THE ANALYSIS OF A CONCRETE CASE OF INTERGRADATION BETWEEN TWO SUBSPECIES. II. ADDITIONAL DATA AND INTERPRETATIONS[1]

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In a recent number of these PROCEEDINGS[2] I presented some of the more important results of an intensive study of intergradation between two subspecies of *Peromyscus*. It was my announced intention to follow that article by a more extended one, to be published elsewhere, and covering in part the same ground. Since, however, such a procedure would involve much needless repetition, both of text and figures, it seems preferable that the earlier paper should merely be supplemented by another brief one, containing the more important additional material. Under the circumstances, an understanding of the present paper presupposes some knowledge of the earlier one.

In the following pages are included (1) a map, showing the actual spatial relations of the various trapping "stations;" (2) a half-tone illustration, representing average specimens of the seven local populations here considered; (3) a table, giving the mean values and standard deviations for all of the characters measured, including some which were not mentioned in the previous report; (4) a discussion of correlation, both intra-racial and inter-racial; (5) a more extended discussion of various theoretical questions involved in an endeavor to interpret this situation.

The position of the collecting stations (Fig. 1) was not chosen arbitrarily, as might be inferred from their irregular distribution. It was determined to some extent by agricultural conditions, but chiefly by the ascertained nature of the populations at various points. Thus after trapping near Chipley and Round Lake, at points only ten miles apart, it became evident that intensive collecting was necessary between these stations. On the other hand, it was not thought worth while to make collections between Graceville and Abbeville, a distance of nearly fifty miles, owing to the close similarity of these two populations.

The picture presented by the series of pelages (Fig. 2) may be profitably compared with the histograms comprised in figure 1 of the February paper, and with the values given in the table below.

The racial differences among the various characters shown in table 1 have, for the most part, been portrayed graphically in the previous paper. But certain other mean values, absolute and relative, deserve consideration here. Three of these have been plotted in figure 3 of the present paper.

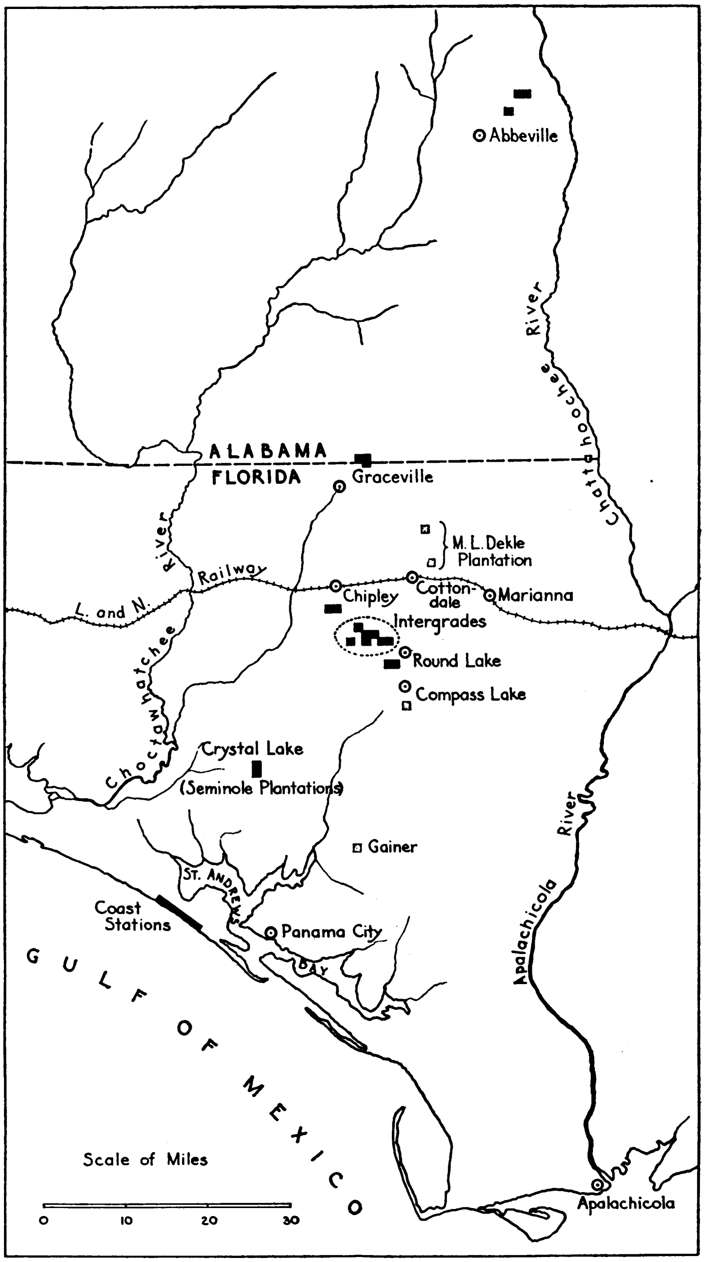

FIGURE 1

Map of area considered in present paper. Squares represent sections of land in which trapping was conducted. (In most cases, the actual township and section were ascertained, and the position of the latter has been correctly indicated on the map.)

