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ELEUTHERODACTYLUS NUBICOLA DUNN

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PATTERN VARIATION IN THE FROG
ELEUTHERODACTYLUS NUBICOLA DUNN

COLEMAN J. GOIN¹

SYNOPSIS: An analysis is made of the color pattern variation in the Jamaican frog, *Eleutherodactylus nubicola* Dunn. A basic pattern, Mottled, may be overlaid by no less than six modifying patterns as follows: Dorsolateral stripes, Middorsal stripe, Broad middorsal stripe, Picket, Interocular bar, and Pelvic spots. It is possible to have more than one of these modifying patterns present in a single individual; one specimen had, at one and the same time, Dorsolateral stripes, Middorsal stripe, and Picket. Evidence is presented that these modifying patterns are inherited in a mendelian manner and Dorsolateral stripes and Middorsal stripe seem to be dominant. Evidence is not yet available that will permit us to determine if the other pattern modifiers are dominant or recessive.

It is pointed out that certain Rhacophoridae from Ceylon and Microhylidae in the Papuan region not only have developed terrestrial breeding habits like those of *Eleutherodactylus*, but that they have several of the pattern modifications described for *E. nubicola*. The significance of the parallelism is at present unknown.

With the possible exception of the African genus *Hyperolius*, the neotropical frog genus *Eleutherodactylus* is the most "difficult" taxonomically of any of the large anuran genera. The reason seems to be threefold—the phenomenal amount of speciation, the morphological similarity of the species, and the intraspecific diversity of color pattern. In earlier papers (Goin, 1947, 1950) I presented evidence that much of this variability in color pattern is due to a series of genes that are inherited in a mendelian manner. So little is known of amphibian genetics that the determination of the genetic basis of color pattern inheritance in these species is of interest in itself, but more importantly, an understanding of it may help to throw light on the evolution and relationship of species within this complex genus, and possibly on the even more fundamental problems of evolution in natural populations.

Eleutherodactylus contains nearly 250 recognizable forms. Many of the species are rather variable in color pattern, with the same basic pattern modifications occurring in species after species. The evidence, discussed below, suggests that these pattern variations reflect the segregations of a number of different genes (and their alleles) which are homologous in the different species.

¹ The author is Professor of Biological Sciences, University of Florida, and Research Associate, Carnegie Museum. Manuscript submitted 16 February 1960.

My interest in this problem first centered on *E. ricordi planirostris*, a species with two phenotypes, which was introduced into Florida and has been abundant locally for a number of years. At the suggestion of my friend, W. Gardner Lynn, I later turned my attention to *E. nubicola* of Jamaica, because this species is known to have a large number of phenotypes and because its eggs can be collected easily along the mountain trails in the Blue Mountains of Jamaica. In the summer of 1948 I was able to collect 25 clutches of *nubicola* eggs which produced 1002 hatchlings. Analysis of the data (Goin, 1950) indicated that, as in *planirostris*, variability in *nubicola* is produced by genes that modify the color pattern and that are inherited in a simple mendelian manner. Additional data gathered on two related species, *alticola* and *pantoni*, indicate a similar mode of pattern inheritance in these forms. I returned to Jamaica in 1957 to gather additional material on *nubicola*; 43 clutches, comprising 1341 hatchlings, were collected on this trip. These, together with the previous material, make a total of 2,343 young *nubicola* from 68 clutches of eggs now available for analysis.

ACKNOWLEDGMENTS

In the course of this work I have become indebted to a great many institutions and people. My field work in 1948 was financed by the American Academy of Arts and Sciences, that in 1957 by the American Philosophical Society. I obtained data on the variability of other species in Jamaica in 1952 by field work done with the aid of a grant from George R. Cooley. As is true of anyone doing natural history work in Jamaica, I am deeply indebted to C. Bernard Lewis and his staff at the Science Museum, Institute of Jamaica. The Forest Department of Jamaica, through its Conservators, E. W. March, E. M. Brown, and J. A. N. Burra, made the Forest Hut at Clydesdale available to me as a base of operations. My neighbor in the Blue Mountains, Bonner E. C. Shekell, formerly of Chester Vale, St. Andrew, rendered me a number of courtesies that made my stay in the mountains more pleasant and profitable. My field companions, Dennis E. Miller, Byrum W. Cooper, and Robert H. Barth in 1948, Albert M. Laessle in 1952, and my wife and two children in 1957, helped appreciably in the collecting of the eggs. My research assistant, Ronald Baxter, aided in tabulating the results. My colleague, Kenneth W. Cooper, contributed materially by his help in analyzing the data and Henry W. Wallbrunn assisted in some of the statistical calculations. Curt Stern most kindly took time from his busy schedule to go over the manuscript and has made several helpful suggestions. As usual, I

am deeply obligated to my wife, Olive Bown Goin, for her skillful assistance in typing and editing the manuscript. This work was completed while I was under tenure of a Grant (G-5628) from the National Science Foundation. To all of the above I am deeply grateful.

