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ART. 10. REMARKS ON EVOLUTION OF COLOR PATTERN IN THE
GOSSEI GROUP OF THE FROG GENUS *ELEUTHERODACTYLUS*

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INTRODUCTION

The *gossei* group (formerly called *luteolus* group) of the genus *Eleutherodactylus* in Jamaica is fairly well known both ecologically and systematically and shows a high degree of polymorphism in color patterns. Furthermore, there are data available to show that at least part of this polymorphism has a genetic basis. In view of this, I have been giving some thought to the variability of color pattern in the species of this group in the light of their possible evolutionary history. As there seems to be a correlation among them, I present my interpretation of the evolution with special reference to the color patterns in this group of frogs.

I make no attempt to give in this paper all of the basic data on which my conclusions are founded since to do so would lengthen it unduly and this information is readily available in the papers cited in the text.

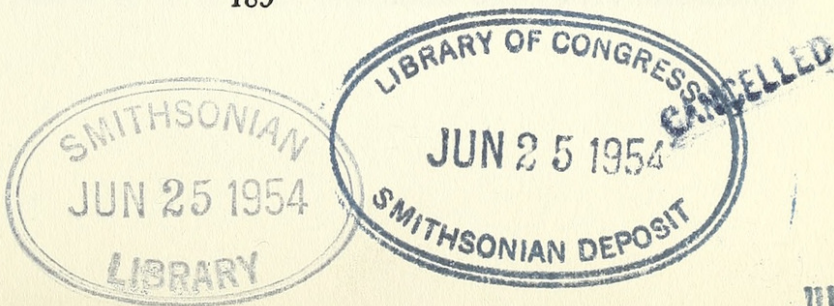
The group of species herein called the *gossei* group may be characterized in general by their terrestrial habits, feebly developed digital disks, smooth back and belly, long vomerine series, and the presence of red in the groin in life. Specimens of *E. alticola* sometimes have fairly short vomerine series (although in other specimens it is quite long) and *E. fuscus* apparently lacks red in the groin in life. The frogs in this group are noisy in life.

This is the predominant group of *Eleutherodactylus* on the Island of Jamaica. In addition, there are several species in the *cundalli* group, which are in the main rather silent, terrestrial species; the aquatic *orcutti*; and the arboreal *jamaicensis*, whose relationships are not well understood. There is, of course, the introduced *martinicensis*. The introduced *planirostris* I would put close to the *cundalli* group.

As Dr. Dunn (1926a: 115) has said, "Jamaica has specialized in the development of the *luteolus* group [= *gossei* group]." Thus, I would conclude that not more than four main stocks of *Eleutherodactylus* (excluding the recently introduced forms) have reached Jamaica, and I believe unquestionably that the differentiation of the species of the *gossei* group has taken place entirely on the Island. How long this stock has been on the Island is, of course, a matter of conjecture, but there seems to be no doubt that we have here seven species evolved from the same basic stem and all closely related.

MATERIAL

I have had the opportunity to study and observe most of the Jamaican species of *Eleutherodactylus* in the field. In my opinion, the *sine qua non* of studying frogs of this genus is observation of the forms in life. Thus, my own field experience in Jamaica has helped me not only in deciding on what should be included in the *gossei* group, but also in concluding that certain other species should not be therein included. I have not seen *E.*



junori or *E. fuscus* in life. I include them in the group with the approbation of Dr. E. R. Dunn and Dr. W. Gardner Lynn, collectors and describers of these respective species, and two of the foremost students of this genus of frogs.

In addition to hundreds of individuals observed in the field but not collected or preserved, and museum specimens of some of the species studied after preservation, I have analyzed the color pattern of the following numbers of specimens in life: *gossei*, 190; *nubicola*, 1302; *alticola*, 417; *pantoni*, 353; *andrewsi*, 17.