Areas heavily shaded represent the major stations, upon which the present discussion is almost entirely based; those lightly shaded are the minor ones. Results from the latter stations are in complete harmony with the others, so far as they go.

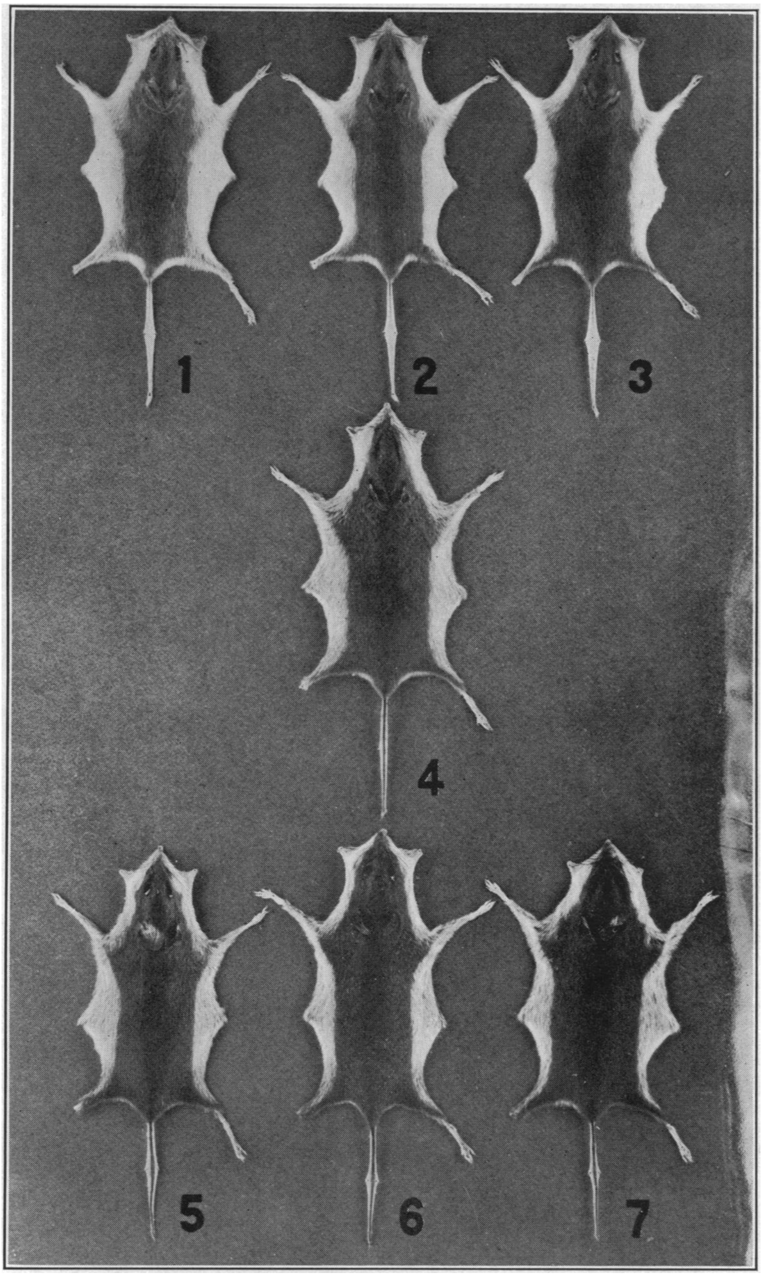

FIGURE 2

Photographs of a series of skins, representing the seven chief local populations here considered. The specimen chosen, in each case, stands close to the average in respect to the values of "colored area," "red," and the "index of saturation." 1, Shore; 2, Crystal Lake; 3, Round Lake; 4, Intergrades; 5, Chipley; 6, Graceville; 7, Abbeville.

Foot pigmentation denotes the depth of pigmentation of the foot, graded according to an arbitrary scale.[3] It will be seen that the mean values for this character present nearly the same relations as those shown by the other pigmental characters in figure 3 of the February article. The single exception is the value for the Graceville collection, which is considerably lower than would have been expected.