Eleutherodactylus nubicola Dunn

Eleutherodactylus nubicola is a montane species found in the Blue Mountains of Jamaica between the altitudes of 4000 and 6000 feet. Lynn (1942) described in detail its life history and embryonic development. The slopes of the Blue Mountains are so steep it is practical to collect only beside the foot trails. The female lays from 26 to 75 eggs which are fertilized by a single male at the time of deposition. The eggs are not scattered, but are gathered together in a single, compact bunch under a rock. Thus it is certain that each clutch is the product of a single set of parents. The female remains with the clutch during intraovular development. It is thus possible for one to determine the phenotype of the female parent of many clutches of eggs collected in the field, although at times the female escapes before her pattern can be noted.

A study of live individuals in the field and preserved specimens in the laboratory indicates that there is a basic pattern, Mottled, with at least six distinctive modifications as follows: Dorsolateral stripes, Middorsal stripe, Broad middorsal stripe, Picket, Interocular bar, and Pelvic spots. Data compatible with a simple mendelian interpretation are now available for all of these patterns except Broad middorsal stripe and Pelvic spots.

In the discussion that follows, the locus for genes affecting Dorsolateral stripe is indicated by S, that for Picket by P, that for Middorsal by M. A dominant gene at the S locus is designated by S, its recessive allele by s, and correspondingly P and p, and M and m, for the other loci.

The following data are now available for pattern inheritance analysis:

(1) For the phenotypic ratios in the wild population, 300 specimens collected along the mountain trails in the same area where the eggs were taken showed the following patterns or pattern combinations (females with eggs are included):

Mottled—222

Dorsolateral stripes—32

Picket—21

Middorsal stripe—21

Dorsolateral stripes plus Middorsal stripe—2

Picket plus Middorsal stripe—2

(2) From mothers of known pattern 1544 hatchlings from 45 clutches of eggs:

Mother—Mottled (34 clutches)

Collected in 1948

26 Mottled, 20 Dorsolateral stripes
 25 Mottled, 28 Middorsal stripe
 25 Mottled, 26 Middorsal stripe
 26 Mottled
 43 Mottled
 58 Mottled
 47 Mottled
 42 Mottled
 53 Mottled
 21 Mottled
 51 Mottled
 33 Mottled
 41 Mottled

Collected in 1957

33 Mottled, 4 Dorsolateral stripes
 5 Mottled, 3 Dorsolateral stripes
 19 Mottled, 12 Dorsolateral stripes
 3 Mottled, 4 Dorsolateral stripes
 43 Mottled, 19 Dorsolateral stripes
 26 Mottled, 14 Middorsal stripe
 16 Mottled, 21 Middorsal stripe
 53 Mottled, 8 Picket
 13 Mottled, 11 Picket
 22 Mottled
 21 Mottled
 13 Mottled
 14 Mottled
 29 Mottled
 26 Mottled
 36 Mottled
 29 Mottled
 39 Mottled
 41 Mottled
 11 Mottled
 37 Mottled

Mother—Dorsolateral stripes (5 clutches)

Collected in 1948

31 Dorsolateral stripes
 9 Mottled, 8 Dorsolateral stripes
 5 Mottled

Collected in 1957

6 Mottled, 16 Dorsolateral stripes
 21 Mottled, 30 Dorsolateral stripes

Mother—Middorsal stripe (4 clutches)

Collected in 1948

29 Mottled, 16 Middorsal stripe
 34 Mottled, 39 Middorsal stripe

Collected in 1957

5 Mottled, 5 Middorsal stripe,
 10 Picket
 16 Mottled, 19 Middorsal stripe

Mother—Picket (2 clutches)