TAXONOMY OF THE GROUP

As I interpret it at present, the *gossei* group in Jamaica comprises the following species:

- E. gossei* Dunn
- E. nubicola* Dunn
- E. alticola* Lynn
- E. pantoni* Dunn
- E. fuscus* Lynn and Dent
- E. andrewsi* Lynn
- E. junori* Dunn

These seven obviously closely related forms are, with one possible exception, quite distinct. In the region of Clydesdale, for example, *andrewsi*, *pantoni* and *gossei* occur together. The voices of all three forms are quite different, as are the clutches of eggs. In other parts of the Island, *gossei*, *pantoni* and *junori* are found together. Several of the species show marked altitudinal limitations. Even in these forms, however, there is overlap and, where the ranges do overlap, the species remain quite distinct in voice, structure of the clutch of eggs, etc. There is, in fact, perfectly good evidence that each of the forms is a distinct species with the exception of *andrewsi* and *junori* the ranges of which, as known at the present time, are adjacent but non-contiguous. These two forms may possibly, although I think it unlikely, be shown to be subspecies of a single species.

This group of frogs is the one which has so long been known as the *luteolus* group. I have recently demonstrated (Goin, 1953) that *luteolus* Gosse is in reality quite a different species and, after having collected it and observed it in life, I am convinced it is not a close relative of any of the above species.

DISTRIBUTION

The ranges of these species may be generalized as follows.

E. gossei. Widespread from sea level to about 4500 feet; apparently absent from most of the dry south coast except on the Liguanea Plain about Kingston.

E. nubicola. The parishes of Portland, St. Andrew, and St. Thomas in the Blue Mountains and adjacent portions of the Port Royal Mountains at elevations between 3500 and 6000 feet.

E. alticola. The Blue Mountains from about 5600 feet to the top of Blue Mountain Peak (7360 feet).

E. pantoni. Widespread from the eastern to the western end of the Island from altitudes of about 500 feet to 4000 feet.

E. fuscus. Known at present only from Dolphin Head, Westmoreland, and Quick Step, St. Elizabeth.

E. andrewsi. In the Blue Mountains from about 3000 to 5000 feet.

E. junori. Known only from Spaldings in the Parish of Clarendon, at an elevation of about 2900 feet.

There are thus two wide-ranging species, *gossei* and *pantoni*. Both *andrewsi* and *junori* have their ranges overlaid by, and contained within, the ranges of both *pantoni* and *gossei*. *E. nubicola* seems to replace *pantoni* in the Blue Mountains above elevations of about 4000 feet, while *alticola* in turn replaces *nubicola* from slightly below 6000 feet to the tops of the highest peaks. On the slopes of the mountains, the ranges of *pantoni* and *nubicola* overlap by only a few hundred feet at about the 4000-foot level while the ranges of *nubicola* and *alticola* overlap by a few hundred feet at about the 6000-foot level. *E. fuscus* is known only from two specimens from Dolphin Head and one from Quick Step. With so few specimens it is impossible to generalize regarding its ecology or distribution, but it is known to occur with *pantoni* at Dolphin Head.

HABITS AND HABITAT

The group as a whole is comprised of terrestrial species. In habits and habitat *gossei* is perhaps the most generalized. It is found in rather dry situations and also in some of the humid cloud forest ravines in the mountains. During the day the frogs seem to spend most of their time under rocks; at night they come out and call from the ground, at times climbing up on rocks and even sometimes on low bushes.

E. pantoni seems to be, next to *gossei*, the most tolerant of dry conditions although it is also found in very humid situations. As with *gossei*, the frogs can be found under rocks during the day. In the evening they can be seen and heard calling from the ground and low rocks.

E. nubicola is an inhabitant of the cloud forest in the Blue Mountains below 6000 feet. Specimens can be collected along the trails during the day by looking under rocks; at night the frogs leave their shelters and sit on the ground or low rocks.

E. alticola inhabits the cloud forest in the Blue Mountains above 5600 feet and ranges up to the wind scrub on the top of Blue Mountain Peak where it is very common. Specimens can be collected by looking beneath the rocks that border the trails.

E. andrewsi I have never taken in the daytime. All of the specimens that I have collected were found along the trail. They were calling from the open rocky region on the trail proper as well as from beneath the bushes beside the trail. I have never seen any of them show any propensity for climbing.

