GENETIC AND DISTRIBUTIONAL STUDIES OF THREE SUB-SPECIES OF *PEROMYSCUS*[1].

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(With Plates VIII–XI, Twenty-seven Text-figures and Six Tables.)

CONTENTS.

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[1] These studies were conducted at the Scripps Institution of Oceanography at La Jolla, California, largely with the aid of a liberal grant from the Carnegie Institution of Washington.

I. INTRODUCTION.

INTENSIVE field studies of various groups of animals, both vertebrate and invertebrate, are making it increasingly evident that the phenomenon of geographic variation within a species, or a group of closely related species, is one of very wide occurrence[1]. Among students familiar with the facts of the case the belief is now probably fairly general that the differentiation of these geographic races or sub-species represents one of the most important ways in which the divergence of organic groups commences. It is consequently surprising, in view of the abundance of some of this material and of the absence of insurmountable technical difficulties in rearing it, that so few geneticists have directly attacked the problem of the inheritance of sub-specific characters. Preoccupation with the simpler, more sharply defined problems of Mendelian inheritance is doubtless responsible in large degree for this attitude. The view is often expressed that the phenomena manifested in specific and sub-specific crosses are too complicated for profitable investigation at present, since the characters involved do not seem to admit of "critical" Mendelian analysis.

It is doubtless true that they do not admit of critical analysis, according to prevailing Mendelian standards, and this fact is certainly an important limitation to the scope of studies conducted with such material. Perhaps it will always remain so. But the question arises whether much of first-rate importance cannot be learned from such studies, despite these handicaps, and whether all knowledge of the genetics of sub-specific differences must await the time when we can resolve them into a definite number of nameable genes, each assigned to its proper linkage group.

It would seem, for example, quite relevant to genetics to decide such questions as the following: whether sub-specific differences are inheritable at all; whether they are subject to appreciable modifications by external influences; whether and to what extent individual variations in these same characters, within a sub-species, are inheritable; to what extent the various characters which differentiate one sub-species

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[1] A valuable general discussion of this subject has been recently prepared by Rensch (1929).

from another are found to be correlated, (1) in dealing with a group of closely related sub-species, and (2) within the limits of a single sub-species; whether the correlation, if it exists, appears to be explainable by the linkage of genetic factors, or by the dependence of the characters in question upon common genetic factors, or by some other cause; whether there is any tendency toward dominance or recessiveness of sub-specific characters in crosses, and whether the aggregate characters of one of the sub-species tend to behave as a unit in this respect; whether there is any evidence of genetic segregation in the F_2 generation of sub-specific hybrids, in back-crosses, etc., and if so whether the character differences in question depend upon single genetic factors, or upon multiple factors; whether, in the latter event, the number of principal factors concerned may be approximately estimated; whether there is any tendency, in these generations, for the several characters which distinguish one sub-species from the other to segregate together, thus increasing any correlations which may previously have been exhibited; finally, whether there is any evidence that sub-specific characters may blend, as a result of crossing, in such a way as to be irrecoverable in later generations.

The foregoing list of questions could be greatly extended. None of them depend for their answers upon "critical analysis" of the usual Mendelian type. To what extent the *Peromyscus* studies of the past fifteen years have contributed to their solution I must leave others to judge. But that studies of the sort here indicated have been urgently called for is evident from the fact that when the present investigations were commenced zoologists were still seriously discussing whether the differences between geographic races of birds and mammals were hereditary at all. So far as I have been able to learn, no real experimental test of this question had previously been made with either of these groups.

The experiments to be discussed in the following pages form part of a rather extended programme which has been conducted by the author and his co-workers since 1914. The results have been reported in numerous papers throughout this period[1].

It has been inevitable that my point of view respecting some of the

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[1] The chief of these, so far as they bear on genetic or distributional problems, are as follows (those most relevant to the present discussion being italicised): Sumner, 1915, 1917, 1917 *a*, *1918*, *1918 a*, *1918 b*, *1920*, *1922*, *1923*, *1923 a*, 1923 *b*, 1924, *1924 a*, 1924 *b*, 1925, *1926*, *1927*, *1928*, 1928 *a*, *1929*, *1929 a*, 1929 *b*; Sumner and Collins, 1922; Sumner and Huestis, 1921, *1925*; Sumner and Swarth, 1924; Collins, 1923; Huestis, *1925*.

theoretical questions involved should undergo considerable change with increasing knowledge of the facts. Thus, for some years, I was disposed to share the view of many taxonomists and others that the characters which distinguish species, sub-species and other "natural" groups belong to a quite different category from the characters which distinguish the various "artificial" races and "mutant" types that have been used in most Mendelian experiments[1]. The obvious differences between these two types of variation, both in their incidence and in their mode of inheritance, cannot be disputed. I am nevertheless now disposed to accept as probable the interpretation which has been given to these differences by most recent geneticists, namely, that they are due largely to differences in the number of genetic factors which are involved in the two cases.

My own change of view-point on this subject has resulted mainly from two considerations: (1) Convincing evidence of genetic segregation, in respect to various colour characters, has been revealed in the course of the *Peromyscus* studies. This was not obvious in the earlier hybridisation experiments which were undertaken (Sumner, 1920), but became increasingly evident with more extended experiments and more thoroughgoing analysis (Huestis, 1925; Sumner and Huestis, 1925), and has been shown most strikingly of all in the series discussed in the present paper. (2) Certain variations of the "mutant" type, occurring sporadically within a species, have been found to be inherited with much the same appearance of imperfect segregation as are the differences between our "natural" species and races. In Mendelian terms, they seem to depend upon a number of partially dominant factors of varying potency. Thus the sharp distinction between one type of inheritance and the other seems to fall away (Sumner, 1928).

The remarks in the last few paragraphs must not be construed, however, as a claim (or admission) that the "multiple factor" interpretation of all specific and sub-specific characters yet rests upon a firm foundation. All that is claimed is that the data thus far derived from the study of *Peromyscus* conform fairly well with the requirements of that theory, while there are thus far few data which seem actually inconsistent with it. As has been remarked more than once previously, evidence for genetic segregation is not necessarily evidence for *complete* segregation of the type familiar to us in the case of known Mendelian allelomorphs.

Throughout the entire course of these studies I have been much less

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[1] Osborn's (1927) antithesis between "speciation" and "mutation" belongs here.

concerned with the mechanism of hereditary transmission, to which, for the most part, they have little relevance, than with the analysis of racial differences, and the light which these may throw upon the process of evolution. To what extent, if at all, the present studies have contributed to this field will be considered in the closing section of the paper[1].

II. DESCRIPTION OF THE SUB-SPECIES EMPLOYED.

No extended account seems called for here, either of the material or the methods employed in the present experiments. The biometric data regarding the "wild" generation of the parent stocks (*Peromyscus polionotus polionotus, P. p. albifrons* and *P. p. leucocephalus*) have been presented in considerable detail in another paper (Sumner, 1926)[2], while the nature of the "characters" here considered, and the means by which they are measured, have been fully discussed in a yet more recent paper (Sumner, 1927).

Briefly, it may be repeated that the species *Peromyscus polionotus* constitutes a group of small, short-tailed mice, occupying portions of the states of Georgia, Alabama and Florida, where it is represented by six recognised sub-species[3]. This grouping may prove, however, to be provisional. *Peromyscus polionotus* appears to be closely related to *P. maniculatus*, the most widely prevalent and geographically diversified member of the genus. Within the species *P. polionotus*, the sub-species *P. p. polionotus* probably represents most nearly the ancestral form. Its range is wider, its habitat more nearly average, and its characters more typical of the genus than those of any other of this group of geographic races. Thus *P. p. polionotus*, viewed dorsally, is of a dark grey-brown colour, not far different from that of many of the other wild mice of various parts of the world. As with most species of *Peromyscus*, the ventral surface of the body, up to a certain level on

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[1] It is a pleasure to acknowledge here, as on many previous occasions, the ever-ready help of my colleague, Dr G. F. McEwen, in various matters relating to mathematical procedure.

[2] The figures presented in the present paper do not, in all cases, correspond with those given in the earlier one for a number of reasons. (1) The earlier figures for *albifrons* were based upon material derived from three more or less isolated localities. It will be pointed out below that these local collections exhibited rather wide differences in respect to certain characters. (2) Instead of using the fraction $\frac{R-V}{V}$ as an index of saturation for red, I now use $\frac{R-V}{R}$ $\left(\text{see Sumner, 1927, in which paper, however, this fraction is written } \frac{R-BV}{R}\right)$. (3) Certain values comprised in the earlier table have been omitted from the later one, while a considerable number of new ones have been added in the latter.

[3] Osgood (1909), Howell (1920).

the sides, is of a whitish appearance, due to the lack of pigment in the tips of the hairs covering this region. The basal half or more of each hair exhibits, however, the usual dark pigmentation. A dorsal stripe of dark hairs extends throughout the length of the tail, this contrasting rather sharply with the white hairs which clothe the remainder of the appendage.

The other sub-species which have been described are of a much paler hue, they occupy less typical habitats, and are considerably modified from the supposedly primitive condition shown in *polionotus*. I shall discuss only two of these sub-species. *P. p. albifrons* is found throughout a rather narrow belt, bordering the Gulf of Mexico, and extending, so far as known, from Mobile Bay eastward to Point St Joe, a distance of more than 160 miles. *Albifrons* is a far paler form than *polionotus*, being of a buff or pale brown hue, not far different from that of many of the rodents of our American deserts. The white, ventro-lateral area is considerably more extended than in *polionotus*, while the hairs throughout much of this area are white to their very bases. The dorsal tail stripe is reduced or vestigial. It is narrow and faintly pigmented, and commonly extends only part way from the base to the tip. In some cases it is lacking altogether.

This process of depigmentation has been carried to extraordinary lengths in the case of the third race, *leucocephalus*, which inhabits an island reef, skirting the coast of north-western Florida. This race has a paler coloration and more extensive white areas than any other wild mouse with which I am acquainted, and the tail stripe is entirely lacking.

This island (Santa Rosa Island), as well as the beaches and dunes of much of the adjacent mainland, consist of extremely white quartz sand, covered to only a limited extent by vegetation. One cannot escape the conviction that these conditions have been responsible for the extraordinary modification of the mice which dwell here. That the modification has progressed so much farther in *leucocephalus* than in *albifrons* is doubtless due to the complete isolation of the former throughout a considerable period of time[1].

The three sub-species here considered also differ in certain other ways. In respect to the depth of pigmentation of certain exposed areas of the skin (ears, soles of the feet, etc.), we have the same graded series as was observed in the case of pelage characters. *Polionotus, albifrons* and *leucocephalus* form a series of decreasing pigmentation. As regards the length of certain bodily appendages (tail and feet), *polionotus* gives

[1] Howell (1920), Sumner (1926).

the lowest values and *leucocephalus* the highest, with *albifrons* intermediate[1]. In ear length, the three races show no probable differences. Nor are there any certain differences in weight or in the mean length of the body (head + trunk).