Collected in 1948

7 Mottled, 4 Dorsolateral stripes,
 3 Picket, 4 Middorsal stripe,
 3 Dorsolateral stripes plus
 Picket, 5 Picket plus Mid-
 dorsals stripe, 5 Dorsolateral
 stripes plus Picket plus Mid-
 dorsals stripe

Collected in 1957

13 Mottled, 11 Picket

(3) From parents of unknown phenotype 799 hatchlings from 23 clutches of eggs:

Collected in 1948	Collected in 1957
5 Mottled, 4 Dorsolateral stripes	4 Mottled, 4 Dorsolateral stripes
23 Mottled, 22 Middorsal stripe	11 Mottled, 15 Dorsolateral stripes
48 Mottled	15 Mottled, 29 Dorsolateral stripes
60 Mottled	31 Mottled, 3 Dorsolateral stripes
34 Mottled	20 Mottled, 14 Dorsolateral stripes,
39 Mottled	10 Interocular bar, 11 Dorsolateral stripes plus Interocular bar
	13 Mottled, 16 Midorsal stripe
	26 Mottled, 17 Picket
	25 Mottled, 25 Picket
	21 Mottled
	29 Mottled
	35 Mottled
	41 Mottled
	27 Mottled
	20 Mottled
	29 Mottled
	26 Mottled
	47 Mottled

Mottled

The Mottled pattern consists of a brown background overlaid by a dark brown or black mottling. The most consistent element is a dark W-shaped mark in the suprascapular region, extending from above the arm on one side to above the arm on the opposite side. The apex of the middle portion of the W is directed anteriorly and located on the midline of the dorsum. The area immediately caudad to the two posteriorly directed apices of the W is generally somewhat lighter in color than the surrounding dorsum. A faint, wavy line of dark pigment is discernible caudad of this lighter area. A dark interocular bar is present. Intensity of pigmentation shows a great deal of individual variation and generally tends to increase with age. In hatchlings the pattern is immediately apparent, but in large, mature individuals it is often obscured by a general darkening of the dorsum.

The main features of this basic pattern may be discerned in the majority of the species of this genus. In *E. nubicola* it seems to be the basic wild pattern upon which the pattern modifications discussed below are superimposed.

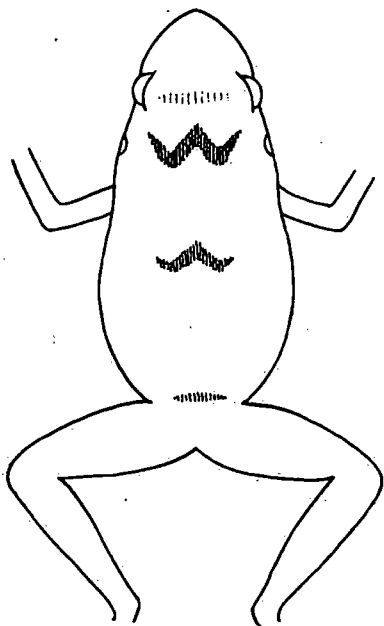


Figure 1. Diagrammatic sketch of Mottled pattern.

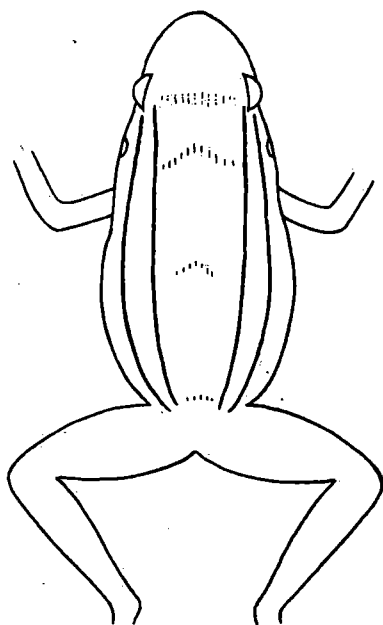


Figure 2. Diagrammatic sketch of Dorsolateral stripes pattern.

Dorsolateral stripes

In this pattern two broad cream-colored bands, one on each side, originate on the posterior margins of the upper eyelids, pass posteriorly above the tympani directly backward through the arms of the W, and terminate above the insertions of the hind limbs. These cream-colored bands obliterate the arms of the W leaving only the Λ -shaped portion between the two stripes in the suprascapular region.