E. junori is known from seven specimens which Dr. Dunn collected at Spaldings in September, 1925. I spent six nights collecting in the rocky hills about Spaldings in late August and early September in 1952 but was not able to collect *junori* or to hear its voice. Concerning this species Dr.

Dunn (1927: 535) says: "This is a tiny, short-legged, short-snouted form, which lives in the woods, and calls exclusively from holes in the rocks. The call can hardly be transliterated, sounding like a child's wooden ratchet. It is a long call, very deceptive and hard to trace, rising to a high pitch and falling again to silence, so that I did not know whether it was a night bird flying past, or whether it was on the ground or in the trees, until I saw the frog calling."

E. fuscus is known from two specimens from Dolphin Head, Westmoreland, and one from Quick Step in St. Elizabeth. I have never seen it alive or heard its call.

I have collected the eggs of *gossei*, *nubicola*, *alticola* and *pantoni*. The breeding habits of these species do not seem to give definite clues as to their relationship. If anything, I would say that they are more a reflection of the size. *E. pantoni*, the largest of these species, lays the largest number of eggs, with as many as 104 in a clutch; *nubicola*, the next smaller in size, lays from 26 to 75 eggs in a single clutch; *gossei* has up to 33 eggs in a clutch; the 20 clutches of *alticola* eggs that I have collected averaged 23 per clutch. The eggs of both *nubicola* and *pantoni* are large and in the main non-adhesive so that they spread out in one or two layers in the nest whereas the eggs of the two moderate-sized species, *gossei* and *alticola*, are both smaller in size and much more adhesive so that they tend to cluster up into little groups somewhat like bunches of grapes. The eggs of all four of these species are laid in hollow places under rocks.

EVOLUTION

The detailed descriptions of the morphology of these species can be found in Lynn (1940) and Lynn and Dent (1943), so I list here only the major features of their morphology. As stated above, the species in the group can, in general, be characterized by long vomerine series, feebly developed digital disks, smooth back and belly, and red in the groin in life.

E. gossei. A moderate-sized species practically invariable in the characters listed above.

E. nubicola. A rather large species with the characters of the group plus the additional character of having the belly quite dark in life.

E. alticola. A moderate-sized species with the characters of the group except for the fact that the vomerine series may vary from long to quite short.

E. pantoni. A large species characterized by the yellow color of the belly in life.

E. fuscus. A large species lacking (at least in the three known specimens) red in the groin in life.

E. andrewsi. A small species.

E. junori. A small species.

It can thus be seen that there are three large species, *nubicola*, *pantoni* and *fuscus*, two moderate-sized species, *gossei* and *alticola*, and two small species, *andrewsi* and *junori*.

As Dunn (1926a: 116) has pointed out, "Adult size is one of the most

ART. 11. GEOGRAPHIC DESIGNATION OF THE MEMBERS OF THE CHADRON FORMATION IN SOUTH DAKOTA

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In 1937, I recognized three members of the Chadron formation of South Dakota* which were locally identifiable by their lithology. At the time, it seemed inadvisable to give these members geographic names, because they were recognizable only locally. The designations A, B and C and 1, 2 and 3 had already been used for purely faunal subdivisions known to be invalid, so I used the names Lower Member, Middle Member, and Upper Member. Work on lower Oligocene sediments in other localities has necessitated occasional references to these members and confusion has arisen as to whether, for instance, the expression "older Chadronian" means "coeval with the Lower Member of Clark 1937" or simply "older part of the early Oligocene." Personally, I do not approve of geographic names for thin, local members of formations, but the overwhelming majority of vertebrate paleontologists favor geographic names in this case. I, therefore, wish, at this time, to designate a standard section for the Chadron formation in South Dakota with geographic names for its members.