Thus far, these sub-species have been spoken of as if they were homogeneous groups throughout the territory occupied by each. This may be approximately true in the case of *leucocephalus*[2], but it is quite untrue of either *polionotus* or *albifrons*. Even during the earlier field studies of 1924, three collections of *albifrons*, which were made at points more or less isolated from one another, showed undoubted and considerable mean differences in respect to pelage colour and other characters (Sumner, 1926, pp. 157–8). In 1927 a series of collections was made, extending from the dunes of the gulf coast, near St Andrews Bay, through the entire range of *albifrons*, to a point far within the range of *polionotus*. As already reported recently,[3] each of these races, particularly *albifrons*, displayed a very perceptible gradient from south to north, as regards the mean value of each of the pigmental characters which were subjected to quantitative treatment. A large and relatively abrupt change was, however, noted in the latter, at a point about 40 miles from the coast, where the transition from a somewhat atypical *albifrons* to a somewhat atypical *polionotus* occurred within the space of a few miles.

III. BREEDING EXPERIMENTS.

A limited stock of cage-bred animals was reared from each of the "pure" races. These "C_1" animals were utilised in some of the hybridisation experiments, and they also served a valuable purpose in showing the effects of captivity upon certain of the characters here considered. The great majority of the mice which were reared, however, were various sorts of hybrids between different sub-species. These are listed below. The numbers in parentheses represent the numbers which were reared to maturity, and the data from which have been included in the present discussion. In most of the groups, a small number of individuals have

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[1] This intermediate position of *albifrons*, in respect to length of appendages, appears to hold only for the population dwelling in the immediate neighbourhood of the coast. Commencing at a point only 20 miles inland, the tail and feet of *albifrons* are no longer than those of *polionotus*. This fact is interesting in view of the fairly uniform gradient which seems to hold for all of the pigmental characters (Sumner, 1929, 1929 *a*).

[2] That is, so far as *local* variations are concerned. Of course there is a high degree of genetic variability within the population of any single locality.

[3] Sumner (1928 *a*, 1929, 1929 *a*).

been rejected, owing to being undersized, or to being manifestly stunted or deformed[1]. Some individuals which died in the cages were decomposed when found, and were thus not available for measurement. In the following list, the order in which the parent races are named has no significance. In each case, reciprocal crosses were obtained. Throughout this paper, the term "back-cross," when unqualified, refers to the first back-cross (commonly with *leucocephalus*), the term "grades" being applied to the second back-cross with *leucocephalus*.

Leucocephalus × *albifrons*[2],	F_1	(75)
„ „	F_2	(125)
„ „	back-cross, 3/4 *leucocephalus*	(70)
„ „	back-cross, 3/4 *albifrons*	(15)
„ „	grades, 7/8 *leucocephalus*	(58)
„ „	F_3	(65)
Leucocephalus × *polionotus*,	F_1	(74)
„ „	F_2	(109)
„ „	back-cross, 3/4 *leucocephalus*	(67)
„ „	back-cross, 3/4 *polionotus*	(16)
„ „	grades, 7/8 *leucocephalus*	(55)
„ „	F_3	(82)
Polionotus × *albifrons*,	F_1	(95)
„ „	back-cross, 3/4 *polionotus*	(76)
„ „	back-cross, 3/4 *albifrons*	(51)

In mating F_1 mice for the production of the F_2 generations, sibs were employed wherever possible, *i.e.* in the great majority of cases. No selection with reference to colour characters was practised. The F_3 generations, on the other hand, resulted from the matings of F_2 individuals which had been selected according to shade. About equal numbers of individuals of "dark," "medium" and "pale" parentage were reared.

In addition to the foregoing sub-specific crosses, I made a number of attempts to obtain inter-specific hybrids between *leucocephalus* and sub-species of *P. maniculatus*. The attempt succeeded in only a single case, as a result of which I obtained a fertile female hybrid between *P. maniculatus sonoriensis* and *P. polionotus leucocephalus*. This F_1 female was successfully back-crossed to a *leucocephalus* male, giving

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[1] In dealing with this species, animals have been arbitrarily classed as "undersized" which fell below a body length of 74 mm. (males) or 76 mm. (females). In addition to the exclusion of all measurements from such mice, the measurements of body parts, though not of colour characters, have been rejected in the case of a small number of others which were obviously deformed. The total number of animals whose measurements have been excluded wholly or in part for these reasons is less than 4 per cent. of the cage-bred animals.

[2] In the following pages, I have dealt separately with the derivatives of the "East Pass" and "Foster's Bank" series of *albifrons*. A large majority of individuals, in each generation, belong to the former class (fifty-nine and sixteen, respectively, in the F_1), and it is these which have chiefly been reckoned with in dealing with this cross.

birth to two young, and to a *maniculatus* male (not, however, *sonoriensis*, but *gambelii*[1]), giving birth to thirteen young.

Reference has been made in preceding papers (Sumner, 1915, 1918*a*; Sumner and Huestis, 1921) to the not altogether normal character of the generations reared in captivity. There is a tendency toward reduction in total size, as well as toward a diminution in the relative length of the tail and feet. These conditions are believed to be in part of a rachitic nature. Since the fall of 1924 cod-liver oil has been regularly included in the dietary of the mice, being given in a mush which likewise contains milk. Although no carefully controlled experiments have been made to test the effect of this substance, it appears to have had a beneficial influence. Scarcely any of the more extreme cases of stunting and deformation, such as appeared in each of the series of animals before administration of cod-liver oil to the mothers, are to be found among those reared after the treatment was commenced[2].

Comparisons have been made between the mean values for the "wild" generation of each of the pure races and the corresponding values for the first cage-bred generation, after rejection of the small percentage of obviously stunted or malformed individuals (see above). What seems a fairer comparison has also been made between the mean values for the cage-bred mice and the means for those wild ones which actually figured as parents, the latter being weighted by the number of their offspring. While it does not seem worth while to present these figures in detail, it may be said that considerable differences appear between the two generations in certain cases. These differences, however, are not, on the whole, consistent. They may be of opposite sign in the different races, and even in the two sexes of the same race. For the most part, they are probably due to random sampling, the number of individuals, and especially of parents, being rather small. On the other hand, it seems likely that the preponderant tendency toward reduction in total size, and in the relative size of certain parts, is real. It accords with what has been observed on a more pronounced scale when the conditions of life have been distinctly unfavourable. Effects of captivity upon pigmental characters are much more problematic. If they exist at all, they are small in comparison with racial differences, and probably do not affect the interpretation of any of the results to be discussed below. This cannot be said unreservedly of such characters as tail and foot length.

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[1] No fertile male *sonoriensis* was available at this time.

[2] However, the majority of those born "before using" are of normal appearance, and their *average* size is only slightly less than those born "after using."

IV. DETAILED RESULTS FROM THE VARIOUS CROSSES.

(*a*) *The* leucocephalus-albifrons *series.*

(Text-figs. 1–10; Plates VIII, IX, X.)

Tables I and III give the mean values and standard deviations for the parent races and various hybrid generations concerned in this cross. As has already been stated, the *albifrons* material collected during the summer of 1924 came from three distinct localities more or less isolated from one another. While it was recognised in the field that these sub-races displayed certain mean differences in respect to colour and some other characters, the extent of these differences (see Text-fig. 1) was unfortunately not realised until after the first generation of hybrids had been reared. As a result individuals derived from two of these localities were employed indiscriminately as parents of the F_1 hybrids in the crosses with *leucocephalus*. In view of the surprisingly large differences between these two *albifrons* stocks, it has been found desirable, for most purposes, to separate the "East Pass" and "Foster's Bank" derivatives[1]. A large majority belong to the former series, while the residuum of Foster's Bank material is not large enough to have any great statistical value.

The results of reciprocal crosses, here and elsewhere, have been thrown together and treated, in each case, as a single population. This procedure seems justified, owing to the apparent lack of any significant differences depending upon the direction of the cross. Mean differences of some magnitude appear in certain cases, but these show no consistent trend, and are doubtless due to chance. The number resulting from one reciprocal cross is sometimes considerably smaller than that from the other, and may be inadequate to reveal any except pronounced differences. Such differences, as already stated, are probably not present among these hybrids.

It will be most instructive, perhaps, to deal seriatim with the various measured "characters" which are represented in Table I.

Body length. As regards both this measurement and *weight* no significant racial differences are to be found between these two sub-species. There is no evidence of heterosis in the F_1 generation, nor any significant increase of variability in the F_2. I have more than once called attention to the greater mean size of the females of *Peromyscus* as compared with the males. This appears to be particularly true of the *polionotus* group.

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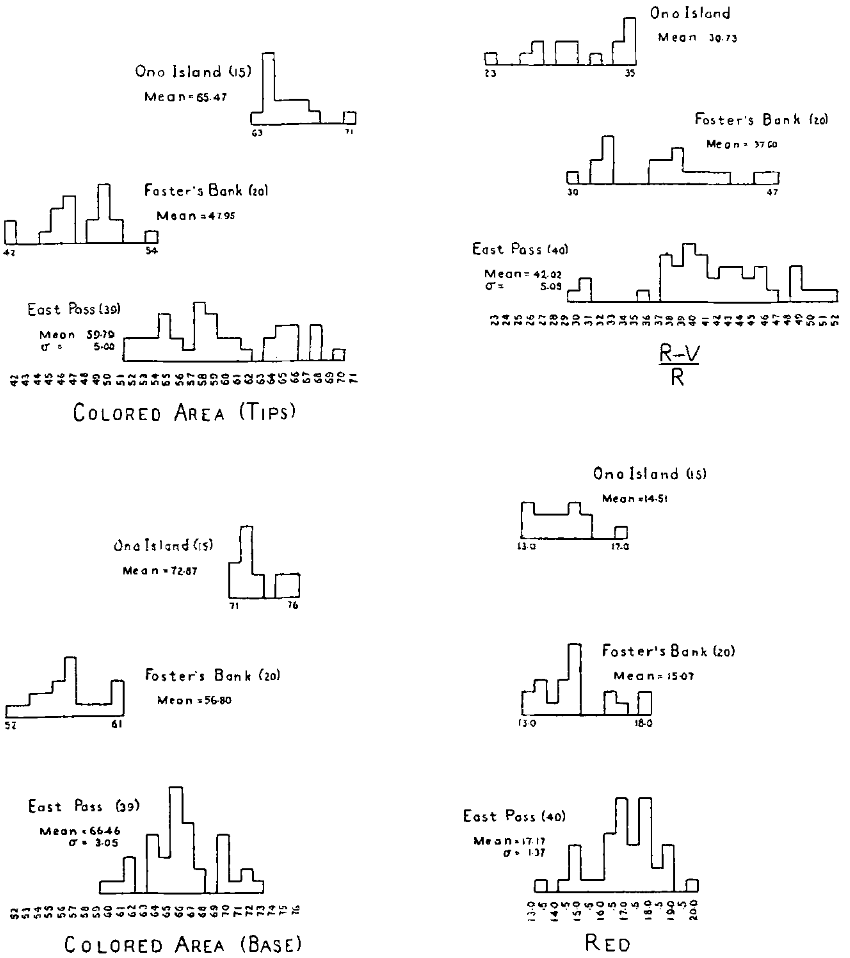
[1] For the position of these localities see Sumner (1926).

Tail length. No facts of genetic interest are to be noted in the present cross in relation to this appendage.