This is one of the most widely distributed pattern modifications in the genus. I have demonstrated fairly conclusively (Goin, 1947) that in *E. ricordi planirostris* this pattern is determined by a dominant gene that is inherited in a simple mendelian fashion.

No clutches of eggs of *E. nubicola* were taken for which the color patterns of both parents were known, but indirect evidence for dominance or recessivity may be sought by use of the Hardy-Weinberg equilibrium formula

$$q^2 SS : 2q(1-q) Ss : (1-q)^2 ss$$

to determine the genotypic ratio in the wild population.

If we assume Dorsolateral stripes to be dominant, then in a population in which 34/300 showed Dorsolateral stripes,

$$2q(1-q) + q^2 = 34/300 = 0.1133$$

therefore

$$(1-q)^2 = 0.8867 \text{ and } 1-q = 0.9416$$

hence

$$q = 0.0584$$

in which case

$$SS = 0.0034 \quad Ss = 0.1100 \quad ss = 0.8867$$

If the assumptions necessary for the application of the Hardy-Weinburg law are made, we can calculate the phenotypic constitution of the clutches of the offspring. Thus of 68 clutches of eggs only approximately 0.46 clutches would be expected to be made up of offspring with Dorsolateral stripes only, 14.08 clutches should contain offspring both with and without Dorsolateral stripes, and 53.46 clutches should be made up of nonstriped individuals only.

Going through the same steps, but assuming Dorsolateral stripes to be recessive rather than dominant, it can be calculated that of 68 clutches approximately 0.87 should contain only offspring with Dorsolateral stripes, 20.44 clutches should contain both types of offspring, and 46.69 clutches should contain no offspring having Dorsolateral stripes.

These two sets of estimates are compared with the actual results in table 1.

TABLE 1.

	Theoretical clutches Dorsolateral stripes dominant	Theoretical clutches Dorsolateral stripes recessive	Actual clutches
Dorsolateral stripes only	0.46	0.87	1
Mixed	14.08	20.44	16
Without Dorsolateral stripes only	53.46	46.69	51
Total	68.00	68.00	68
	$\chi^2 = 0.53^*$ $P = <0.5>0.3$	$\chi^2 = 2.14^*$ $P = <0.2>0.1$	

* Lines 1 and 2 are summed for calculation of χ^2 .

While these results give no certain statistical basis for choosing between the two assumptions, I believe that it logically may be assumed that the gene for Dorsolateral stripes is dominant in *E. nubicola* because it has been shown to be dominant in both *E. alticola* (Goin,

1950) and *E. r. planirostris* (Goin, 1947). As Sturtevant (1948: 230) has concluded, "there can be no doubt that, in general, related species have essentially the same complements of genes."

The pattern of Dorsolateral stripes has been recorded in at least the following species of *Eleutherodactylus* and is probably present in many others as well.

albipes
alticola
armstrongi
atkinsi
audanti
bogotensis
cuneatus
gossei
gundlachi

intermedius
juniori
lentus
ockendani
orcutti
orientalis
pantoni
pictissimus
planirostris

polytychus
portoricensis
rhodopis
richmondi
ricordi
rufifemoralis
turquinensis
wienlandi

Picket

This pattern consists of a light area on the dorsum, bounded anteriorly by the posterior margin of the middle section of the W mark. The lateral margins of this light area apparently coincide with the median margins of the cream-colored bands in individuals with Dorsolateral stripes. When both Dorsolateral stripes and Picket are present in the same individual, the entire area between the stripes posterior to the Λ -mark is occupied by the light picket.

On the basis that 23 out of the sample of 300 individuals of the wild population had the Picket pattern and 277 lacked it, an analysis similar to that made for the inheritance of Dorsolateral stripes may be made for Picket (see table 2).

Here the evidence is consistent with the assumption that the gene for Picket pattern is dominant.

I have found this pattern in only three other species: *gossei*, *pantoni*, and *polytychus*.

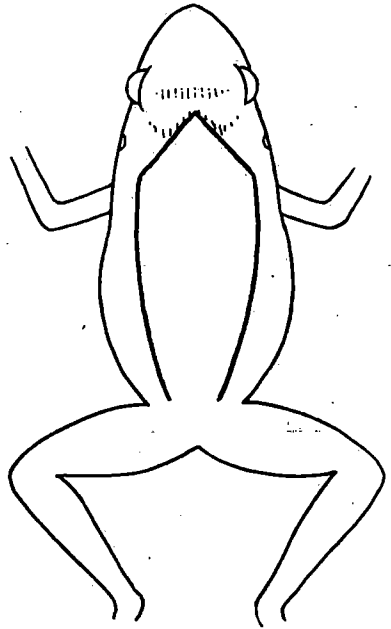


Figure 3. Diagrammatic sketch of Picket pattern.