The standard section for the Chadron formation in the Big Badlands is the south fork of Indian Creek, Pennington County, from Sec. 34, T.3S., R.12E. to Sec. 10, T.4S., R.12E. The member formerly designated as the Lower Member shall be called the Ahearn member, from the name of a ranch formerly at the mouth of the south fork of Indian Creek. The member formerly known as the Middle Member shall be called the Crazy Johnson member. The member formerly known as the Upper Member shall be called the Peanut Peak member.

These last two names are the alternative local names given to the prominent butte in the southern part of Sec. 10, T.4S., R.12E., which is called both "Crazy Johnson Butte" and "Peanut Peak", referring to attempts by a man named Johnson to raise peanuts on top of it. The standard section for these two members is the north face of this butte, illustrated in Plate XXI, upper figure, of the Annals of the Carnegie Museum, v. 25, art. 21, referred to above.

It is obvious that more widely used geographic names would be preferable to these. However, the three members are all fossiliferous and are most characteristically developed at this locality, and no other geographic names are available here. It seems advisable, therefore, to let geologic practicability override euphony and lexicographic elegance in this case.

In the original definition of the three members, the Ahearn (Lower) member was described as characteristically including red sediments. It was assumed that all of these reds were inherited, either from a lateritic soil on the uplands or from the Spearfish and Opeche formations of the Black Hills.

*J. Clark. The stratigraphy and paleontology of the Chadron formation in the Big Badlands of South Dakota. Annals of the Carnegie Museum, 1937, v. 25, art. 21, p. 261-350.

Careful restudy has confirmed the presence of inherited reds in clay pebbles and small laminae interbedded with greenish sediments. However, small hematite concretions also occur, with ramifying extensions which could not have undergone transportation. Also, in some cases a red-stained zone of hematite concentration surrounds bone inclosed in even-grained, otherwise green sandstone. It is evident, therefore, that both inherited and epigenetic reds occur within the Ahearn member. The diagenetic nature of the red-orange color in the Peanut Peak and Crazy Johnson members has been further confirmed by recent field studies; it is apparent that three different types of red beds are represented in the Chadron of South Dakota.

In the original paper, bentonitic material was not reported for the western-derived Chadron sediments (p. 284). It was first detected by Ray Alf, now of Webb College, California, who wrote an unpublished paper on the subject. I have since confirmed Mr. Alf's observation. All three members contain ash, which differs from the ash of the overlying Brule in being completely bentonitic, while the Brule ash consists partly of fresh shards.

Additional information and interpretation will be presented in a forthcoming paper on the faunas of the three members.

constant characters in this group." I agree with him that adult size is a valid specific character.

I believe that much of the evolution in the group on the Island of Jamaica has been ecological rather than geographic in nature. With so many of the species overlapping in range, and not showing any marked ecological differences, I puzzled for a long time about how they could have evolved, until I happened to recall a statement by Dunn (1926b: 37) concerning ecological speciation, "where the nearest relative is in the same region and the same habitat but of a quite different size."

I consider *gossei* the most generalized species, and such forms as *andrewsi*, *junori* and *alticola* the more specialized. *E. pantoni* and *nubicola* certainly lie between these two extremes. Not enough is known of *fuscus* to place it precisely, but from its rarity I am inclined to think it is most likely a specialized species.

When adult size is considered, the distribution of the species forms a definite pattern. Thus, on the lower slopes of the Blue Mountains, there are three species occurring together, the large *pantoni*, the moderate-sized *gossei*, and the small *andrewsi*. As we go up the mountain slopes, the large *pantoni* is replaced by the large *nubicola*, and only *above* the range of the moderate-sized *gossei* does the moderate-sized *alticola* appear. Likewise, in the vicinity of Spaldings there are three species, the large *pantoni*, the moderate-sized *gossei* and the small *junori*. So far as is known, the ranges of the small *junori* of the central mountain mass and the small *andrewsi* of the Blue Mountains do not come in contact. Thus we have in the group two species of approximately the same size occurring together only in the case of *pantoni* and the very rare *fuscus* in the western portion of the Island. Whether or not there is ecological separation between these two species has not been determined.