Foot length. In this case there is a rather pronounced racial difference[1]. *Leucocephalus* has a greater mean foot length than any of the collections of *albifrons*, the difference being most prominent when comparison is made with the East Pass series. There is, notwithstanding, no increase of variability in the F_2 generation over the F_1. Indeed we find just the



Text-fig. 1. Pelage characters of three local collections of *Peromyscus polionotus albifrons*. Here and elsewhere, each square represents an individual.

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[1] It is possible to compare only individuals of the same sex, since males have relatively larger feet than females.

opposite relation in both sexes, though these differences have no statistical significance. In this connection it should be stated that genetic differences in foot length are masked by a high degree of non-genetic variability. The weighted mean of the coefficients of parent-offspring correlation between two generations of the "pure" races employed in this cross, together with those between the F_1 and F_2 hybrid generations, is only + 0·076. This is based upon 210 offspring. The corresponding figure for the coloured area, in the same series of animals, is 0·501[1].

Ear length. Nothing instructive is to be noted here.

Skeletal measurements. As regards these, a number of differences between these sub-species are shown, some of which are perhaps of statistical significance. These measurements seem to show that *albifrons* (at least from East Pass) has a slightly greater number of caudal vertebrae than *leucocephalus*, as well as a slightly longer pelvis and shorter skull. There is, however, no pronounced tendency for these characters to give intermediate values in the F_1 generation of hybrids, and there is certainly no tendency for the F_2 generation to show a higher range of variability than the F_1.

When we pass to characters relating to pigmentation of the hair or skin, a wholly different situation is found. In respect to all of these characters, so far as determined, there are racial differences of considerable magnitude, while a comparison of the various hybrid generations reveals many facts of genetic interest.

Tail stripe. This longitudinal stripe of dark hairs is present on the dorsal surface of the tail in most species of *Peromyscus*, as well as in some other genera of rodents. It is, however, totally lacking in *leucocephalus*, the tail of which is entirely white, and it is present in *albifrons* in a much reduced condition, or may be lacking altogether. It has been pointed out in earlier papers (1915, 1918, 1927, etc.; also Grinnell, 1922) that the relative width of this stripe undergoes interesting local variations within certain species. In general, dark races have a noticeably broader stripe than paler ones. In *P. p. albifrons*, and in certain hybrids where the tail stripe is usually incomplete, its length rather than its width has been determined, and this has been expressed as a percentage of the length of the entire (exposed) part of the tail. This percentage may vary from 0 to 100. Figures based on length alone do not, of course, adequately express differences in the degree of pigmentation of this stripe, since they represent only one dimension, whereas the stripe may be said

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[1] In the case of foot length, certain of the generations are not available for parent offspring correlations owing to practical considerations which need not here be discussed.

to have three dimensions (that is, if the *depth* of pigmentation may be counted as one of these). Thus a "100 per cent." stripe in *albifrons* is, at best, much less of a stripe than is the 100 per cent. stripe found in most *P. p. polionotus*, which is both wider and of a deeper shade. Furthermore, the stated length of an incomplete tail stripe is often merely a rough approximation, owing to the rather arbitrarily chosen termination, which is unavoidable in cases where scattered black hairs occur throughout much of the length of the tail. After making due allowance for these difficulties, however, the length of the tail stripe is still to be regarded as a highly important character in the study of sub-specific hybrids in *P. polionotus*. Its range of individual variability far exceeds that due to observational error, and the genetic nature of many of the differences is obvious from an inspection of some of the graphs.

An extraordinary difference is to be noted in the tail stripe length of the two local collections of *albifrons* used in the present hybridisation experiments. Whereas the East Pass collection gives values from 7 to 100, with a mean of 41·73, the series from Foster's Bank for the most part lacks a tail stripe altogether, the highest value being 7. It is obviously necessary to treat these two groups separately.

Text-fig. 2 shows the various generations which have been derived from crossing *leucocephalus* with East Pass *albifrons*. The mid-value between that of the two parental means (0 and 41·73) is about 21. We find, however, in the F_1 generation, a mean of 3·81, while slightly more than half of this generation are of the 0 grade[1]. Thus, lack of a tail stripe is incompletely dominant over its presence, a fact which will be illustrated in a number of ways later.

Comparison between the F_1 and F_2 generations is highly instructive. Whereas in the former the highest value is 27, in the latter we have seven cases exceeding that value, while the highest reaches 96. The mean, likewise, has advanced from 3·81 to 9·33, while only 36 per cent. of the individuals are now of the 0 grade[2]. All of these relations are, of course, in keeping with the above supposition that we have to do with an incomplete dominance of absence of tail stripe over its presence, and with the reappearance in the F_2 generation of individuals which are homozygous for some of the recessive factors.

Standard deviations have been computed for this character in the

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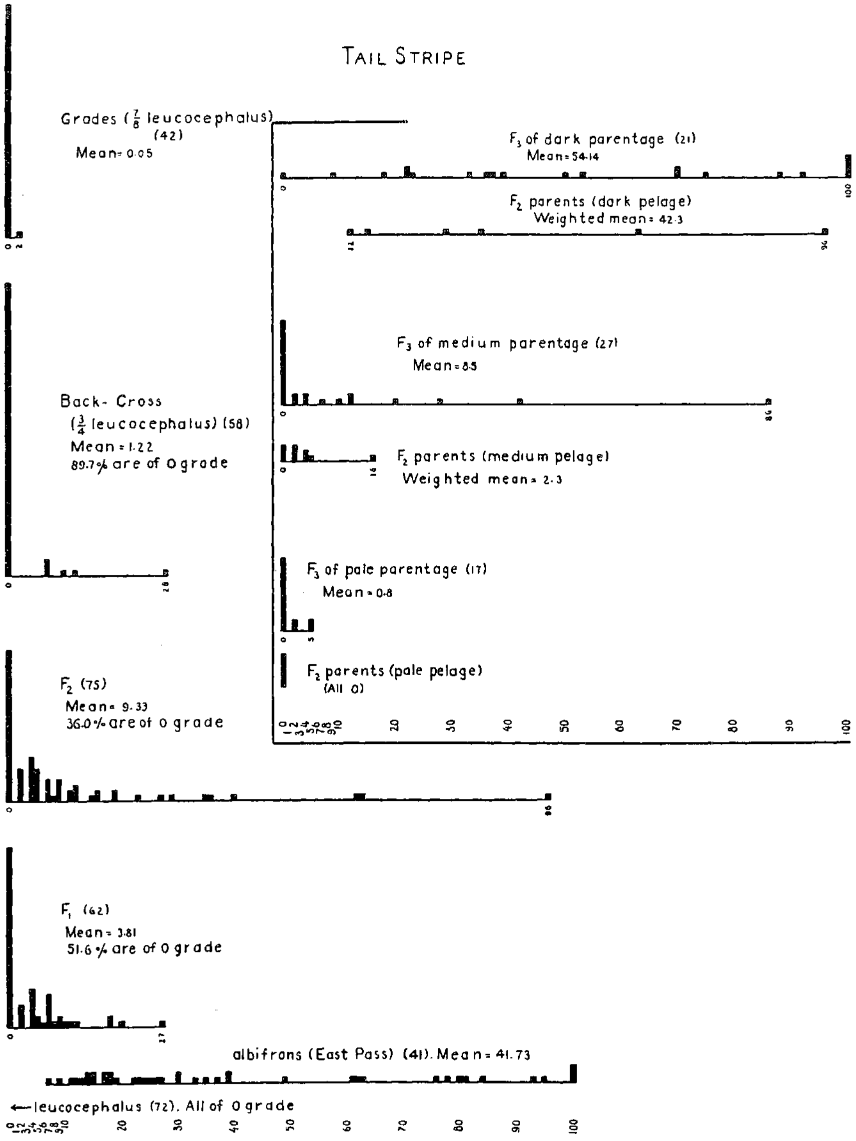
[1] That this is not due to the accidental choice of *albifrons* parents having low-grade tail stripes is shown by the mean figure of the latter (weighted by the number of their offspring). This figure is 40·42.

[2] The weighted mean of the values for the F_1 parents is 4·29.



Text-fig. 2. Tail stripe values for *leucocephalus* (0), *albifrons* of the East Pass series, and the various generations of hybrids. Here and elsewhere, the values given for length of tail stripe represent percentages of the total exposed part of the tail.

various generations, though this is scarcely a legitimate procedure, owing to the extreme asymmetry of the distributions. It is obvious, however, that the variability is far greater in the F_2 generation than in the F_1.

Back-crosses with the paler parent race (*leucocephalus*) give a mean value for the tail stripe of 1·22, while 90 per cent. of the individuals are of the 0 grade. For the "grades" (7/8 *leucocephalus*), all but one of the forty-two individuals belong to the 0 grade, the single exception giving the lowest measurable grade (2).

It is a matter of interest that the degree of dominance is nearly alike in the two generations in which it is possible to test this. Thus the mean value for the F_1 generation (3·8) is removed only nine hundredths of the distance from 0 to the weighted mean of the *albifrons* parents (40·42), while the mean of the back-cross generation (1·22) is eleven hundredths of the distance from 0 to the weighted mean of the F_1 parents of that generation (10·71)[1]. It happens that all of the back-cross parents of the "grades" lacked the stripe in any measurable degree, and this condition is virtually repeated in the latter generation.

The limited series of crosses derived from *albifrons* of the Foster's Bank series are far less instructive. Only four individuals out of this collection were employed as parents, three of these having a tail stripe of the 0 grade. The F_1 hybrids between these and *leucocephalus* numbered only sixteen, while the F_2 generation numbered twenty-nine, the back-crosses with *leucocephalus* twelve, and the grades seventeen[2]. Certain of the relations shown by this series are contradictory, owing probably to the limited numbers (*e.g.* the lower variability of the F_2 generation as compared with the F_1). It is significant, however, that the great majority of individuals, both in the F_1 and F_2 generations, are of the 0 grade, while the highest value in either generation is 5. The slight development of the tail stripe in the Foster's Bank mice thus represents a hereditary difference.

The point last referred to brings up the question how far, in general, these differences in the development of the tail stripe are hereditary. Within the East Pass series alone, the values range from 7 to 100, while individuals giving values from 9 to 76 were mated with *leucocephalus* as parents of the F_1 hybrids. It may seem that little of an instructive nature can be learned from the use of such heterogeneous material.