TABLE 2

	Theoretical clutches Picket dominant	Theoretical clutches Picket recessive	Actual clutches
Picket only	0.22	0.40	0
Mixed	9.81	15.07	7
Without Picket only	57.97	52.52	61
Total	68.00	67.99	68

$$\chi^2 = 1.074$$

$$P = 0.3$$

$$\chi^2 = 6.003$$

$$P = <0.02>0.01$$

Middorsal stripe

In adults showing this pattern, the dorsum is marked by a narrow, cream-colored median line which extends from the snout to the vent and there branches to continue along the posterior margin of each leg to the sole of the foot, where it terminates at the juncture of the fourth and fifth toes. Ventrally a narrow, cream-colored, median line extends from the tip of the chin to the crotch. This is the only one of the patterns that is manifest on the ventral side of the body. The midventral portion of this line tends to become obliterated with increasing size (hence age) but even in the largest specimens a median line on the chin and throat is still evident. In hatchlings the middorsal portion of the stripe extends only as far forward as the anteriorly-directed apex of the W but in mature individuals it continues on to the snout.

Using the same method of analysis, on the basis that 25 in a sample of 300 individuals of the wild population had the Middorsal stripe pattern and 275 lacked it, similar calculations were made. The results are shown in table 3.

Some additional evidence may be obtained from the clutches of females having Middorsal stripe. Of five such clutches, each contained offspring showing Middorsal stripe. This is to be expected if

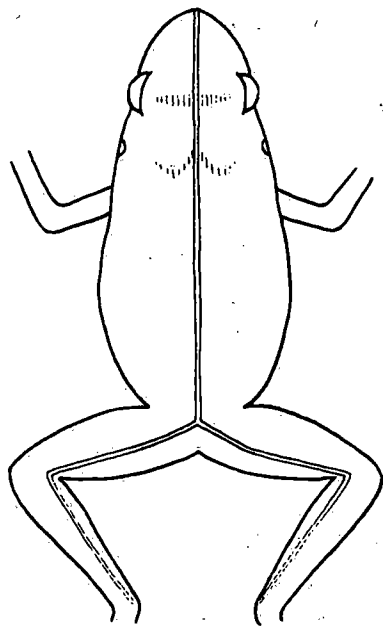


Figure 4. Diagrammatic sketch of Middorsal stripe pattern.

the gene for Middorsal stripe is dominant; if Middorsal stripe is recessive, each of these females must have mated with a male carrying the recessive gene. Since only 25 out of 300 adults in the population showed the pattern, then

$$25/300 = 0.0833 = (1-q)^2$$

and

$$(1-q) = 0.2886 \text{ and } q = 0.7114.$$

TABLE 3

	Theoretical clutches Middorsal stripe dominant	Theoretical clutches Middorsal stripe recessive	Actual clutches
Middorsal stripe only	0.24	0.47	0
Mixed	10.62	16.12	11
Without Middorsal stripe only	57.14	51.40	57
Total	68.00	67.99	68
	$\chi^2 = 0.0021$ $P = >0.95$	$\chi^2 = 2.4915$ $P = >0.1 < 0.2$	

The distribution of the genotypes in the population may accordingly be estimated:

$$\begin{aligned} MM &= 0.506 \\ Mm &= 0.411 \\ mm &= 0.083 \\ \hline &1.000 \end{aligned}$$

Still assuming the gene for Middorsal stripe to be recessive, each of the five females must have been mm in genotype. Since each female produced both Middorsal striped and non-Middorsal striped progeny, all five females must have mated with heterozygous males (Mm). But genotypically Mm frogs make up only 0.411 of the population, and the likelihood that, on chance alone, a given set of five females would each be mated with an Mm male is only $(0.411)^5$, or a P of 0.012—a poor likelihood. It seems most probable, then, that Middorsal stripe is also dominant.