It thus seems to me that the evolution has been about as follows: A moderate-sized *gossei* or pre-*gossei* parent stock gave rise to a large-sized *pantoni* stock with differences in size permitting them to occupy the same major habitat and both of them becoming widespread.

E. pantoni, in turn, gave rise to the small *junori-andrewsi* stock. It may seem strange for me to consider *pantoni*, the largest species in the group, as a close relative, and probably the parent of, the *andrewsi-junori* stock, the smallest species in the group. For anyone who doubts their close affinity, however, I would suggest that he examine and compare specimens of *andrewsi* with immature specimens of *pantoni* that are equal in size to *andrewsi* and have only the pattern of pelvic spots.

E. andrewsi and *junori* have perhaps speciated geographically from a pre-*andrewsi-junori* stock or, and I consider this more probable, they both may be independent derivatives of *pantoni*.

I believe the same *gossei* or pre-*gossei* stock gave rise to the large *nubicola* in the cloud forest region of the Blue Mountains between 4000 and 6000 feet, with *nubicola*, in turn, giving rise to the moderate-sized *alticola* which occupies the higher peaks of the Blue Mountains above the range of *gossei*.

The little-known *fuscus* is apparently related to *pantoni*.

My concept of the evolution of this group is illustrated diagrammatically in Fig. 1.

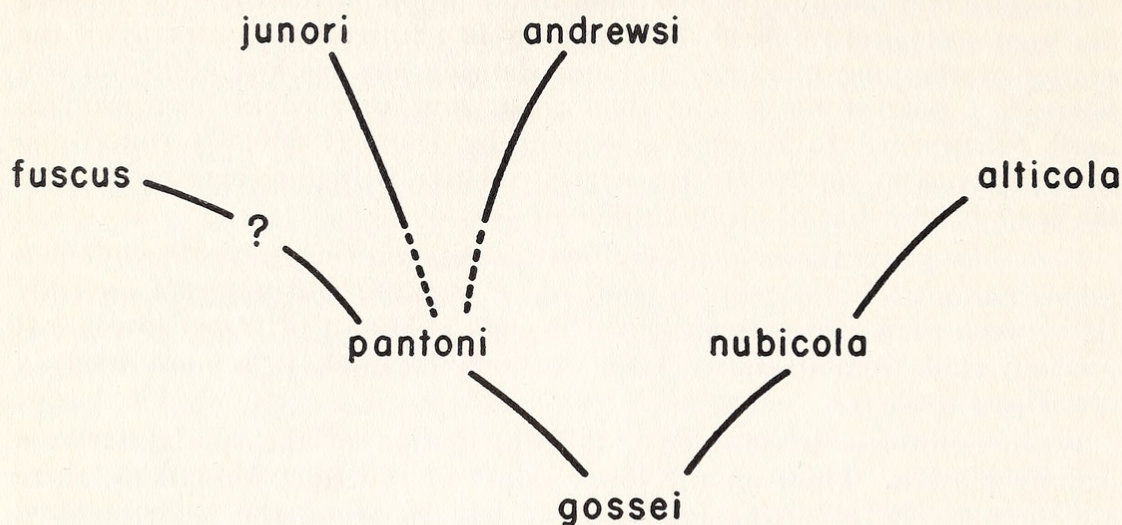


FIG. 1. SUGGESTED PHYLOGENY OF THE *gossei* GROUP OF THE FROG GENUS *Eleutherodactylus*.

COLOR PATTERNS OF THE GROUP

While it is impractical to define all of the minor pattern modifications in this group of *Eleutherodactylus*, there seem to be at least eight basic types of patterns, and these are described below. The citation at the end of the description of each pattern is to the figure of this pattern, from an actual specimen, in Lynn's "Amphibians" [of Jamaica] (Lynn, 1940).