$\frac{Ca}{R}$ is the value obtained by dividing the measurement for "colored area" by that for "red." Since the latter figure is used here as an index of the paleness or darkness of the dorsal region of the pelage (a high value denoting a pale pelage, and vice-versa), this fraction is roughly indicative of the total amount of pigment present. The "curve" for this fraction presents the same peculiarities as those for the other pigmental characters. The range of variability among these local races, in respect to this value, is naturally greater on the whole than that shown by either of the characters upon which it is based, taken singly.[4]

$\frac{R - V}{R}$ may be regarded as an "index of saturation," as regards red.[5] High values of this fraction indicate a relatively rich coloration, low values an approach to neutral gray. Disregarding the collection from the white sand dunes of the coast, it is seen that the pelages are progressively grayer as we proceed inland. The low saturation of the color of the coast-dwelling specimens is due to the greater proportion of white hairs in their fur. In this case, therefore, low saturation is associated with high luminosity, while in the case of the dark interior race (*polionotus*) low saturation is associated with low luminosity.

Our present discussion of *correlation* will be confined to pigmental characters. In the earlier section of this report, it was shown that the only characters displaying any consistent trend in their geographic variation were those relating to pigmentation. It is hence a matter of considerable interest to determine the extent of the correlations, both intra-racial and inter-racial, which are shown among these various characters. To what extent, if any, do these characters tend to vary together within a single local population, and to what extent do they tend to vary together, as we pass from one locality to another?

The correlation between the extent of the colored area of the pelage and the depth of pigmentation of the foot is found to be slight or wanting within each of the seven local populations here considered. Five of these correlations are positive and two are negative, the weighted mean of the seven coefficients being +0.099.[6]

On the other hand, these same two characters are found to vary together markedly as we pass along our geographic gradient from the coast inland. When we view these races in succession, we find that the mean area of the

TABLE I

	SEX	ALBIFRONS (COAST)		ALBIFRONS (CRYSTAL LAKE)		ALBIFRONS (ROUND LAKE)		POLIONOTUS-ALBIFRONS INTERGRADES	
NUMBER OF INDIVIDUALS		51		58		54		43	
		MEAN	σ	MEAN	σ	MEAN	σ	MEAN	σ
Body length (head + trunk)	♂	78.27 ±0.24	1.67	76.12 ±0.22	1.66	76.38 ±0.22	1.78	77.22 ±0.35	2.52
Body length (head + trunk)	♀	82.83 ±0.28	2.21	82.11 ±0.35	2.90	80.96 ±0.42	3.02	82.78 ±0.34	2.27
Body length (head + trunk)	Both	80.86 ±0.28	3.02	79.42 ±0.34	3.84	78.42 ±0.30	3.32	79.80 ±0.38	3.67
Tail length (actual)	Both	55.67 ±0.23	2.40	49.66 ±0.24	2.71	49.02 ±0.23	2.47	50.30 ±0.26	2.52
Tail length (corrected)*	Both	55.41		49.93		49.60		50.37	
Foot length (actual)	♂	18.35 ±0.05	0.33	16.78 ±0.06	0.48	17.02 ±0.06	0.46	17.37 ±0.07	0.55
Foot length (actual)	♀	18.26 ±0.06	0.46	17.03 ±0.05	0.38	16.82 ±0.06	0.42	17.37 ±0.06	0.40
Foot length (corrected)*	♂	18.37		17.45		17.27		17.68	
Foot length (corrected)	♀	18.02		16.85		16.79		17.43	
Ear length (actual)	Both	15.53 ±0.04	0.44	14.41 ±0.04	0.46	14.37 ±0.04	0.44	15.20 ±0.06	0.55
Tail stripe length**	Both	16.14		17.61		44.67		88.73	
Foot pigmentation	Both	0.20 ±0.04	0.44	0.55 ±0.06	0.60	1.00 ±0.08	0.81	1.58 ±0.07	0.65
Colored area of pelage†	Both	56.69 ±0.61	6.50	61.66 ±0.36	3.82	66.16 ±0.40	4.29	71.10 ±0.57	5.52
Pigmentation of ventral hair	Both	0.00		0.04		0.20		1.77	
Red	Both	18.15 ±0.14	1.43	17.35 ±0.15	1.55	15.74 ±0.14	1.54	11.80 ±0.22	2.08
$\frac{Ca}{R}$	Both	3.15 ±0.05	0.51	3.59 ±0.04	0.44	4.26 ±0.06	0.65	6.27 ±0.15	1.48
$\frac{R - V}{R}$ ‡	Both	37.34 ±0.53	5.52	41.86 ±0.40	4.22	37.88 ±0.45	4.82	36.69 ±0.63	6.02

TABLE I (*Continued*)