This Middorsal stripe pattern occurs in at least the following additional species:

abbotti
alticola
antillensis
auriculatoides
avocalis

bakeri
cundalli
dimidiatus
gossei
junori

lanciformis
matudai
pantoni
portoricensis

Independent Assortment

For considering whether the three modifications of the basic Mottled phenotype that have been discussed so far are determined by genes that are multiple alleles, or whether these genes occur in different loci, evidence is provided by the presence of three modifications of the pattern in a single clutch. The most complex series of offspring from a single clutch is the set of 31 young from a Picket mother which contains 7 of the 8 combinations of patterns possible with these three modifiers. The presence in one clutch of all three modifications plus the basic pattern precludes the possibility that the three pattern modifiers are all allelomorphic *inter se* or to the basic pattern gene. Let us assume then that three different pairs of genes are involved, and that the gene modifying the color pattern is dominant.

Since there are unmodified Mottled offspring in this clutch, it would not have been possible for either parent to have been homozygous for Dorsolateral stripes, or Picket, or Middorsal stripe. As both Dorsolateral stripes and Middorsal stripe occur among the offspring in approximately a 1 : 1 ratio, and as the mother showed neither, the dominant genes for both of these patterns should have been present in the father. Since Picket is present in the mother and in approximately one-half of the young, the dominant gene for this character should not have been present in the father. Thus, on the basis of the argument given above, the mother must have been heterozygous for Picket and homozygous recessive for Dorsolateral stripes and Middorsal stripe, and the father must have been heterozygous for both Dorsolateral stripes and Middorsal stripe, and homozygous recessive for Picket. There should be, according to the laws of chance, a nearly equal distribution of the eight possible phenotypes in the offspring. The theoretical phenotypical composition of a clutch from this cross is compared below with the actual ratio of the 31 offspring of the female with Picket pattern.

	ss Pp mm × Ss pp Mm	
	Offspring	
	Theoretical	Actual
Mottled	3.875	7
Dorsolateral stripes	3.875	4
Picket	3.875	3
Middorsal stripe	3.875	4
Dorsolateral stripes plus Picket	3.875	3
Dorsolateral stripes plus Middorsal stripe	3.875	0
Dorsolateral stripes plus Picket plus Middorsal stripe	3.875	5
Picket plus Middorsal stripe	3.875	5

Moreover, if the parents were $ss Pp mm \times Ss pp Mm$, each of the three modifiers (Dorsolateral stripes, Picket, and Middorsal stripe), when considered individually, should be equally distributed among the offspring. Below the theoretical number is compared with the actual number of each of the three traits considered independently:

	Theoretical	Actual	P ²
Dorsolateral stripes present	15.5	12	0.14
Dorsolateral stripes absent	15.5	19	
Picket present	15.5	16	0.50
Picket absent	15.5	15	
Middorsal stripe present	15.5	14	0.36
Middorsal stripe absent	15.5	17	

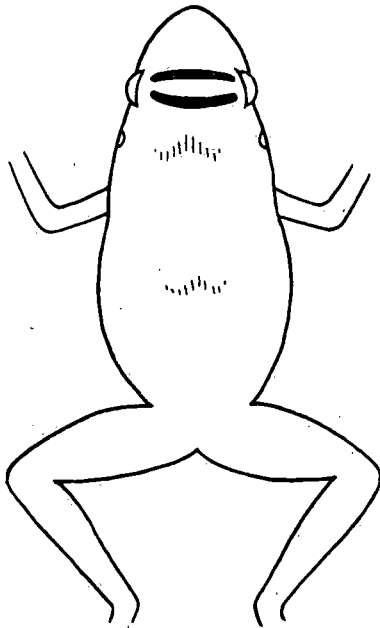


Figure 5. Diagrammatic sketch of Interocular bar pattern.

The actual ratios obtained for Middorsal stripe and Picket patterns are obviously very close to the expected ratios, and a ratio as divergent or worse than 12 to 19, as represented in the Dorsolateral stripes series, would be expected in a random sample about 14 percent of the time. The data are thus consistent with the hypothesis that there are three pairs of independent genes.

Interocular bar

A sharply defined, cream-colored, slightly convex bar passes across the top of the head from the upper eyelid of one side to the upper eyelid of the other side. Both anteriorly and posteriorly it is margined by buff-brown or black.

I had no data on this character.

