in contrast to high arboreal) frog, its vocal forerunner was not a member of the assemblage of *Eleutherodactylus* which have loud and resounding metallic voices (category III above), but rather from a species with a less penetrating call. A trill could have developed from the very rapid repetition of a two-note call resulting first in a vibrato and thence in a true trill. In any event, if the peculiar call of *E. barlagnei* is the result of need to have itself heard above the roar of its montane rivers, the frog has (as far as human ears are concerned) been remarkably unsuccessful, since its voice is not readily heard above the noise of the cataracts which it inhabits.

There are no data for the calls of *poolei, heminota,* or *bakeri,* reported in the literature, and I have not heard any of them in the field. Considering the relationships between *poolei* and *flavescens* (both are the only known Antillean *Eleutherodactylus* with notched digital discs) and between *heminota* and *armstrongi* (which are very similar in, and at times indistinguishable on the basis of, dorsal pattern), I imagine that *poolei* has a two-note call like *flavescens* and *heminota* a single note metallic call as does *armstrongi.*

ZOOGEOGRAPHY AND RELATIONSHIPS

Of the members of the *auriculatus* group, 6 are Cuban (two, *varians* and *auriculatus,* occur as well on the Isla de Pinos), 14 are Hispaniolan (none occurs on any of the offshore islands), 11 are Puerto Rican (with *cochranae* and *antillensis* extending eastward into the Virgin Islands), 1 is restricted to the Virgin Islands, and 5 are Lesser Antillean. The group is absent from the Bahamas, and almost certainly absent from Jamaica (see, however, the discussion of *E. jamaicensis* Barbour below).

Perhaps one of the most striking results of the present study is the relative abundance of species of the *auriculatus* group in relation to the total number of species of *Eleutherodactylus* on the three Greater Antillean Islands and the Virgins. Of 30 species of *Eleutherodactylus* in Cuba, 6 are *auriculatus* group (20%); of 34 species on Hispaniola, 14 are *auriculatus* group (41%); of 14 Puerto Rican species, 11 are *auriculatus* group (79%); of 4 Virgin Island *Eleutherodactylus* (two of which are non-endemic and Puerto Rican as well), 3 are *auriculatus* group (75%). The coincidence of percentages for Puerto Rico and the Virgin Islands is noteworthy only in that the Puerto Rico-Virgin Islands herpetofaunas are extremely similar, most species in the latter islands showing very close relationships (usually on the subspecific level) with those of Puerto Rico. The Virgin Island fauna is in actuality a derived and depauperate Puerto Rican fauna. Thus, if *auriculatus* group members form a high percentage of Puerto Rican species, it is expected that they would also form the majority of Virgin Island species – and such is indeed the case.

If total number of species of a group is to be regarded as a function of area involved (and this is by no means necessarily the case), then the disparity between the number, both of species of *Eleutherodactylus* and of the *auriculatus* group members, on Cuba and Hispaniola is at once apparent. Cuba, with an area of 111,463 square kilometers, is considerably larger than Hispaniola, with an area of 77,250 square kilometers. Cuba has both fewer species of *Eleutherodactylus* (30 vs. 34) and many less *auriculatus* group members (6 vs. 14) than does Hispaniola. On one hand, Cuba is a relatively simple island, attenuate in shape, with three major massifs, the highest (the Sierra Maestra) culminating in the Pico Real del Turquino with an elevation of 2005 meters. Hispaniola, on the other hand, is a much more complex island, with several high and much dissected ranges, separated by low and at times xeric (or relatively so) valleys of considerable extent, and culminating in Pico Duarte with an elevation of 3175 meters. Even a casual glance at topographic maps of these two islands demonstrates the far greater complexity of Hispaniola than that of Cuba. Finally, Puerto Rico is simple, with, in essence, a central massif (the Cordillera Central) and a more or less extensive, in places arid, coastal plain. The highest Puerto Rican peak is Cerro de Punta with an elevation of 1338 meters.

DARLINGTON (1957: 515) has suggested that Cuba and Jamaica were ports-of-entry for West Indian vertebrates arriving from the Central American mainland. Assuming that such has been the case with the *auriculatus* group, it is obvious that Jamaica is an unsatisfactory port-of-entry by virtue of its lack of any species of *Eleutherodactylus* associated with the present group (see however, the discussion of *E. jamaicensis* beyond). Cuba with its small number of species seems also not altogether satisfactory. However, two factors concerning the group in Cuba are pertinent: 1) on Cuba, one island-wide species of the *auriculatus* complex has differentiated subspecifically (*varians*) and 2) the Isla de Pinos, of all Greater Antillean satellite islands, has members of the *auriculatus* group (*auriculatus* and a subspecies of *varians*). These two facts alone bespeak a long residency of members of the complex on Cuba.