								MINOR COLLECTIONS		
	SEX	POLIONOTUS (CHIPLEY)		POLIONOTUS (GRACEVILLE)		POLIONOTUS (ABBEVILLE)		ALBIF. (GAINER)	ALBIF. (COM-PASS L)	POLION. (M. L. DEKLE)
NUMBER OF INDIVIDUALS		58		53		60		3	1	22
		MEAN	σ	MEAN	σ	MEAN	σ	MEAN	MEAN	MEAN
Body length (head + trunk)	♂	76.37 ±0.26	2.00	78.84 ±0.20	1.58	78.16 ±0.31	2.55	77.50	74.00	78.45
Body length (head + trunk)	♀	82.81 ±0.36	3.04	83.38 ±0.44	3.28	83.34 ±0.36	2.89	82.50		81.55
Body length (head + trunk)	Both	79.92 ±0.37	4.14	80.98 ±0.31	3.40	80.67 ±0.33	3.75	80.83		80.00
Tail length (actual)	Both	50.71 ±0.25	2.75	50.10 ±0.25	2.66	51.00 ±0.22	2.54	46.83	50.50	49.52
Tail length (corrected)*	Both	50.74		49.70		50.66				
Foot length (actual)	♂	17.29 ±0.06	0.48	17.46 ±0.06	0.45	17.32 ±0.07	0.56	17.30	16.70	17.25
Foot length (actual)	♀	17.52 ±0.05	0.40	17.39 ±0.06	0.41	17.43 ±0.06	0.46	16.60		17.11
Foot length (corrected)*	♂	17.51		17.61		17.53				17.38
Foot length (corrected)	♀	17.38		17.21		17.08				17.03
Ear length (actual)	Both	15.21 ±0.05	0.51	15.26 ±0.05	0.53	15.12 ±0.04	0.50	14.97	14.00	14.92
Tail stripe length**	Both	98.02		100.00		100.00		13.70	66.67	100.00
Foot pigmentation	Both	1.80 ±0.06	0.65	1.47 ±0.07	0.72	2.02 ±0.06	0.70	0.00	0.00	1.64
Colored area of pelage†	Both	74.51 ±0.29	3.15	76.63 ±0.24	2.51	77.22 ±0.24	2.78	62.33	69.00	75.27
Pigmentation of ventral hair	Both	1.96		2.00		2.00		0.00	0.00	1.86
Red	Both	10.43 ±0.10	1.08	9.67 ±0.10	1.11	9.99 ±0.10	1.13	16.47	15.00	11.10
$\frac{Ca}{R}$	Both	7.22 ±0.08	0.85	8.03 ±0.09	0.99	7.83 ±0.08	0.96			6.89
$\frac{R - V}{R}$ ‡	Both	32.81 ±0.38	4.19	32.02 ±0.40	4.24	30.13 ±0.42	4.78			31.55

* Probable values for a standard body length of 80 mm.

** Expressed as percentage of length of exposed part of tail.

† In this case the area of hair which is pigmented throughout its entire length.

‡ V designates "blue violet" (designated BV in *J. Mammalogy*, 1927).

colored part of the pelage increases steadily, there being no exception to this (February paper, figure 1). Likewise, the mean depth of foot pigmentation increases steadily, with a single exceptional case (present paper, figure 3).

When these seven local collections are thrown together, and treated statistically as a single population, the correlation between the last-named pair of characters is found to be +0.613, this figure being based upon 358 individuals.[7]