Mottled. The mottled pattern consists of a brown background overlaid by a mottling of dark brown or black. The most consistent element of this pattern is the arrangement of dark pigment in a W-shaped mark on the back in the suprascapular region. This W-shaped mark extends from above the arm on one side of the back to above the arm on the opposite side with the apex of the middle portion being directed anteriorly and being located precisely on the midline of the back. Generally the area of the back immediately caudad of the two posteriorly directed apices of the W is somewhat lighter than the surrounding dorsum. Posterior to this lighter area, a fainter wavy line of dark pigment is discernible. In addition, a dark interocular bar is present. It is of interest to note that the W-shaped mark described above is the one so easily recognized in many different species of *Eleutherodactylus*. Most of the variation in the mottled pattern is apparently due to differences in intensity of pigmentation. While there is a great deal of individual variation, there appears to be a general tendency for intensity of pigmentation to increase with age. In hatchlings the pattern as described above is immediately apparent, but in large mature individuals it is quite often obscured by a general darkening of the dorsum. (Plate IV, Fig. 6.)

Dorsolateral stripes. This pattern consists of two broad cream-colored bands, one on each side, originating on the posterior margins of the upper eyelids, passing posteriorly above the tympani directly backward through

the arms of the W and finally terminating on the back above the insertions of the hind limbs. As the cream-colored bands pass through and thus obliterate the arms of the W, all that is left of it is the central portion forming an inverted V-shaped mark in the suprascapular region between the two lateral stripes. (Plate VI, Fig. 11, c.)

Picket. In this pattern there is a light area bounded anteriorly by the posterior margin of the middle section of the W-mark. Behind the two posterior apices of the W the lateral margins of this light area appear comparable to the median margins of the cream-colored areas in individuals which have dorsolateral stripes. Thus when both dorsolateral stripes and picket patterns occur in the same individual, the light picket occupies the entire area between the dorsolateral stripes posterior to the V-mark. (Plate VI, Fig. 11, b.)

Mid-dorsal stripe. This pattern in the adults consists of a narrow cream-colored median line extending from the snout to the vent, there branching and continuing on the posterior margin of each leg to the sole of the foot, terminating at the juncture of the fourth and fifth toes. Ventrally, a median, narrow, cream-colored line extends from the tip of the chin to the crotch. It should be noted that this is the only one of the patterns herein described that carries over onto the ventral side of the body. The midventral portion of this pattern tends to become obliterated with increasing size (hence age) of the individual, but is discernible as a median line on the chin and throat in the largest specimens. In hatchlings the mid-dorsal portion of this line extends only as far forward as the median anteriorly directed apex of the W but in mature individuals it continues on to the snout. (Plate VI, Fig. 11, a.)

Broad mid-dorsal stripe. This pattern consists of a sharply defined, light, cream-colored stripe running from back of the head to the vent along the median dorsal line. Throughout most of its distance it is about as wide as the greatest diameter of the eye. Its margins are sharply defined by black or very dark brown. (Plate IV, Fig. 7, e.)

Pelvic spots. The major feature of this pattern consists of a rather small but conspicuous, coal-black, more or less rounded patch along the back above each groin. (Plate VII, Fig. 13.)

Interocular bar. This consists of a sharply-defined, cream-colored, slightly convex bar across the top of the head from the upper eyelid of one eye to the upper eyelid of the other eye. It is margined both anteriorly and posteriorly by buff brown or black. (Plate VII, Fig. 12.)

Purple. This pattern occurs only with dorsolateral stripes and may be a modification of it. It consists of a moderately narrow mid-dorsal stripe, from tip of snout to groin, Indian purple in color, two dorsolateral stripes of pearl gray extending from the eyes to just behind the groins, each in turn bordered by Indian purple. The background between the median Indian purple stripe and the Indian purple stripe forming the inner margin of the dorsolateral stripe is seal brown. (Plate IV, Fig. f.)

Of the eight color patterns described above, I have recently published data (Goin, 1950) indicating that the following patterns are genetic in nature:

E. nubicola. Dorsolateral stripes, picket, mid-dorsal stripe, mottled.

E. alticola. Dorsolateral stripes, mid-dorsal stripe, mottled.

E. pantoni. Dorsolateral stripes, mottled.

Goin and Cooper (1950: 2) pointed out that individuals both with and without dorsolateral stripes occurred in a single set of hatchlings of *E. gossei*.