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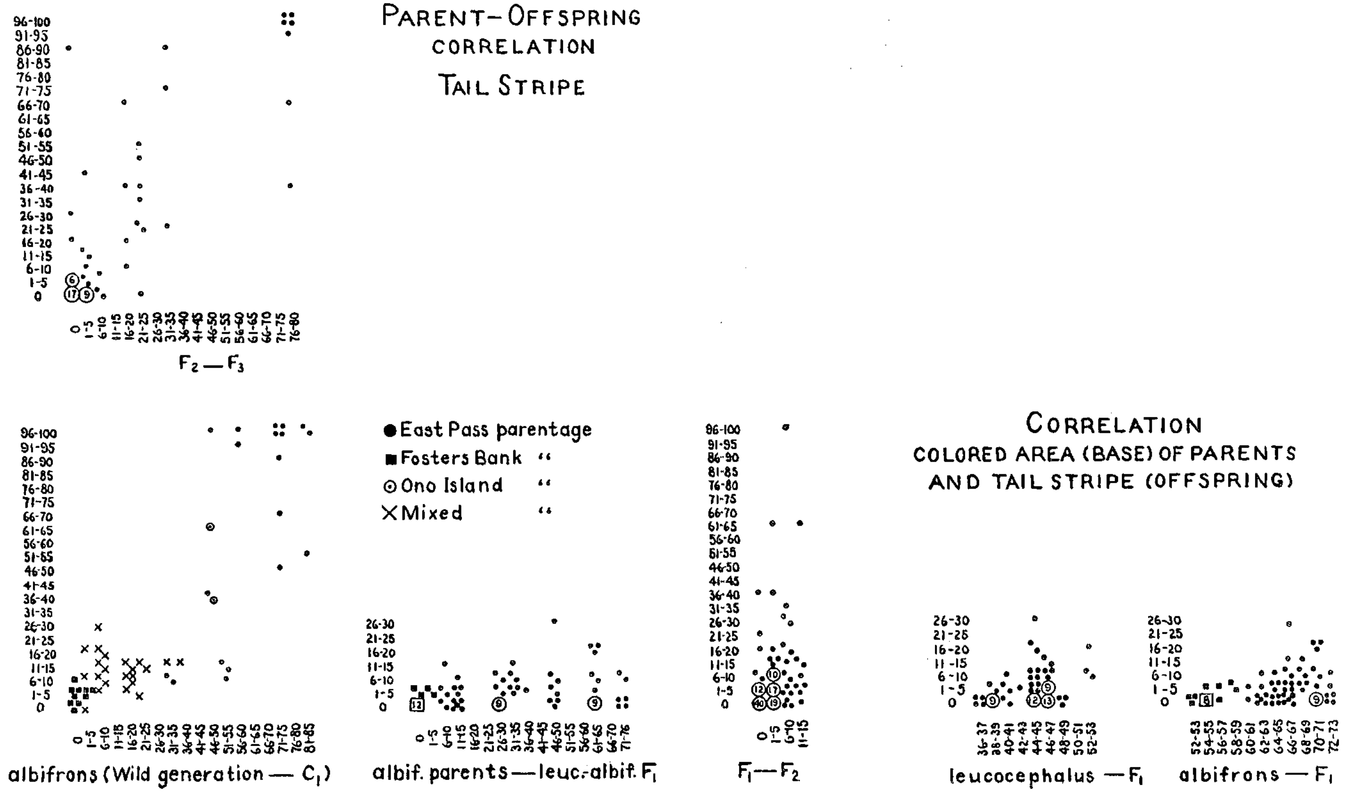
[1] Several F_1 mice having relatively high tail-stripe values figured as the parents of a considerable proportion of the back-cross generation.

[2] In addition to these last, there are twenty-one F_2 individuals of mixed descent, these having both East Pass and Foster's Bank grandparents.



Text-fig. 3. Correlations between tail stripe (parents) and tail stripe (offspring), and between coloured area (parents) and tail stripe (offspring) in the *leucocephalus-albifrons* cross. Abscissas denote mean value of parents; ordinates the individual offspring. Derivation of *albifrons* stock is indicated by symbols in first, second, and fourth figures of lower row; in the other two figures no distinction is made. Where the number at a given locus is too great to be represented by individual dots, this is indicated by the figure in the circle or square.

However, there is abundant evidence that these great differences within a single local population are largely non-genetic.

Owing to the great variability of this character, and to its asymmetrical distribution, the computation of parent-offspring correlations would not here be justified. But the correlation may none the less be portrayed graphically (Text-figs. 2, 3). In Text-fig. 2 we have the values exhibited by an F_3 generation of selected parentage. As already stated (p. 282), the "pale," "medium" and "dark" sections of the F_3 generation were derived from F_2 parents which had been selected according to the shade and extent of the coloured area of the pelage. The magnitude of the tail stripe played little or no part in the choice. The conditions here portrayed make it clear both that the differences in the length of the tail stripe are in part genetic, and that they are closely correlated with differences in the general pigmentation of the pelage.

Text-fig. 3 further illustrates the undoubted, though feeble and erratic, correlation which exists between parents and offspring in respect of the degree of development of the tail stripe.

Allowing, then, for great differences in the "expression" of this character, due to non-genetic causes, is it possible to estimate the number of genetic factors concerned in the difference between total lack of a tail stripe and its presence *in any degree*? Comparison between the arrays for the F_1 and F_2 generations (Text-fig. 2) makes it quite unlikely that we have to do with a simple one-factor difference. In the F_2 generation we should have 25 per cent. of pure dominants, all of which would be of 0 grade, according to hypothesis. But to this number should be added half of the heterozygotes, since about that proportion of F_1 animals were of 0 grade in this respect. Thus, about 50 per cent. of 0 grade individuals, instead of the 36 per cent. actually found, would be expected in the F_2 generation, if we had to do with a one-factor difference.

That the entire difference between the *leucocephalus* and the *albifrons* condition, in respect to tail stripe, is not due to a single pair of allelomorphs is even more certain. When each of the forty-eight F_2 individuals which display this character is compared with its own *albifrons* grandparent, we find that in only three cases is the value equal to or greater than that of this grandparent. No others approach the latter very closely. Although this does not, of course, constitute an accurate estimate of the number of pure segregants for the character in question, the number is obviously far too small for a monohybrid ratio. On the hypothesis of a single factor difference, about nineteen individuals, out of the seventy-five in the F_2 generation, should be homozygous for the *albifrons* tail stripe factor. The number actually found lies between the expected numbers for two and for three factors. We shall find reasons for believing that even that estimate would be too low.

Foot pigmentation. Owing to the complete lack of pigmentation in the foot of *leucocephalus,* and its merely occasional presence in *albifrons,* this character cannot profitably be considered in the present cross. Reference will be made here only to the higher mean value found in all of these generations of *leucocephalus-albifrons* hybrids, in comparison even with *albifrons* itself. This fact will be referred to in connection with the next cross.

Coloured area of the pelage. As stated above, the entire ventral and portions of the lateral surfaccs of the body, in both *leucocephalus* and *albifrons,* are clad with hairs which are white from base to tip. In contrast to this area (peripheral in the flat skin), is a dorsal (central) region, in which the hair is pigmented, partly at the base only, but for the most part throughout its entire length. Thus, when examined by transmitted light, and viewed from the inside of the skin, a central, semi-opaque area is seen, which is bordered by a translucent margin of varying width. The former is constituted by all the pigmented hairs of the pelage, including both those which are pigmented at the base only, and those which are pigmented from base to tip. The semi-opaque area thus seen is usually outlined rather sharply, and may be measured by means of a planimeter. When stated as a percentage of the entire area of the animal's skin it is a character of prime importance[1].

The mean value of this character in *leucocephalus* is 45·54, extreme variants ranging from 37 to 54. In *albifrons* of the East Pass series, the mean is 66·46, the range in variation being from 60 to 73. The *albifrons* from Foster's Bank show a far lower value, the mean being 56·80, and the range from 52 to 61. Finally, the small Ono Island series (not used in the hybridisation experiment) give the high mean value of 72·87. Fortunately, most of the hybrids were derived from crosses with the East Pass series, in which the range of variability is relatively small and does not closely approach that of *leucocephalus.*

Text-fig. 4 shows the behaviour of this character in the various generations of hybrids (excluding the F_3), while the means and standard deviations appear in Tables I and III. The mean value for the sixty-two

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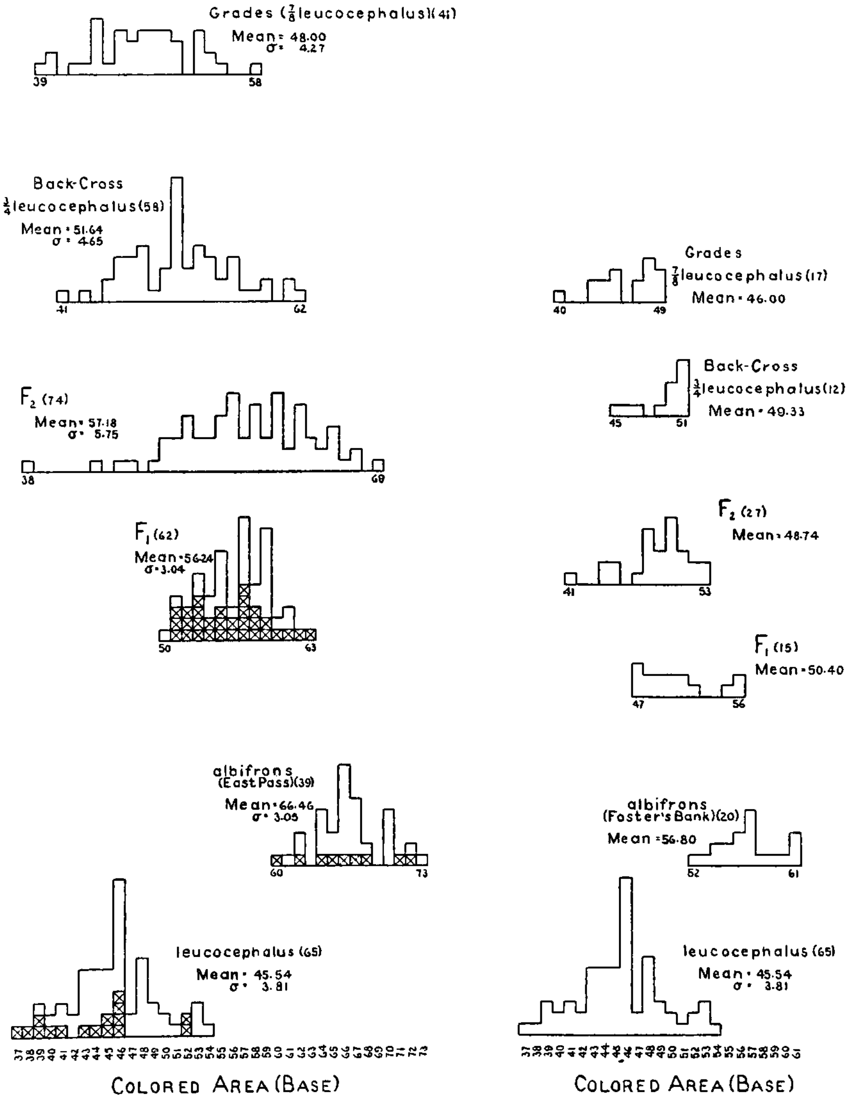
[1] Sumner (1926, 1927). Values thus obtained are obviously far from being absolute ones. Since the procedure is constant, they are, however, strictly comparable with one another.



Text-fig. 4. Values for coloured area of pelage (here the area occupied by hairs pigmented at base) for *leucocephalus*, *albifrons* (of two local sub-races) and the various hybrid generations, excluding F_3. Cross-hatched squares represent parents of the next generation.

F_1 mice (56·24) is very nearly an average of the weighted means of the *leucocephalus* and *albifrons* parents. Thus, there is no appreciable tendency toward dominance in respect to this character. In accordance with the latter fact there has been no appreciable shifting of the mean in the F_2 generation. The slight difference found is probably of no significance.