² Binomial estimate of likelihood, on sampling error, of getting as bad or worse fit to 1:1 ratio.

when I first published on inheritance in *nubicola* (Goin, 1950). When I discussed the evolution of the *gossei* group (Goin, 1954) I reported its occurrence in *gossei* and *junori*, and later (Goin, 1957) I recorded it in *nubicola*. I am now able to report that Interocular bar in *nubicola*, like other pattern modifications, is apparently mendelian in nature.

In a clutch of 56 eggs from an unknown parent, 55 of the eggs hatched. The hatchlings showed the following patterns: 20 Mottled, 10 Interocular bar, 14 Dorsolateral stripes, and 11 Dorsolateral stripes plus Interocular bar. Thus it would seem that Interocular bar well might be the phenotypic effect of a simple dominant, or recessive, color-pattern gene—21 with the bar, 34 without—and also that it assorts independently of Dorsolateral stripes. Such a thesis is certainly consistent with what we know concerning the inheritance of the other color pattern modifiers. The presence of the character in two other species in the group is also suggestive. The fact that Interocular bar has not yet been found with color patterns other than Dorsolateral stripes is, I suspect, due simply to the rarity of the gene in the population.

Broad middorsal stripe

A sharply defined, broad, cream-colored stripe runs from back of the head to the vent along the median dorsal line. For most of its length it is about as wide as the greatest diameter of the eye. Its margins are sharply defined by black or very dark brown.

This is the only pattern modification so far known that might completely mask another. It is quite possible that the presence of Broad middorsal stripe would prevent the phenotypic expression of Middorsal stripe.

There are at present no data on the inheritance of this character. The possibility that it may be an allele to the gene for Middorsal stripe should not be overlooked.

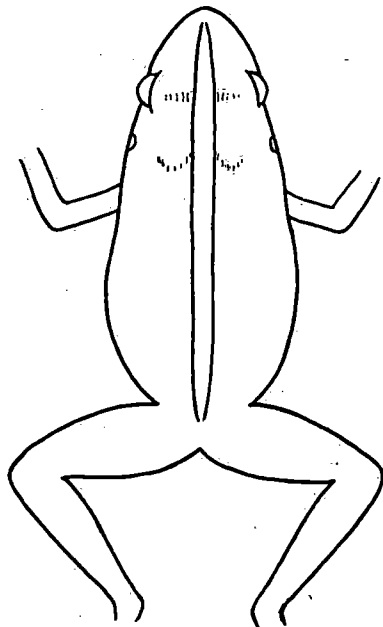


Figure 6. Diagrammatic sketch of Broad middorsal stripe pattern.

I know of this character in the following species:

alticola
gossei

intermedius
nubicola

rhodopis

Pelvic spots

A rather small but conspicuous, black, more or less rounded patch is present on each side of the back above the groin.

This pattern differs in two major respects from those so far discussed. It varies greatly in its conspicuousness and it is expressed by the addition of pigment rather than by deletion. (All of the other pattern modifications in *nubicola* are brought about by diminution or absence of pigment, resulting in the presence of pale, cream-colored areas.) In some mature individuals the pigmented pelvic spots are fairly conspicuous, in others they are rather dim. This variability seems to be due in part to variation in intensity of the spots themselves and in part to variation in the dorsal ground color of the individual.

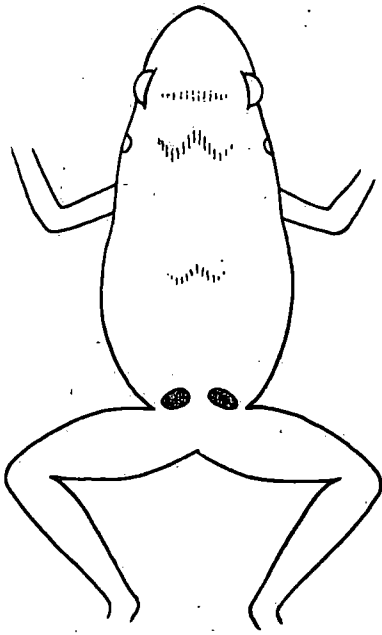


Figure 7. Diagrammatic sketch of Pelvic spots pattern.

Very dark, conspicuous Pelvic spots are invariably present in *E. andrewsi*, and I have seen paler, less conspicuous Pelvic spots in *pantoni* and *gossei* as well as *nubicola*. Judging from published descriptions, this character seems to be fairly widespread in the genus.