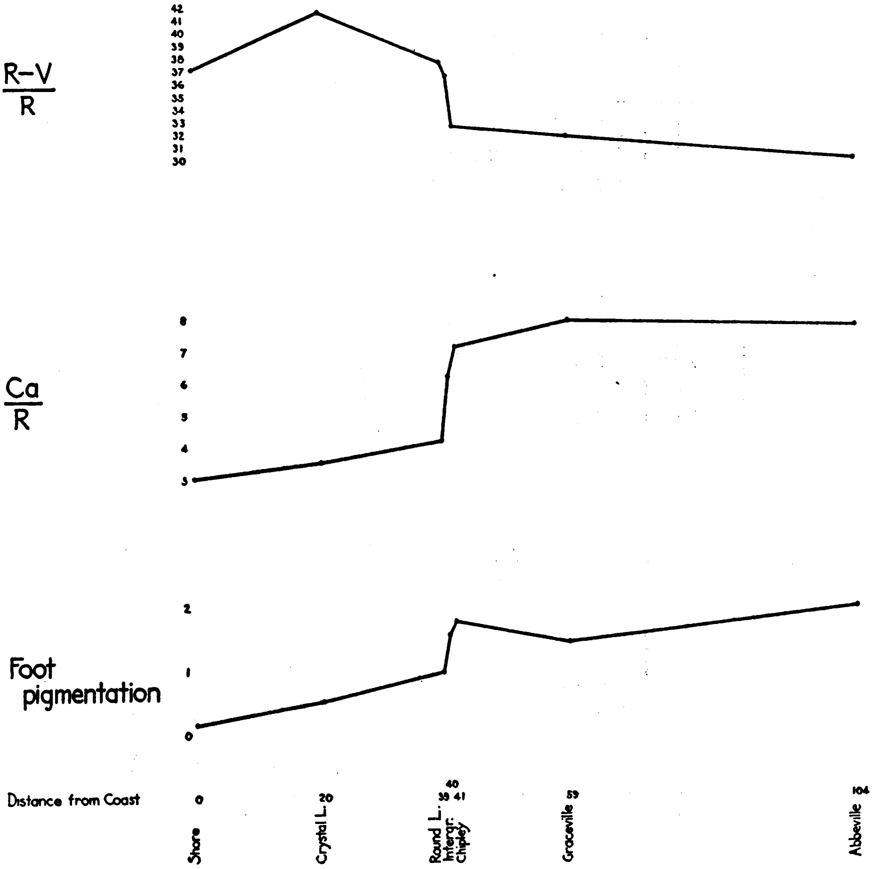

FIGURE 3

Graphs, based upon average values for foot pigmentation, Ca/R, and $\frac{R}{R - V}$.

Certain other correlations between pigmental characters deserve mention here. As regards the correlation between foot pigmentation and red, we find that in six cases out of seven the coefficient is negative, the weighted mean being −0.129. When, on the other hand, we treat our entire material as a single population, this correlation rises to −0.643.[8]

Previous studies which I have made of other species of *Peromyscus* have revealed these same relations, as regards the two characters here considered, viz.: (1) darker races, as a rule, have darker feet; (2) within each separate race, there is little or no correlation between the pigmentation of the feet and that of the pelage.[9]

Considering finally the correlation between red and pigmented area, the mean of the intra-racial coefficients (all negative) is −0.363; that based upon the combined populations (357 individuals) being −0.864.

How are we to explain this coexistence of a high inter-racial and a low (or non-existent) intra-racial correlation between these same characters? In some previous discussions of the subject, I adopted the hypothesis that the two characters in question must have undergone simultaneous but independent genetic change, through the influence of some environmental agency. Such a conclusion would be inevitable if it were really true that the characters in question were not at all (or only slightly) bound together genetically within the organism, in such a way that an alteration of one would necessarily entail an alteration of the other. But, in reaching this earlier conclusion, I failed to recognize the fact that little or no correlation might be detected between the measurements of two characters in a given population, even in cases where these two characters were dependent upon absolutely identical genetic factors.

It is evident that the variations within a single population, upon which intra-racial correlations depend, cannot be altogether comparable with the variations which have led to the evolution of one race from another. There are strong reasons for believing that the former are to a considerable extent of the nature of "somatic modifications," which may affect various regions of the body, quite independently of one another, whereas the latter must of necessity depend upon "mutations," or hereditary variations, by whatever name these may be called.

That a considerable fraction of the intra-racial variability in pigmentation, here measured, is due to non-genetic causes is shown by the relatively low coefficients (averaging about 0.3) denoting parent-offspring correlation with respect to these characters. On the other hand, the fixity of the inter-racial differences, under changed conditions of environment, is evidence that these latter differences are mainly, if not wholly, of the genetic order.

It seems certain, in other words, that the difference between an average *polionotus* and an average *albifrons* is to a much greater extent dependent upon genetic factors than is the difference between a pale and a dark *polionotus* or between a pale and a dark *albifrons*.

The fact that we obtain low correlations, within our local races, in respect to various pigmental characters, is in no way inconsistent, therefore, with the supposition that these characters depend very largely upon the same genetic factors, or at least upon closely linked factors. As additional evidence in favor of this supposition may be cited the marked increase which we frequently encounter in the correlation between any two pigmental characters, in the F_2 hybrid generation, and in back-crosses, as compared with F_1 hybrids and pure races.[10] It is hardly necessary to point out that no such an increase in correlation in the F_2 generation would follow automatically from the increase of variability in both of these characters, which occurs in the F_2 generation, as compared with the F_1. It results from the circumstance that the variability of the "segregating" generations is due more largely to genetic differences than is that of first crosses.

If the foregoing reasoning is correct, it is evident that selection with reference to one of these pigmental characters—say, coat color—would be certain to involve ultimately the modification of any other—say, foot pigmentation—even though these two characters were found to be feebly, if at all correlated within particular local populations.

This renders superfluous the alternative hypothesis earlier adopted by me, namely, that these various characters have undergone simultaneous and independent genetic change under the influence of some environmental agency. The existence of such a process of parallel modification is here inferential, whereas the known facts discussed above are demonstrably competent to produce the results in question.