Of the six Cuban species, two (*varians, auriculatus*) are island-wide, and one (*eileenae*) is almost so, extending as far east as Camagüey Province. Three (*ronaldi, bartonsmithi,* and *leberi*) are restricted to Oriente Province (none is known to be strictly highland however, and of the three, *ronaldi* has the widest distribution in the province). The rather high percentage (three species) which are almost island-wide in distribution again suggests a long residency, since none of the Hispaniolan species has so broad a distribution (although *abbotti* is rather widespread).

I visualize that Hispaniola was colonized from Cuba; the physiographic and ecological diversity of Hispaniola, with high mountains having both pine and rain forest, extensive mesic and arid lowlands, isolated valleys, and peninsulas, provided a background for the evolution of a large number of species. Hispaniola, in contrast to Cuba, has four species of *Hyla,* two of which are lowland, one from intermediate elevations, and the fourth from upland localities. The ranges of none is even today especially well documented. The occurrence of only one, moderately-sized *Hyla* in the uplands (*H. heilprini,* which is not particularly common and breeds in mountain streams) has made available these upland forest habitats to arboreal *Eleutherodactylus,* with the result that of the fourteen Hispaniolan members of the group, eleven (*audanti, haitianus, minutus, montanus, patriciae, pituinus, wetmorei, heminota, bakeri, auriculatoides, armstrongi*) are restricted to upland situations, and three of these (*wetmorei, auriculatoides, armstrongi*) are strongly arboreal.

I believe that Puerto Rico (including the Virgin Islands) was again serially invaded from Hispaniola. No other native arboreal frogs occur on Puerto Rico with the exception of the *auriculatus* group *Eleutherodactylus*; of the three Puerto Rican non-group members, one (*karlschmidti*) inhabits mountain streams, and three (*richmondi, unicolor,* and *lentus*) are terrestrial. *Hyla* is present, but restricted to the northwest, and has possibly been introduced. Thus on Puerto Rico, which is topographically much less complex than Hispaniola or Cuba, *auriculatus* group members took over various habitats which elsewhere are occupied by members of other groups of *Eleutherodactylus*. The two most aberrant members of the assemblage, *brittoni* and *wightmanae*, are Puerto Rican. The single Virgin Island endemic (*schwartzi*) is doubtless a local derivative of the *portoricensis-coqui* complex.

Perhaps the major conflict with the above postulated history is the fact that Cuba, which we assume to be the port-of-entry, has so many less species in the group than Hispaniola; Cuba also, in contrast to Hispaniola, has a single species of *Hyla*, which is altitudinally widespread. Explanations for this apparent discrepancy may be the relative simplicity of Cuba, as noted above, in contrast to the complexity of Hispaniola, and to the fact that many of the niches occupied by *auriculatus* members elsewhere (grass, low herbaceous plants) are occupied in Cuba by members of other groups (*E. varleyi* is a grass frog; *E. atkinsi*, *E. zugi*, and *E. gundlachi* habitually utilize low herbaceous plants).

Of the five Lesser Antillean members of the *auriculatus* group, three (*urichi*, *martinicensis*, *johnstonei*) are typical *auriculatus* members in aspect, call, and structure. *E. pinchoni* of Guadeloupe is a tiny frog which occupies herbaceous and grassy cover, and *E. barlagnei* is an inhabitant of torrential mountain streams. As might be expected, the latter species is highly modified for this sort of existence, having webbed feet and digits with dermal flanges. The coloration and pattern of *barlagnei* is cryptic, matching quite well the vertical wet boulder faces and rocks which it inhabits in montane streams. I have discussed (1966) the interrelationships of these five frogs and details need not be repeated here. I conclude that the Lesser Antillean *auriculatus* members represent an invasion from South America (at least one species, *urichi*, occurs on the mainland in Venezuela, Guyana, and Guiane Française, but has two races on the southern Lesser Antilles). The occurrence of two endemic species (*pinchoni*, *barlagnei*) on Guadeloupe, the largest of the Lesser Antilles, along with *E. martinicensis*, is not correlated with the large size of the island itself. Rather, I suggest that these two endemic species have evolved *in situ* in the western or Basse-Terre mountainous portion of Guadeloupe. Despite the fact that similar niches occur on the other volcanic inner-chain Lesser

Antilles, they are not occupied by either *pinchoni* or *barlagnei*, or any other species of amphibian.