Corollary Discussion

The genus *Eleutherodactylus* is remarkable not only for the extent of its pattern variability but also for its life history and mode of embryonic development. Mating takes place and the eggs are laid on land. The young hatch, not as tadpoles, but as miniature replicas of the adult. It is not simply a case of metamorphosis before hatching, for the embryo fails to develop many of the typical tadpole char-

acters (e.g., functional gills, mouth parts, sucking disk) and does develop a flattened, respiratory tail.

A most remarkable instance of parallelism is shown by certain members of two other unrelated families of frogs (Rhacophoridae and Microhylidae) on the opposite side of the world. They have independently developed similar terrestrial breeding habits and similar patterns of embryonic development (tadpole structures lacking, respiratory tail present) and show, moreover, series of color pattern modifications essentially similar to those found in *Eleutherodactylus*.

Rhacophorus microtympanum (Günther), a member of the family Rhacophoridae, lives in the mountainous regions of Ceylon. It lays about 20 eggs on land in situations similar to those occupied by *E. nubicola*, and its embryo is of the eleutherodactyloid type. Kirtisinghe (1957: 11, 66-67) has pointed out the striking parallelism between this species and *E. nubicola* of Jamaica. The following patterns, as described for *nubicola*, also occur in *R. microtympanum*:

- (1) mottled pattern with dark pigment arranged in the shape of a W-mark on the back in the suprascapular region,
- (2) a pair of pale, dorsolateral stripes, one on each side from the eye to the groin,
- (3) a narrow middorsal stripe,
- (4) a pale interocular bar bordered posteriorly and anteriorly by darker pigment. (See Kirtisinghe, 1957, fig. 50)

In the Papuan region live a number of species belonging to several genera (*Sphenophryne*, *Oreophryne*, *Asterophrys*, etc.) of the family Microhylidae. Many of these species are highly variable in color pattern. Indeed, Parker's (1934: 163) description of color pattern variation in *Oreophryne variabilis* (Boulenger) from Mt. Bonthain, southern Celebes, reads like the description of some species of *Eleutherodactylus*. The following patterns are described:

- (1) a mottled pattern with a distinct, dark W-shaped mark on the back in the suprascapular region,
- (2) a pair of broad, yellow, dorsolateral light stripes from eye to groin,
- (3) a narrow middorsal stripe from snout to groin.

Parker also describes interocular light bars and ocellar dark spots in the groin in other species of this genus.

These Papuan microhylid genera are all probably rather closely related and are the only genera of Microhylidae anywhere in the

world known to have not only terrestrial breeding habits but also an eleutherodactyloid pattern of embryonic development with the young hatching as tiny frogs.

Thus members of three different families of frogs, from three distinct geographic regions, have independently developed very similar reproductive habits and embryos and at the same time show the same kinds of color patterns and pattern variability. It is perhaps significant that all three types are found in mountainous regions, and while not at present confined to mountains, they may well have evolved as montane forms. But the evolutionary significance of this striking parallelism is still not clear.

LITERATURE CITED

Goin, Coleman Jett

1947. Studies on the life history of *Eleutherodactylus ricordii planirostris* (Cope) in Florida with special reference to the local distribution of an allelomorphous color pattern. Univ. Florida Studies, Biol. Sci. Series, vol. 4, no. 2, xi + 66 pp., 6 pls., 7 text figs.
1950. Color pattern inheritance in some frogs of the genus *Eleutherodactylus*. Bull. Chicago Acad. Sci., vol. 9, no. 1, pp. 1-15, 1 pl.
1954. Remarks on evolution of color pattern in the *gossei* group of the frog genus *Eleutherodactylus*. Ann. Carnegie Mus., art. 10, pp. 185-195, 2 figs.
1958. Further studies on color pattern inheritance in the frog, *Eleutherodactylus nubicola*. Year Book Amer. Philo. Soc. for 1957, pp. 248-250.

Kirtisinghe, P.

1957. The amphibia of Ceylon. Privately published, Ceylon, xiii + 112 pp., 74 figs.

Parker, H. W.

1934. A monograph of the frogs of the family Microhylidae. British Mus. (Nat. Hist.), London, viii + 208 pp., 67 figs.

Sturtevant, Alfred Henry

1948. The evolution and function of genes. Amer. Sci., vol. 36, no. 2, pp. 225-236.

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