There is, however, an obvious and very considerable increase in variability when we pass to the second hybrid generation. The latter (seventy-four skins available) has a range from 38 to 69, with a standard deviation of 5·75, whereas these values, in the F_1 generation, range from 50 to 63, giving a standard deviation of 3·04. The two lowest values in the F_2 fall below the mean value for *leucocephalus*, while the three highest values equal or exceed the mean for *albifrons*[1].

In the back-cross (F_1 × *leucocephalus*, in either direction), the fifty-eight animals show a range from 41 to 62, a mean of 51·64, and a standard deviation of 4·65. The mean is approximately midway between the mean of *leucocephalus* (wild generation) and that of the F_1 generation, while the variability is higher than in the F_1, though lower than in the F_2. Four individuals give values equal to or below the mean for *leucocephalus*, while none reach the mean for *albifrons*.

The small group (fifteen) of back-crosses with the other parent race (*i.e.* 3/4 *albifrons*) give a range of from 52 to 69, and a mean of 61·27. This figure is very nearly midway between the F_1 mean and that of the East Pass *albifrons*. The *albifrons* parents and grandparents of this group were almost wholly East Pass derivatives.

Of the second back-crosses or "grades" (first back-cross × *leucocephalus*, in either direction), we have forty-one individuals, giving a mean of 48 and a standard deviation of 4·27. The mean is approximately midway between the mean of the back-cross generation and that of *leucocephalus*.

Passing to the limited number of hybrids involving the Foster's Bank series of *albifrons*, it is evident (Text-fig. 4) that the mean value of the coloured area for this series is much closer to that for *leucocephalus* than is that for the East Pass series. Accordingly, the F_1 generation of hybrids likewise gives a much lower mean. The relations between the F_1 and the first and second back-crosses are such as might be expected,

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[1] Unless otherwise specified, the mean of the entire population of a given parent generation is intended. While the weighted mean of the actual parents is probably a fairer index of the latter's genetic contribution, this has not always been computed, owing to the labour involved, as well as to the fact that such means commonly differ but little from those of the total population to which the parents belong.

considering the small numbers of individuals. The difference between the F_1 and F_2 means is unexpected, but this probably has no significance.

The facts discussed in the last few paragraphs make it plain that the differences between *leucocephalus* and either strain of *albifrons*, in respect to the extent of the coloured area of the pelage, are not dependent upon a single pair of Mendelian factors. If we may assume that they are explainable on a Mendelian basis at all, one naturally enquires whether the number of factor differences may be determined.

It has already been stated that two F_2 individuals of the *leucocephalus*-East Pass cross fall below the mean value of *leucocephalus*. Indeed one gives a value as low as any but the palest single specimen of *leucocephalus*. However, in view of the wide range of variation within *leucocephalus* itself, it is more pertinent to ask how many F_2 animals give values equal to or lower than *their own leucocephalus grandparents*. It happens that there are two such, these being the same two individuals as have already been referred to. One gives a value equal to that of its *leucocephalus* grandparent, the other a value one unit less.

It would, of course, be unjustifiable to conclude forthwith that these particular two individuals, and no others, are pure segregants for the factors concerned in determining the racial differences in the magnitude of the coloured area. For, in the first place, even an individual having the same genetic constitution as a given ancestor would not necessarily agree with the latter precisely. It might give a lower or higher value, and a departure in either direction would be equally probable. We should not be warranted, therefore, in including only those individuals which equalled or *surpassed* their parents in respect to a given character, since this number would tend to be too low[1].

However, there is another circumstance working in the opposite direction. If we suppose that a number of factor differences are concerned here, it is likely that the various genetic classes in the segregating generations would overlap rather broadly, owing to non-genetic variability. For this reason, an individual not homozygous for all of the colour-restricting factors derived from *leucocephalus* might nevertheless equal or surpass its *leucocephalus* ancestor in respect to the character in question.

Since we have no means of determining which of these two opposing tendencies would exert the greater influence, let us make the arbitrary

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[1] The word *surpass* is here employed in the sense of having a *smaller* value for coloured area than the *leucocephalus* ancestor, since *leucocephalus* differs in this direction from *albifrons*.

assumption that their effects would balance one another, and provisionally count as pure *leucocephalus* segregants (for these factors only) the actual number of individuals which give equal or lower values than their *leucocephalus* ancestors.

Thus, as already stated, we have, in the present F_2 generation, two segregants supposedly "pure" for the *leucocephalus* allelomorphs which influence the magnitude of the coloured area. This frequency (1 in 37), stands between the expected frequencies in cases where two and three pairs of Mendelian factors are concerned in a cross. However, in the other direction, it happens that not one of the F_2 individuals attains as *high* a grade as its *albifrons* grandparent. This would lead us to suspect that we have to do with more than two factor differences.

Passing to the back-crosses with *leucocephalus*, we find but a single individual, out of a total of fifty-eight, which gives a lower value than the mean of its *leucocephalus* ancestors. This is not far from the proportion of 1 in 64, which would be the expected proportion were six factor differences concerned in the cross.

The "grades" (7/8 *leucocephalus*) yield seven cases, out of a total of forty-one, in which the extent of the coloured area equals or falls below that of their *leucocephalus* ancestors. Thus we have about 17 per cent., a proportion very close to that to be expected were six factors concerned (see Text-fig. 15). This is in close agreement with the figure indicated by the back-cross generation, but not at all in harmony with that which might be inferred from the number of *leucocephalus* segregants in the F_2 generation. Needless to say, none of these figures have any great measure of probability, owing to the small numbers concerned, and to the further uncertain elements in the situation which have been referred to above.

One weighty reason for believing that we have to do here with a considerable number of factor differences is based upon the distribution of cases in the population of "grades" (7/8 *leucocephalus*). For purposes of comparison I have computed the expected proportions belonging to each phenotypic class, which would result from such a cross, on the supposition that we had to do with two to ten pairs of factors respectively[1]. The proportional numbers of these classes, expressed in per-

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[1] The terms of this series are derived from the expansion of $(1+3)^n$, where n equals the number of supposed allelomorphic pairs concerned. If the more heavily pigmented race (in this case *albifrons*) be represented as $AABBCC$..., etc., and the less heavily pigmented race (*leucocephalus*) be represented as $aabbcc$..., etc., the frequencies plotted in these graphs are those for genetic combinations containing the various possible numbers of capital letters, ranging from the completely heterozygous condition ($AaBbCc$..., etc.) to a

centages, are shown graphically in Text-fig. 15. It is evident from this figure that a very asymmetrical distribution is to be expected until about five or six factors are reached. Furthermore, the asymmetry is of such a nature that the mode is displaced in the direction of the pure race to which the hybrids have been successively crossed. Thus, in the present case, if only a few factor differences were concerned, the genetic classes which approach most closely to "pure" *leucocephalus* should be piled up on one side of the distribution surface, while those classes which show the effects of the cross with *albifrons* should be present in gradually decreasing numbers, tapering off to a low minimum for the completely heterozygous class, equivalent to the F_1.

This asymmetry is so marked in all of the polygons up to those for five or six factors that it should manifest itself even in the small population (forty-one individuals) with which we have to deal in the present case, and even when we take account of the considerable amount of non-genetic variability and of probable departures from the ideal scheme assumed in the preceding footnote. A glance at Text-fig. 4 shows that nothing of the sort has occurred. The distribution is approximately symmetrical. This same fact will be referred to again in connection with another character in the present cross, and with both characters in another cross.

Considerable asymmetry is to be noted in the small series of Foster's Bank crosses, but this asymmetry is not of the type which is called for by the considerations here discussed, and it is likewise manifested in generations where it should not occur. The relations are probably accidental.

In the foregoing argument, both *leucocephalus* and *albifrons* were treated provisionally as if they were genetically homogeneous in respect to the character under consideration. As might have been anticipated, this is distinctly not the case, a fact which serves to further complicate the picture presented to us.

Parent-offspring correlations for the "pure" races and the various generations of hybrids have been computed for this and some other

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condition homozygous for the *leucocephalus* factors (*aabbcc*..., etc.). Any strict comparison between these polygons and the frequency distributions in an actual 7/8 cross involves, of course, several assumptions, viz. that Aa is approximately midway between AA and aa; that the effects of A, B, C, etc. are approximately equal; and finally that all of the "capital" genes belong to one of the two sub-species, while all of the "lower case" ones belong to the other. Since, however, we are not trying to determine the actual number of factors concerned, even roughly, but merely endeavouring to set a minimum value for these, I believe that the foregoing objections may fairly be waived.

characters. The weighted mean of these coefficients of correlation between the successive generations (excluding that between F_2 and F_3) is + 0·375. The degree of correlation is doubtless somewhat increased by the fact that the derivatives of the local sub-races of *albifrons* have not been segregated from one another in these computations[1].

The correlation between selected groups of F_2 individuals and their F_3 offspring (see p. 282) is + 0·751. The high value of this coefficient is due to the fact that three groups, representing the extremes of shade and the medium condition, were selected, and were subjected to assortative mating. The effect upon the correlation was, of course, much the same as if several pairs of pure *leucocephalus* and *albifrons* had been included among the F_2 parents.

Graphs (Text-fig. 6) showing the distribution of these offspring of selected F_2 parents are instructive[2]. The wide differences between these group means is obvious.

Red. This is the value of the reading obtained through the red colour screen in the Ives Tint Photometer. It is expressed as a percentage of the light which is simultaneously reflected from a standard white block (magnesium carbonate). The value obtained with the red screen is employed in preference to those obtained with either of the others used by me merely because it is the highest of these values. In the present discussion it is employed merely as an index of the paleness or darkness of the pelage, high values denoting pale skins and *vice-versa*[3].

From Table I and Text-fig. 5 it appears that *leucocephalus* gives a mean value for this character of 25·4, the individual figures ranging from 20 to 37. The East Pass collection of *albifrons* gives a mean of 17·17, the range being from 13·5 to 20. There is no overlapping between the actual parents of the F_1 generation, the lowest value for *leucocephalus* being 21·5, the highest for *albifrons* being 19.

The mean value of the Foster's Bank *albifrons* is 15·07, that of the fifteen Ono Island skins being 14·51.