The foregoing discussion of correlation was written substantially as here presented before I became aware of the similar treatment by Bubnoff[11] of the problem last considered. This author found that certain characters of the shells of fossil ammonites were distinctly correlated when groups of closely related species were compared. He thereupon put to test the question "whether also this correlation exists among all the individuals of one species," finding that "measurement gave the surprising, but undoubted, result that within the variants of a species this correlation is not present, that each character varies by itself and is not necessarily bound up with corresponding alterations of another." (p. 165, translated.)

Bubnoff's interpretation of these facts appears to be identical with my own, namely, that the variations which distinguish these related species are "genotypic" alterations of form, while those which appear within the various species are somatic modifications ("zufällige Variante," in his words) and do not involve correlative changes. It is contrary to all analogy, however, to suppose that intra-specific differences in these characters of the shells of ammonites are wholly of the non-genetic sort. Nor does it seem probable that Bubnoff has found here a satisfactory criterion for separating species.[12]

In my previous communication upon this series of animals, certain fundamental theoretical questions were reserved for later consideration. While any discussion of these questions must at the present time be largely speculative, I believe that we are already in possession of sufficient facts to warrant a preliminary effort in this direction. Indeed, there would be little incentive for engaging in such detailed observations and descriptions, if we were debarred from the possibility of attempting these interpretations.

Two chief problems present themselves in reference to the phenomena which have been discussed in these papers. (1) How did these races of mice become differentiated from one another? (2) How are we to explain the curious relations which we encounter in their geographic distribution? These questions may be considered in the order given.

Notwithstanding my earlier arguments for a more direct effect of environment in evolution (these I still regard as valid in certain cases) I will concede that the facts in the present instance seem to lend themselves better to an explanation based upon the selection of germinal variations which, in their origin, bore no specific relation to factors of the environment. I have already indicated my belief that the pale race *albifrons* arose from a dark race, similar to or identical with, the present *polionotus*. The most plausible explanation of these color changes, I think, is that we have to do with protective coloration, achieved through the differential survival of paler variants.

It is easy to discern, within every geographic race in nature, the small hereditary differences, through the accumulation of which one race may have been derived from another. Each such race presents a wide range of variability in respect to every character which has been measured, while it is experimentally demonstrable that these individual differences are in part genetic. Given an adequate basis for selection, tending to accumulate the differences in one direction or the other, it is easy to imagine how the divergence may have occurred.

It cannot, of course, be proved that any *new* germinal changes have occurred during the entire process by which these local races have become differentiated from one another. According to the currently accepted interpretation of selection, even such striking divergence as was obtained by Castle, with his hooded rats, resulted from a simple process of sorting-over of existing genetic materials. It is not at all impossible that genetic factors adequate for the production of *albifrons*, and even of the more extreme form, *leucocephalus*, were already present in the original *polionotus* stock. On the other hand, the occurrence of one highly aberrant individual[13] which falls within the limits of *leucocephalus*, in respect to extensity of color pattern, suggests that this sorting process may be supplemented by occasional mutations, i.e., actual changes in genetic factors.

Before leaving this subject, however, I wish to disclaim the belief that all organic diversity is the result of selection, based upon utility. Much of it probably is; much of it, no less probably, is not.

It must here be recalled that none of the subspecific differences in *Peromyscus*, so far as these have been investigated, have been found to depend upon single Mendelian factors.[14] If the Mendelian scheme is really of universal application, we have to do with numbers of independently segregating factors, affecting each character. This, although the characters themselves, as stated above, may be closely correlated. The divergence of the races has been due, in every case, to the accumulation of small genetic differences; never to large abrupt changes or "saltations."

The facts cited in the foregoing paragraph lead us directly to the second of the two questions set forth above: How are we to explain the curious relations which we encounter in the geographic distribution of *polionotus* and *albifrons?* We have just seen that the latter race could not have arisen from the former by a single act of mutation. Thus the fairly abrupt transition between one race and the other, geographically speaking, can receive no such simple interpretation.

Among the curious relations here referred to there are two which deserve particular attention. One is the fact that such a highly depigmented condition should occur so far inland where there are no white beaches or dunes, at least ones which are exposed to view at the present time, and where the ground is largely covered by vegetation. The other is the fact that the boundary between the ranges of these two subspecies is as sharp as it is, despite their mutual fertility.