As these patterns are known to be inherited in these species, I believe that Sturtevant's (1948: 230) conclusion "there can be no doubt that, in general, related species have essentially the same complements of genes" makes it safe to assume that they are genetic in the entire group.

As I pointed out (Goin, 1950), the genes involved seem to control patterns that overlie and modify the basic mottled pattern. It should also be pointed out here that these patterns are not mutually exclusive so that various combinations of them can, and do, obtain. Thus, a *pantoni* may have dorsolateral stripes, mid-dorsal stripe, and picket at one and the same time. Hence there are many more phenotypic expressions possible than there are basic patterns involved.

The species in the group exhibit these basic patterns as follows:

E. gossei. Mottled, dorsolateral stripes, picket (?), mid-dorsal stripe, broad mid-dorsal stripe, pelvic spots, interocular bar, purple.

E. pantoni. Mottled, dorsolateral stripes, picket, mid-dorsal stripe, pelvic spots.

E. nubicola. Mottled, dorsolateral stripes, picket, mid-dorsal stripe, broad mid-dorsal stripe, pelvic spots.

E. alticola. Mottled, dorsolateral stripes, mid-dorsal stripe.

E. junori. Mottled, dorsolateral stripes, mid-dorsal stripe, interocular bar.

E. andrewsi. Pelvic spots.

E. fuscus. Mottled.

I have seen all of these patterns in their pure form in the species listed above except picket pattern in *gossei*. I have seen specimens of *gossei* which have a pattern somewhat like picket but certainly not the same clear-cut pattern exhibited by *pantoni* and *nubicola*.

When the presence of these various patterns in the species is correlated with the suggested evolutionary history presented above, a rather striking fact stands out—that, as we pass from the rather generalized parent stocks to the more specialized filial species, there is a reduction in the number of color patterns present. Furthermore, the patterns that drop out or become fixed are not necessarily the same in the different evolutionary lines so that whereas we have the generalized *gossei* with many patterns, *alticola*, at the terminus of one evolutionary line, retains only mottled, dorsolateral stripes and mid-dorsal stripe, and in *andrewsi*, at or near the terminus of another evolutionary line, every known specimen shows only pelvic spots.

E. nubicola, which I have assumed to be between *gossei* and *alticola*, has six of the eight patterns shown by *gossei* and has none that are not present in *gossei*; and *alticola* has three of the six present in *nubicola* but none that are not present in *nubicola*. Along the other line, *pantoni* has five of the eight patterns present in *gossei* but none not present in *gossei*; *junori* has three present and one not at present known in *pantoni*; finally, as mentioned above, the pattern of pelvic spots seems to be fixed in *andrewsi*.

The three known specimens of *fuscus* are all mottled.