In the F_1 generation of the *leucocephalus*-East Pass cross we have a mean value of 19·32, the extremes being 15·5 and 24. The mean here

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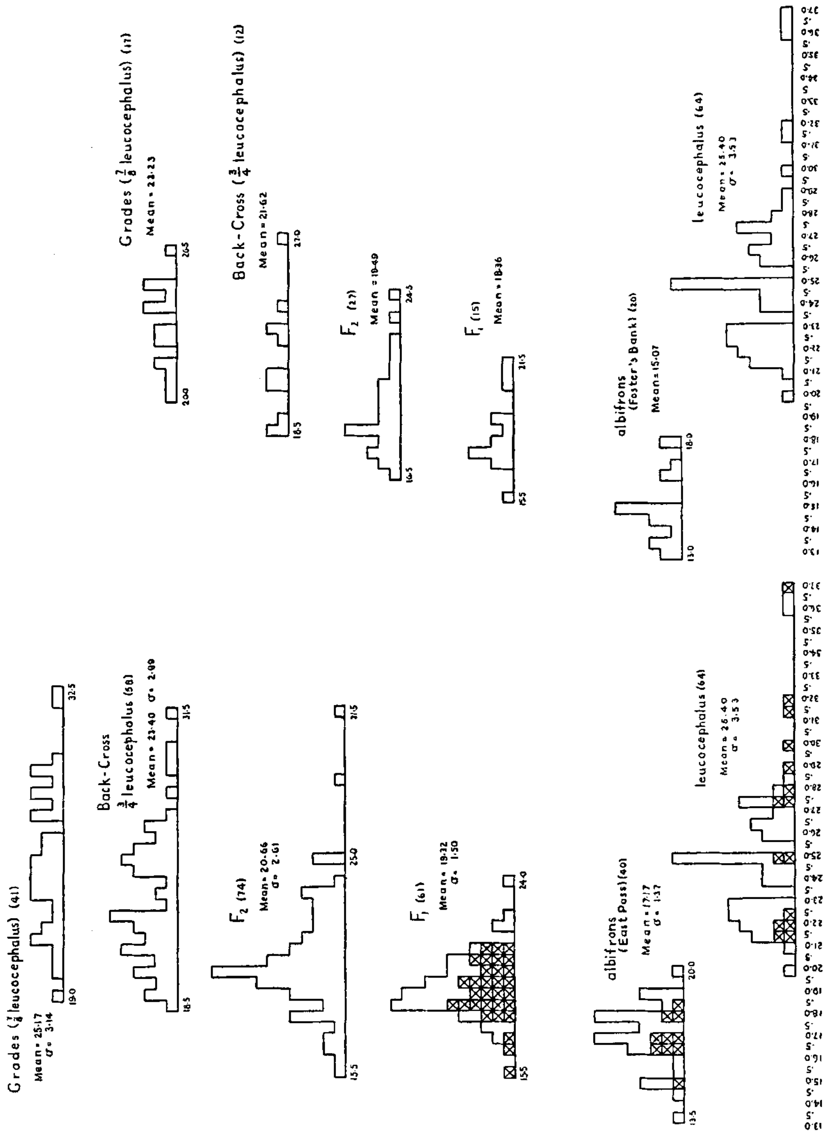
[1] The computations were well under way before the extent of these local differences was realised, and it has not been thought worth while to repeat these laborious calculations.

[2] Selections based upon the inspection of living animals, before their pelage measurements are known, are necessarily inexact.

[3] For an extended account of my procedure in using this instrument, see Sumner (1927). Let me repeat here that the colour values obtained in these studies are not absolute ones, nor do they approach the accuracy required in physics. All that is claimed is that the figures are reasonably comparable for the various series of skins here considered.

is appreciably lower than either the mid-value between the means of the parent races (21·28) or between the weighted means of the actual



Text-fig. 5. Values for "red" (readings through red colour-filter in the Ives Tint-Photometer) for the same populations represented in Text-fig. 4.

parents (21·41). It would thus appear that there is a slight tendency toward dominance of the darker condition over the paler, a relation which will be found to be even more pronounced in the *leucocephalus-polionotus* cross to be described below. It is of interest to recall that this is just the reverse of the relation manifested in the case of tail stripe length, in which the unpigmented condition is incompletely dominant over the pigmented. This situation is the more curious, since depth of coat colour (which is merely the reciprocal of the value of "red") is positively and strongly correlated with tail stripe.

In the F_2 generation we meet with the following salient facts. The mean is 20·66, being thus somewhat higher than the mean for the F_1 generation as a whole (19·32), and still more so in comparison with the weighted mean of the parents of the F_2 animals (19·14). This difference, which appears to be significant, is in the expected direction, representing a shift in the direction of the recessive condition. The same relation has already been noted in the case of tail stripe, and will be met with again in the *leucocephalus-polionotus* cross.

More important still is the increase in variability. The standard deviation for "red" has risen from 1·50 in the F_1 to 2·61 in the F_2. Likewise, the upper limit of the range has risen from 24 to 31·5, there being two individuals far exceeding the mean condition in *leucocephalus*. The lowest values, however, are the same in the two generations.

In the back-cross between the F_1 generation and *leucocephalus*, we have a mean value for fifty-eight individuals of 23·4, and a standard deviation of 2·99. The highest single value is, however, no higher than in the F_2 generation. The small series (fifteen) comprised in the back-cross with *albifrons* is not comparable with the others, since two of the collections of *albifrons* are represented in their ancestry.

The "grades" (7/8 *leucocephalus*) give a mean value of 25·17, which is close to that for "pure" *leucocephalus*, while nearly half of the total number equal or exceed, in this character, the mean value for the latter race.

The conditions shown in the limited number of crosses between *leucocephalus* and the Foster's Bank series of *albifrons* are evident from inspection of the graphs. The same tendencies are manifest as in the East Pass derivatives, the differences being due (1) to the much smaller numbers in the former series, and (2) to the considerably lower mean value for "red."

Considering, as previously, the proportion of seemingly "pure" segregants in the various hybrid generations, we find that in the F_2 generation, three individuals of East Pass lineage give a value equal to and three a value higher than the *leucocephalus* grandparent. If these six were regarded as segregants which were pure for the *leucocephalus* factors (see p. 296) we should have about one out of twelve in the total population, *i.e.* more than the expected number, if only two-factor differences were concerned.

Conversely, four F_2 individuals equal or *fall below* the value for the *albifrons* grandparent, *i.e.* about one in eighteen.

Among the back-crosses, we have twelve out of fifty-eight which would be "pure" segregants according to the suggested criterion, a proportion which would likewise correspond roughly with a two-factor difference[1].

Passing to the "grades," we have nineteen individuals out of forty-one (about 46 per cent.) which reach or surpass the mean of the *leucocephalus* ancestors. The expected proportion of pure segregants resulting from such matings is 42·2 per cent., on the assumption that we have to do with three factor differences.

Thus, if the foregoing reasoning were to be accepted, we should have a character difference between these two sub-species which depends upon two or at most three principal pairs of Mendelian factors. This is quite unexpected in view of the fact that racial differences in the extent of the coloured area were found to depend almost certainly upon a considerably greater number of factors than this, and of the further fact, to be discussed later, that these two "characters" are probably dependent, to a large extent, upon the same factors.

Inspection of the distribution polygon for the generation of "grades" (Text-fig. 5) reveals no more evidence of a pronounced asymmetry of distribution than was to be observed in the distribution of values for "coloured area" (p. 297). As judged by this criterion, a moderately large number of factor differences must be concerned in the case. An effort to reconcile these various contradictions will be made after the other crosses have been considered.

Parent-offspring correlations comparable with those computed for coloured area (see above) give a weighted mean for the various generations (excluding the correlation between F_2 and F_3) of $+ 0{\cdot}264$. This is a considerably lower figure than that for coloured area (0·375), a fact which probably depends upon the higher proportion of non-genetic variability in the character "red," as derived from tint-photometer readings of the pelages.

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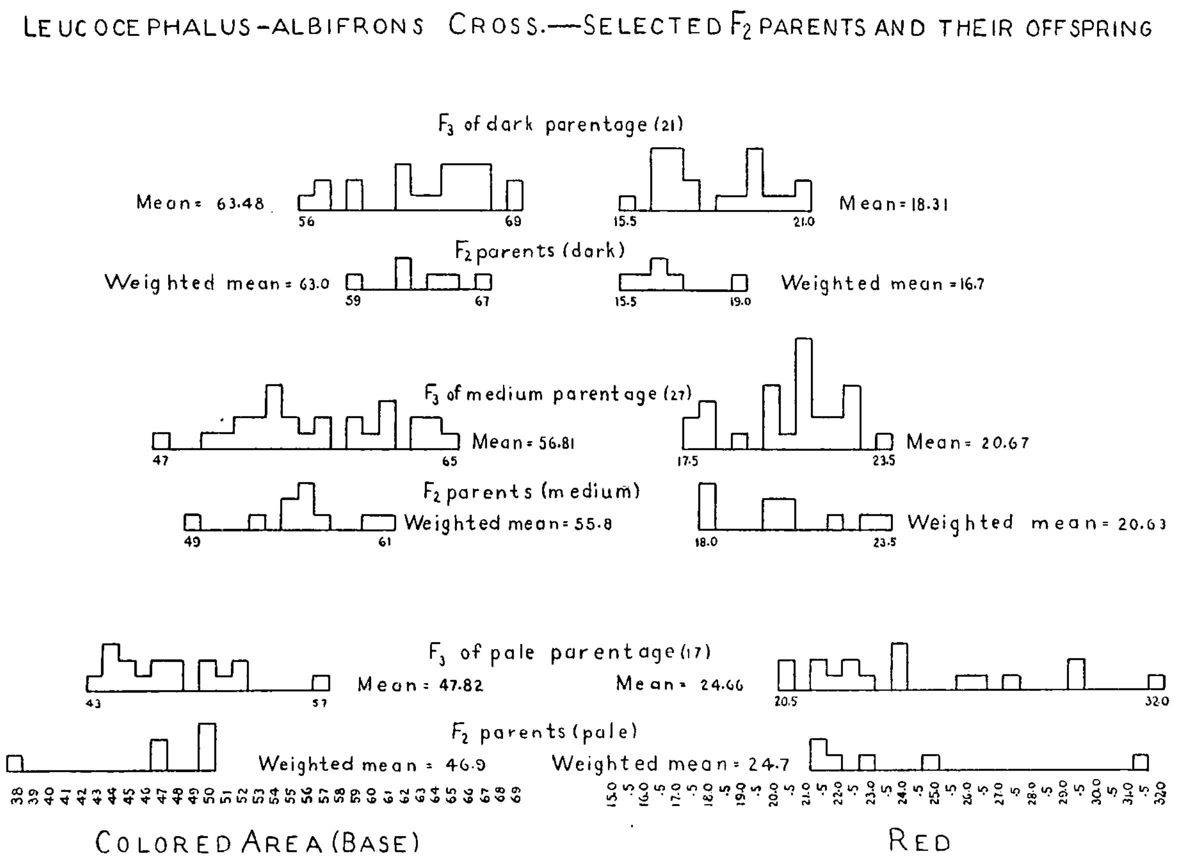
[1] Of these twelve, it is to be remarked that nine have as their mother (and likewise in some cases as grandmother) the same *leucocephalus* individual, and that the value of "red" for this individual is considerably below the average.



Text-fig. 6. Two pelage characters in selected F_2 parents and their F_3 offspring (*leucocephalus-albifrons* cross). The basis of selection was relative paleness or darkness, depending upon both depth and extensity of pigmentation.

The correlation between the selected series of F_3 animals and their F_2 parents is $+ 0{\cdot}743$. This is slightly, though not significantly, lower than that for coloured area. Text-fig. 6 gives the distribution of values in the offspring of each group of selected parents.

$\frac{A_b}{R}$. Since "red" is here used as an index of the paleness of the pelage, the reciprocal of this $\left(\frac{1}{R}\right)$ may be regarded as indicative of the depth of pigmentation. The total amount of pigment in the pelage is of course roughly proportional to the coloured area multiplied by the density of pigmentation, *i.e.* $A \times \frac{1}{R}$ or $\frac{A}{R}$.[1] This is, of course, far from being an exact quantitative expression for the amount of pigment present, and in any case it is obvious that we are not dealing here with another character, independent of both "coloured area" and "red," even supposing that the last two are independent of one another.