As regards the first of these problems, an appeal might be made to ecological conditions which have long ceased to exist. Perhaps at the time when *albifrons* was differentiating from *polionotus* there was much less top-soil and vegetation throughout this entire region, thus leaving the underlying pale sand more fully exposed to view. Or possibly the evolution of this race dates back to a time when the coast line, with its rampart of glistening white sand, lay considerable farther inland than at present. Unfortunately, such geological evidence as is available does not favor this supposition.[15]

On the other hand, it is possible that a fuller knowledge of the habits of these mice would reveal the need of their harmonizing with backgrounds of pale sand, even in territories where most of the soil is covered by vegetation. In support of such a contention, certain facts may indeed be cited: (1) the exposed soil of almost the entire *albifrons* zone, so far as my observations go, is sandy, and the sand, while mostly far from white, is distinctly pale, as compared with the soil somewhat farther north; and (2) the burrows of these mice appear to be nearly always located in patches of bare soil, while areas covered densely with weeds are distinctly unfavorable places for trapping them. Thus the need for concealing coloration might be greater than would at first be suspected. However, even this supposition would not account for the extreme depigmentation of *albifrons*, a process which has been carried farther than in any except a few of our most highly modified desert types.

Viewing all the available evidence, it seems more likely that the entire differentiation of *albifrons* from its *polionotus*-like ancestor occurred upon the present gulf shore, where these animals abound upon areas of intensely white sand, largely uncovered by vegetation. Here the new race may have found an optimum habitat[16] and multiplied rapidly in consequence. This region may be supposed to have become, accordingly, a new "center of distribution" from which the expanding population pressed inland, displacing and absorbing the darker form, *polionotus*, until its advance was halted by the centrifugal pressure of the latter. The width of the zone occupied by the new race would depend upon the relative rates of multiplication of the two populations. This interpretation is essentially that offered by Grinnell, in his account of the origin of the chestnut-backed chickadee.[17] While it is, in the present instance, purely hypothetical, it seems to meet with fewer difficulties than any of the alternative explanations here considered.

But there is one highly important element in the situation which still remains to be accounted for. This is the fact which has previously been emphasized, that the transition between these two subspecies is at present so abrupt. One obvious explanation has already been rejected, namely, that our two races became differentiated in localities more remote from one another, and that they subsequently (and rather recently) came into contact. Aside from the utter lack of evidence for such a past geographic relation, is the presumable present contact of these two races, along a wide front, and the known existence of numerous similar cases elsewhere. These circumstances make it unlikely that we chance to be witnessing the first meeting of two previously separated populations.

In order to account for the lack of a more abundant intermediate population in our transitional area, we seem driven to one or both of two assumptions. These are (1) that there is a high degree of assortative mating, within each subspecies, and (2) that the intermediate or hybrid individuals are less viable *in either environment* than are the "pure" types.

Granted the operation of one or both of the above principles, it still remains unexplained why these races should not freely invade one another's territory, even if they do not intermingle genetically. We may dismiss at once the suggestion that there exists here some intangible ecological barrier, despite the apparent lack of one. For it seems quite improbable that a barrier rigid enough to produce such a sharp delimitation of races would entirely escape notice.

Nor would even a conspicuous and well-defined difference in soil color on the two sides of this subspecific boundary line be sufficient to bring about such a hiatus. It happens that in passing from south to north we actually encounter in this vicinity a transition from paler to darker soils, representing a difference in the respective geological formations.[18] But there appears to be no close correspondence between the geological boundaries and the "peromyscological" ones, and in any case there is abundant evidence that selective elimination, on the basis of concealing coloration, is far from intense among these animals.[19] The discrimination on the part of their enemies would need to be well-nigh absolute in order to maintain a condition such as we actually find here.

It must be confessed that the causes responsible for the abrupt transition between the ranges of *polionotus* and *albifrons* are at present obscure. It is difficult to see how the mutual pressure of two expanding populations would, in itself, suffice to maintain a boundary at all sharp, where they came into contact. Careful field studies might reveal the existence of "social" or "psychical" factors, analogous to those which keep apart the races of mankind.

One question which is sometimes raised is whether the "intergrading" forms between two subspecies represent transitional stages in the evolution of one subspecies from the other, or whether they represent hybrids between the two after their differentiation has been accomplished. This question appears to me to be rather academic. If one of the races is still in the process of differentiating from the other, the "intergrading" forms will necessarily represent, in part, transitional stages. On the other hand, interbreeding doubtless occurs between the two races, both during and after their differentiation from one another, and thus part of the population will be of hybrid origin in any case. A little reflection shows that, genetically, there would be no necessary difference between such "hybrids" of the *n*th generation and individuals representing the various factorial combinations which would occur during the evolution of one geographic race from another.

Supplementary Note.—The foregoing paper had gone to press before I received the highly interesting article by W. Meise (Rassenkreuzungen an den Arealgrenzen, *Verh. d. deutschen zoöl. Gesellsch.* 32, Jahresvers., 1928, 96–104). Considerable parallelism will be noted between the two articles as regards both the problems discussed and the points of view of the two authors.