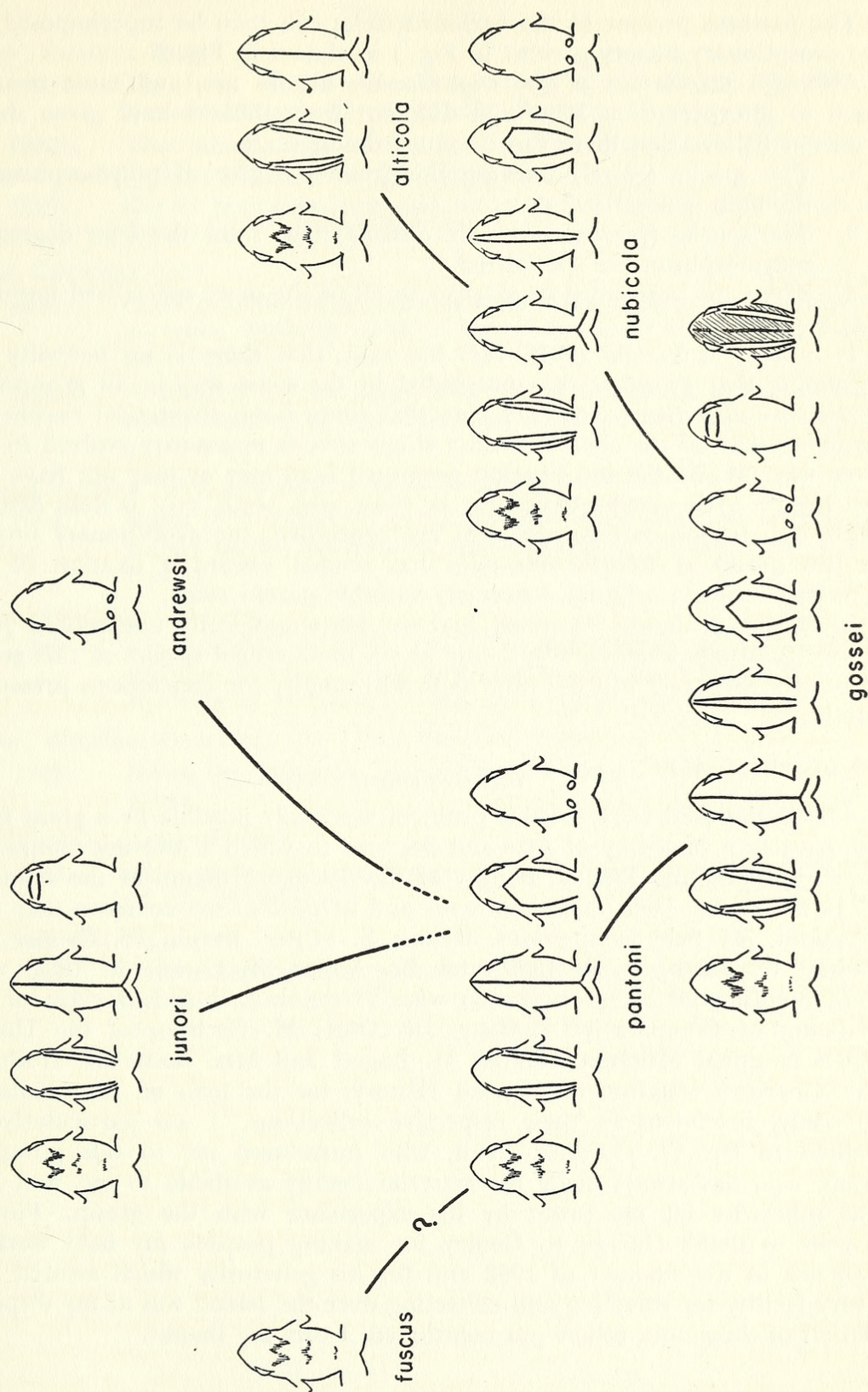


FIG. 2. SUGGESTED PHYLOGENY OF COLOR PATTERNS IN THE *gossei* GROUP OF THE FROG GENUS *Eleutherodactylus*.

The patterns present in the various species can then be superimposed on the evolutionary history present in Fig. 1 as shown in Fig. 2.

Although the details of the evolutionary history are, and must remain, open to interpretations somewhat different from those I have given them, I do not believe that there can be much doubt that:

1. The species (*gossei*) showing the greatest degree of polymorphism is the most generalized.
2. The species (*junori*, *andrewsi*, *alticola*) that show the least degree of polymorphism are specialized.
3. The same patterns do not occur in all of the more specialized terminal species.

It is true, as Wright (1940: 181) has said, that there is no necessity for supposing that evolution has proceeded in the same way in all groups. It also seems to me to be equally true that there is no theoretical reason for assuming that all the characters in a single species necessarily evolved in the same way. While the information presented here may or may not have any bearing on such specific characters as voice, size, teeth, etc., it does demonstrate that insofar as color patterns are concerned, the evolutionary process in this group of *Eleutherodactylus* has tended toward a fixation of the genotype from an original, extremely variable parent stock.

In closing it should be stated that the herpetologically unexplored John Crow Mountains undoubtedly house as yet undescribed species of this group of frogs. Only time will tell how these will modify the conclusions presented herein.

ACKNOWLEDGMENTS

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