Of the two parent races here considered, *leucocephalus* gives a mean value of 1·82, *albifrons* (East Pass series) a mean value of 3·9. The figures for the weighted means of the actual parents are 1·72 and 3·95 respectively. The mean for the F_1 generation is 2·93, that for the F_2 being 2·82, which is slightly nearer the value for the paler of the two races (*leucocephalus*). The expected increase of variability in the second hybrid generation is to be observed here. Conditions with respect to the back-cross generation and the grades are made evident in Text-fig. 7 and Tables I and III.

A quest for cases in which hybrid descendants have equalled or surpassed (here fallen *below*) their *leucocephalus* ancestors in respect to the value of $\frac{A}{R}$ results in contradictory findings. Whereas the number of supposedly pure segregants in the F_2 generation points to the presence of not more than three factor differences, the proportion among the grades is about that for six factors. The distribution of frequencies in the latter generation (Text-fig. 7) likewise points to a relatively large number of factors.

The weighted mean of the parent-offspring correlations for the two pure races here involved, and for the various hybrid generations (excluding that between F_2 and F_3), is $+ 0{\cdot}312$. This is intermediate between the figures for coloured area and red. The correlation between the selected F_2 parents and the F_3 generation is $+ 0{\cdot}762$. It was thought possible that this fraction $\frac{A}{R}$ would prove to be a better

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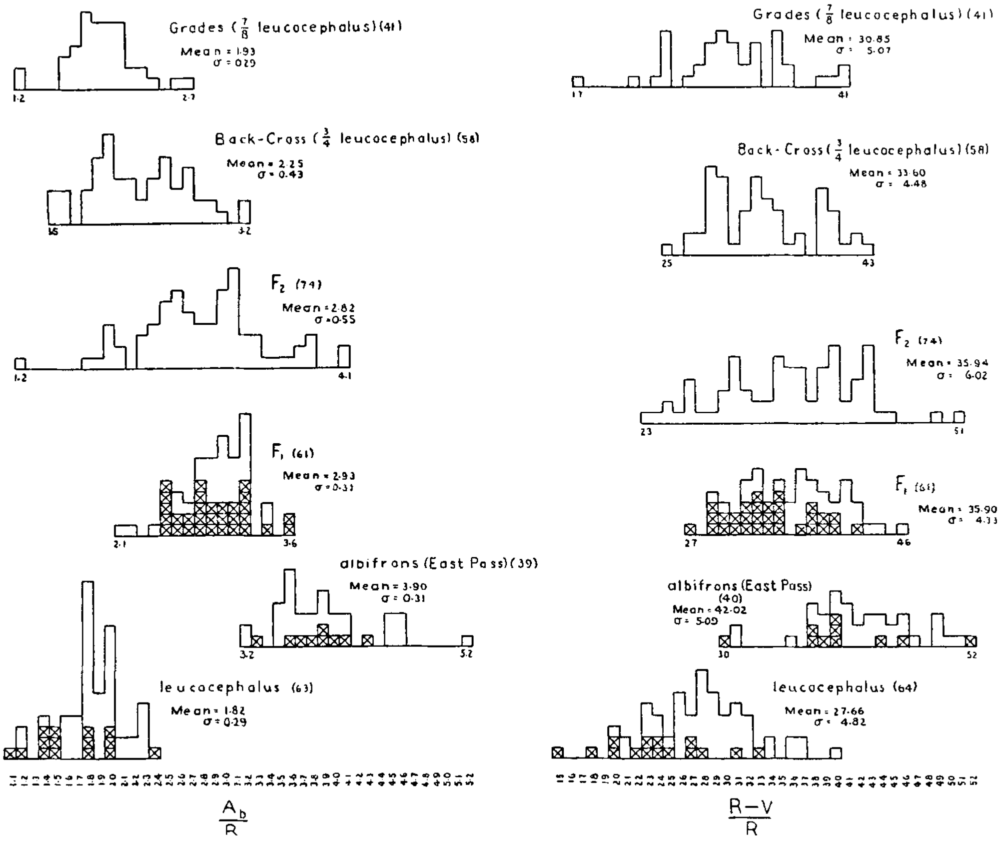
[1] Sumner, 1929 $\left(\frac{Ca}{R}\right.$ was used in the former paper$\left.\right)$. I shall here designate the area of hair pigmented at the base by A_b, the area pigmented at tips being designated as A_t.

index of genetic differences in pelage pigmentation than either of the values from which it is derived. It is evident that this is not the case.

$\frac{R-V}{R}$. The exact meaning of this fraction has been explained in my recent paper on technique (1927), and need not be discussed at any length here[1]. Briefly speaking, the fraction represents an index of



Text-fig. 7. Values for fraction: coloured area ÷ red, and for index of saturation, in *leucocephalus*, *albifrons* (East Pass series), and hybrids (excluding F_3).

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[1] Since there is no "free" blue or violet in the pelage of a mouse, the reading with the blue-violet screen (V) represents the amount of non-selective reflection, *i.e.* the amount of "white" light which is reflected from the skin. $R-V$ represents the amount of "free" red, after deducting that which is present as a component of the white light. In the paper referred to, this fraction was written "$\frac{R-BV}{R}$," but the formula here employed accords better with algebraic notation, since BV ("blue-violet") is a single quantity. In my first paper on the *polionotus* group (1926), I employed a different index $\left(\frac{R-V}{V}\right)$.

saturation as regards red. High values indicate a richly coloured skin (brown or yellowish), low values an approach to neutral grey. It will be found that these differences relate to a "character" which is to a considerable degree independent of the other pigmental "characters." Pale pelages may vary greatly in their richness of colour, and the same is true of dark ones. Certain correlations exist, however, between saturation and shade, as will be pointed out.

Leucocephalus, owing in part to the presence of large numbers of white hairs within the coloured area of the pelage, gives a low average value for this fraction (27·66); *albifrons* giving much higher values (East Pass, 42·02; Foster's Bank, 37·6; Ono Island, 30·73). Only the East Pass derivatives will be considered here.

In the F_1 generation we have a mean of 35·90, which does not differ widely from the mid-point between the means of the parent races (34·84). When, however, we compare the F_1 mean with the weighted mean of the actual parents of the F_1 generation, we have a considerably greater difference ($35{\cdot}90 - 31{\cdot}44 = 4{\cdot}46$). This would seem to imply a partial dominance of the more richly coloured condition over the greyer one, a relation which will be found to hold with yet greater force for the *leucocephalus-polionotus* cross.

The F_2 mean (35·94) is almost exactly the same as that for the F_1,[1] but there is a marked increase in variability, the standard deviation being 6·02, as compared with 4·33. The mean value for the back-cross generation is 33·60, this likewise being a figure far in excess of the mid-value between the weighted means of the *leucocephalus* and the F_1 parents of this generation (29·38). The mean for the grades (30·85), however, is very close to the weighted mean of their parents (31·08).

Decidedly curious relations are encountered when we consider the number of F_2 individuals which equal or surpass their grandparents in respect to this "character." On the one hand, there are five individuals out of seventy-four which give values equal to or lower than their *leucocephalus* grandparents; on the other hand, thirty-nine individuals, or more than 50 per cent., give values equal to or higher than their *albifrons* grandparents! Furthermore, even in the F_1 generation, there are two individuals which fall below their *leucocephalus* grandparents, and eight which equal or exceed their *albifrons* grandparents.

There are doubtless genetic factors concerned here which influence the degree of saturation of pelage colour, independently of its shade. Of this further evidence will be offered below. Likewise, the fraction

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[1] The weighted mean of the F_1 parents of the F_2 generation is 33·97.

$\frac{R-V}{R}$ seems to be the only means at hand of expressing these differences in degree. But the value of this fraction appears to depend upon such a variety of unknown factors that little of a definite nature has thus far been learned of its relation to the inheritance of pelage colour. Perhaps the explanation offered in the concluding section (p. 358) for the unexpectedly high number of seemingly pure segregants affords the best clue to this situation.

That the proportion of non-genetic variability is much higher than in the case of the colour characters hitherto considered is evident from a consideration of parent-offspring correlations. The weighted mean for the *leucocephalus-albifrons* series (pure races and hybrids, excluding F_2-F_3) is $+ 0{\cdot}094$; that for the F_2-F_3 coefficients being $+ 0{\cdot}381$.

Segregants showing aggregate "pure-race" pelage characters. It has been shown for each of the pigmental "characters" thus far considered that a certain number of individuals, in the various segregating generations of hybrids, reach or surpass the degree of depigmentation found in their own *leucocephalus* ancestors. Thus far, one "character" at a time has been considered. It is of interest now to enquire how many individuals in each hybrid generation reach or surpass the mean of one or the other parent race in respect to the entire complex of pigmental characters. In other words, what proportion, if any, of our segregants may be fairly classed as average *leucocephalus* or *albifrons* in respect to coloration[1]?

For this purpose, it would obviously be improper to include as "average" only those individuals which reach or surpass the parental mean value for every one of the characters. For such a standard would exclude all but a small proportion of individuals in a stock of the pure race itself[2]. Accordingly, in considering *leucocephalus* segregants, a limiting value was chosen for each character such that 4/5 of the parent stock of this race would be included. In the case of *albifrons*, the limiting value for each character was such that 5/6 of the parent stock would be included. The reasons for this procedure are as follows.

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[1] The fact that thirteen and eleven F_2 individuals, respectively, out of seventy-four (18 and 15 per cent.) fall within the extreme limits of *leucocephalus* and *albifrons*, in respect to all of the pigmental characters, is of little significance in view of the fact that even in the F_1 generation 16 and 7 per cent., respectively, fall within these limits.

[2] Thus, if half of the individuals of a race exceed the mean in respect to character A, only a fourth will exceed the mean in respect to both A and B (supposing that the two are not correlated); only an eighth in respect to A, B and C, etc. Correlation will increase these probabilities somewhat, of course, but the correlations here considered are not as a rule high within the pure races.

In *leucocephalus*, individual differences have been recorded for only three pigmental characters, coloured area, red and the index of saturation $\left(\frac{R-V}{R}\right)$. The other two pigmental characters considered in the present paper (foot pigmentation and tail stripe) are not here included, since their value in *leucocephalus*, with insignificant exceptions, is 0. Likewise the fraction $\frac{A}{R}$ is excluded, since it does not represent a character independent of the first two named above. If we were considering three uncorrelated characters, it is evident that the proportion of a *leucocephalus* population which would be included in the upper (or lower)[1] 4/5 in respect to all of these characters at once would be $(4/5)^1$, or about 51 per cent. Actually, it was found that 34 (54 per cent.) of the sixty-three skins comprising the parent stock of *leucocephalus* fell within the limits set. This agreement is closer than would have been expected, considering that the three characters are all correlated with one another.

In the case of *albifrons*, one further character (tail stripe) has been added to those considered for *leucocephalus*[2]. I have therefore adopted as a limiting value for each of these characters a value such that 5/6 of the *albifrons* population would fall within this limit. Thus, if the four characters were uncorrelated $(5/6)^2$, or about 48 per cent., would fall within this limit with respect to all four. In reality, eighteen out of thirty-nine East Pass *albifrons*, or about 46 per cent., conform to this standard.