Of the northern Lesser Antilles, the genus is absent from Anguilla and St. Barthélemy, although *johnstonei* occurs (because of introduction?) on St. Martin, all of which lie on the Anguilla Bank. *E. johnstonei* has a split distribution in the Lesser Antilles; it occurs from Grenada north to Martinique, is absent from Dominica and Guadeloupe, and resumes on the Leeward Islands (Montserrat and to the north) with the exceptions noted above. Detailed comments and analyses of the distributions of the Lesser Antillean frogs may be found in my paper cited above. There seems to be no evidence to contraindicate that in the Lesser Antilles, since all *Eleutherodactylus* are *auriculatus* group members, after an early invasion from South America there has been differentiation (at times striking) on this chain of islands.

To summarize the above distributional data and historical synopsis, the members of the *auriculatus* group show a typical Antillean double invasion, one branch from South America and arriving in the Lesser Antilles, and a second in the Greater Antilles from Central America, where it spread from its original port-of-entry in Cuba eastward throughout the Greater Antilles.

DISTRIBUTION ON THE MAJOR ISLANDS

The distribution of the Cuban and Isla de Pinos forms has already been discussed above. It may be profitable to comment as well on the ranges of the *auriculatus* group species on Hispaniola and Greater Puerto Rico.

Of the Hispaniolan species, *wetmorei*, *bakeri*, *heminota*, and *armstrongi* are restricted to the south island (*sensu* WILLIAMS, 1961). Of the remaining forms, *auriculatoides*, *montanus*, *patriciae*, *haitianus*, *minutus*, and *pituinus* are restricted to the uplands of the Cordillera Central in the República Dominicana. *E. audanti* occurs at high elevations both on the north and south islands, although its distribution on the former is much less than on the south. *Abbotti* is practically islandwide, with some major exceptions such as the dry Península de Barahona and a rather large area in extreme southeastern República Dominicana; its distribution in northern and central Haiti is poorly documented. Of the two remaining species, *poolei* is known only from the northern Haitian mountains, and *flavescens* occurs in the northern and eastern portions of the República Dominicana. Of all Hispaniolan *auriculatus* group members, only *abbotti* has both a broad geographic range and a wide altitudinal tolerance (from sea level to 5600 feet). *E. audanti*, the only member of the group except for *E. varians* of Cuba which has differentiated subspecifically with races in the Massif de la Selle-Sierra de Baoruco, the Sierra de Neiba, and the Cordillera Central, has the broadest exclusively upland distribution of any Hispaniolan member of the group. I suspect that the three races of *audanti* have developed due to the isolation of the three mountain massifs which this frog occupies, as well as to the high elevations (4750 feet and above) which it inhabits in each of the occupied ranges.

In Puerto Rico, *coqui* and *antillensis* are virtually island-wide; *gryllus*, *eneidae*, *brittoni*, *hedricki*, *portoricensis*, and *wightmanae* are more or less upland frogs which occur throughout the interior highlands, whereas *cochranae* is widespread in the lowlands (*fide* RIVERO & MAYORGA, 1963), and occurs as well on the Virgin Islands as far east as Tortola. Only *cooki* and *locustus* are rather restricted, the former to the Sierranía de Panduras and the latter to the El Yunque massif, and the southeastern mountains (RIVERO & MAYORGA, 1963: 82–83).

In the Virgin Islands, in addition to the essentially Puerto Rican *cochranae* and *antillensis*, occurs *schwartzi*, an endemic species known only from Tortola and Virgin Gorda. No *Eleutherodactylus* are known from the northeasternmost Virgin, Anegada, although both *antillensis* and *schwartzi* are found on Virgin Gorda.

PROBLEMATICAL SPECIES

Eleutherodactylus jamaicensis Barbour

The sole Jamaican *Eleutherodactylus* which might possibly be associated with the *auriculatus* group is *E. jamaicensis*. This arboreal species has digital discs and a granular belly, and thus agrees with the balance of the assemblage in these features. However males appear to lack a vocal sac, and the tooth rows are long. There are no inguinal glands. The voice is a series of "shick...shick...shick... shick", rapidly repeated and in groups of four. The calling sites are arboreal, almost always bromeliads moderately high (6 feet and above) in mesic forest. The structural differences between *jamaicensis* and the balance of the group, and its rather different voice (although the latter might be related to the telegraphic clicking call of several *auriculatus* group members) seem to me to be sufficiently trenchant to exclude it from this assemblage, at least temporarily. *E. jamaicensis* may, however, be a lone relict and somewhat aberrant member of the *auriculatus* group on Jamaica.

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