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[1] These studies were conducted under the joint auspices of the Scripps Institution of Oceanography and the Carnegie Institution of Washington.

[2] Vol. **15,** no. 2, Feb., 1929.

[3] Sumner, *J. Exp. Zoöl.*, **30,** 1920, 402; *J. Mammalogy*, **8,** 1927, 185.

[4] This is because we are virtually dealing with a third power. *Ca* (which is an area) is multiplied by $1/R$. The *depth* of pigmentation (in one sense, at least) varies inversely with the value of R.

[5] Sumner, *J. Mammalogy*, **8,** 1927, 177–206.

[6] One of the minor collections, containing 22 specimens, gives a coefficient −0.046.

[7] A method of computing correlations in such aggregate populations, without the labor of calculating a new set of deviations, product moments, etc., has been developed by my colleague, Dr. G. F. McEwen. The formula, which is derived directly from that for the correlation coefficient, with corrections for approximate means, is as follows:

$$r = \frac{\Sigma(x_1y_1) + n_1(m_{x1} - m_x)(m_{y1} - m_y) + \Sigma(x_2y_2) + n_2(m_{x2} - m_x)(m_{y2} - m_y) + \dots}{n\left[\sqrt{\dfrac{n_1(\sigma_{x1}^2 + (m_{x1} - m_x)^2) + n_2(\sigma_{x2}^2 + (m_{x2} - m_x)^2) + \dots}{n}}\right] \times \left[\sqrt{\dfrac{n_1(\sigma_{y1}^2 + (m_{y1} - m_y)^2) + n_2(\sigma_{y2}^2 + (m_{y2} - m_y)^2) + \dots}{n}}\right]}$$

in which the subscripts 1, 2, etc., are attached to values for the various single local populations, while the corresponding values, without subscripts, are those for the aggregate population. This formula reduces to:

$$r = \frac{n_1r_1\sigma_{x1}\sigma_{y1} + n_2r_2\sigma_{x2}\sigma_{y2} + \dots + n_1a_1b_1 + n_2a_2b_2 + \dots}{[\sqrt{n_1\sigma_{x1}^2 + n_2\sigma_{x2}^2 + \dots + n_1a_1^2 + n_2a_2^2 + \dots}\,] \times [\sqrt{n_1\sigma_{y1}^2 + n_2\sigma_{y2}^2 + \dots + n_1a_1^2 + n_2a_2^2 + \dots}\,]}$$

in which a_1, etc., $= m_{x1} - m_x$, etc., and b_1, etc., $= m_{y1} - m_y$, etc.

[8] It is obvious that the correlation should be negative in the case of these two characters, since high values for "red" denote low degrees of pigmentation, and vice-versa.

[9] Sumner, *Ecology*, **6,** 1925, 365, 366.

[10] Huestis, R. R., *J. Exp. Zoöl.*, **41,** 1925, 464; Sumner and Huestis, *Biol. Bull.*, **48,** 1925, 51. Extensive evidence of this sort will be presented in a subsequent paper, dealing with the results of hybridization experiments.

[11] Bubnoff, S. von, *Zeitschr. indukt. Abst. Vererbungslehre*, **21,** 1919, 158–168.

[12] Dürken, B., *Ibid.*, **27,** 1922, 27–47.

[13] February paper, figure 1, lower left.

[14] Sumner, *J. Exp. Zoöl.*, **38,** 1923, 245–292; Huestis, R. R., *Ibid.*, **41,** 1925, 429–470.

[15] This I learn from Dr. C. Wythe Cooke, of the U. S. Geological Survey.

[16] This and certain other subspecies are found largely in association with the "beach oats" (*Uniola paniculata*) which presumably serves them as an important food-plant. This tall grass is abundant among the dunes of the gulf shore.

[17] Grinnell, J., *Auk*, **21,** 1904, 364–382.

[18] Dr. C. Wythe Cooke writes to the author: "The northern limit of *Peromyscus polionotus albifrons* as described in your letter of December 12, appears to coincide with the northern boundary of the Citronelle formation [Pliocene], which passes through Vernon, Wausau, and Round Lake. The Citronelle is covered almost everywhere by a mantle of deep, loose, salmon-colored sand, very similar to beach or dune sand, which contrasts sharply with the red or brown loams derived from the Tampa, Glendon and Marianna limestones which lie north of the Citronelle area." My own field notes refer to a transition from predominantly pale sand to predominantly reddish and brown soils, occurring near to, but not at, the boundary of the ranges of *polionotus* and *albifrons*.

[19] Sumner, *J. Mammalogy*, **2,** 1921, 75–86; **7,** 1926, 158.