Turning to our hybrid population, we do not find a single individual among the seventy-four comprised in the F_2 generation of the *leucocephalus*-East Pass cross which falls within the limits here adopted, in respect to all of the pigmental characters. Four F_2 individuals, to be sure, fall within these limits in respect to all of the values (including also tail stripe and foot pigmentation) except the index of saturation $\left(\frac{R-V}{R}\right)$. But all of these skins are of a richer colour than any but the upper fifth of the pure *leucocephalus* stock (here excluded). This in spite of the fact that a considerable number of other F_2 pelages (twenty among seventy-four) give values of $\frac{R-V}{R}$ which fall within the four-fifths limit for *leucocephalus*.

In the back-cross with *leucocephalus*, we have five individuals out of

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[1] Upper or lower, depending on the character. The 4/5 which vary in the direction *away from albifrons* is here intended.

[2] Foot pigmentation has not been included here, since the great majority of East Pass *albifrons* agree with *leucocephalus* in showing a 0 grade for this character. Certain hybrids, nevertheless, exhibit a low degree of foot pigmentation.

fifty-eight which conform to the standards that have been set for an "average" *leucocephalus*. Eight other individuals would have been included except for the excessive value for $\frac{R-V}{R}$. Here, again, it must be pointed out that there is no lack of individuals in this series (there are twenty-one out of fifty-eight) which fall within the limits set for this character.

Among the grades, nine out of forty-one animals measure up to the required standards for all of these characters. Of the twenty-two which fall within the limits in respect to coloured area, only five fail to do so with respect to red, while eleven fail to do so with respect to the index of saturation. This in spite of the fact that nearly 60 per cent. of this entire lot of animals fall within the limits with respect to the latter character.

I have likewise looked into the number of possible *albifrons* segregants in the F_2 generation[1], as judged by the standard referred to above. There is not one individual among the seventy-four which falls within the limits set in respect to all of the pigmented characters, although six of them would do so except for their giving too low values for the index of saturation.

To sum up the preceding enumeration, there is not a single individual, in an F_2 population of seventy-four, which measures up to the standards set either for an average leucocephalus *or an average* albifrons, *in respect to aggregate pigmental characters. In the first back-cross with* leucocephalus, *five individuals showing average characters for the latter race appeared in a population of fifty-eight. In the second back-cross ("grades"), there are nine cases in a population of forty-one.*

It must not, of course, be supposed that such an enumeration as the foregoing reveals the exact number of segregants which are pure for all *leucocephalus* colour factors. It merely gives an approximate answer to the question: How many individuals are there in which segregation is so nearly complete that they equal or surpass[2] the average *leucocephalus* phenotypically?

One circumstance which was noticed during the life of the animals is reflected in the figures which have here been considered. This is the fact that most of the paler variants among the F_2 and back-cross generations (including grades) are of a distinctly richer colour than *leucocephalus*, with which they would otherwise be closely comparable. That this is not

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[1] The number of offspring derived from back-crosses with *albifrons* is too small to be considered here.

[2] *I.e.* surpass it in the direction away from *albifrons*.

due to any lack of segregants having a low index of saturation has already been pointed out[1]. It is due to the complete absence, in these hybrid generations, of any positive correlation between pallor and low saturation, such as obtains in *leucocephalus*. Quite the contrary, we meet with a positive correlation between pale shade and *rich* colour in both the F_1 and F_2 generations of this cross.

The question naturally arises whether the *leucocephalus*-like derivatives of the *leucocephalus-albifrons* cross agree with the former race in characters other than pigmentation. The other racial differences upon which stress has chiefly been laid are length of tail and foot. But these differences concern mean values only. The distribution frequencies for both characters overlap broadly in the two races. No such detailed analysis of these values seems desirable here as was presented in the case of colour characters. It need only be stated that the five back-cross individuals above referred to, as well as the nine among the grades, fall within the range of *leucocephalus* with respect to both tail and foot length, while in an actual majority of these cases the measurements of tail and foot equal or exceed the mean values for these members in *leucocephalus*.

Correlations. Considerable attention has been devoted to correlations between the various characters thus far discussed. Table V presents such coefficients as have been determined for the parent stocks and for the various crosses. Correlations between various characters and size (body length) have likewise been computed, though they are not here included. The latter render possible the computation of "corrected" values for various characters which are strongly influenced by size.

The facts revealed by the correlation coefficients and graphs (Text-figs. 8, 9, 10), so far as the *leucocephalus-albifrons* (East Pass) cross is concerned, may be summarised as follows:

(1) All linear measurements (tail, foot, ear, pelvis, femur, skull length, skull breadth), as well as weight, show, as might have been anticipated, rather high positive correlations with body length in nearly all of the populations here considered. In general, there are no differences of interest, in the magnitude of these correlations, between the various races or generations of hybrids or between the sexes[2].

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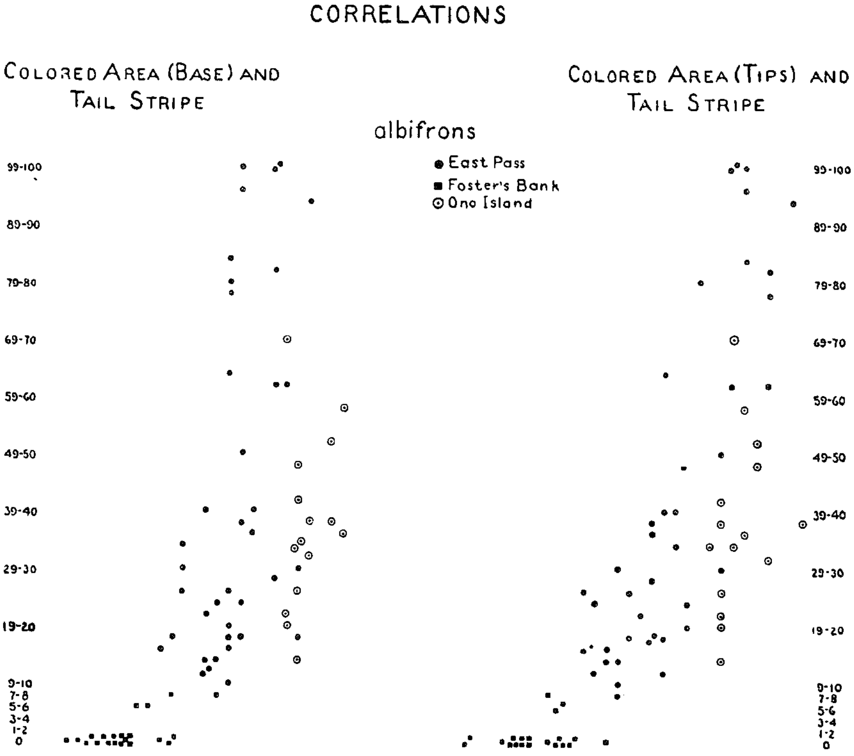
[1] Nor is it probably due to any effects of captivity. The mean index of the C_1 *leucocephalus* is slightly *lower* than that of the "wild" generation of *leucocephalus*, though slightly higher than the weighted mean of their own parents.

[2] There is a moderately strong probability of a correlation between body length and the number of caudal vertebrae, when both the *leucocephalus-albifrons* and the *leucocephalus-polionotus* series are considered. There are eleven positive coefficients out of

(2) There are no constant correlations between body length and any of the pigmental characters. Occasional single figures are of moderate statistical significance, but the relations shown by the various series are so contradictory that the existence of any true correlation is doubtful.

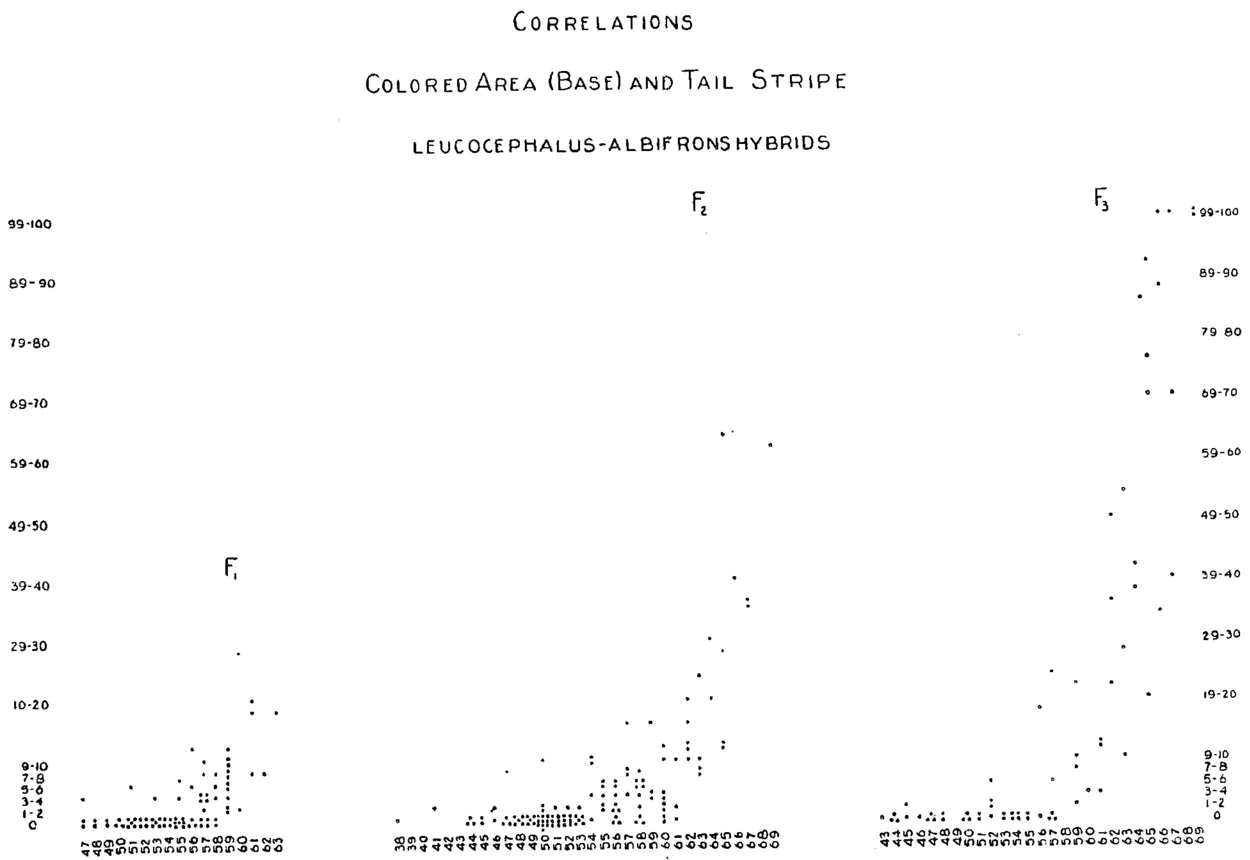
As regards the correlations between various characters, other than body length, I have restricted the computations mainly to characters which differ in the races that have been crossed.



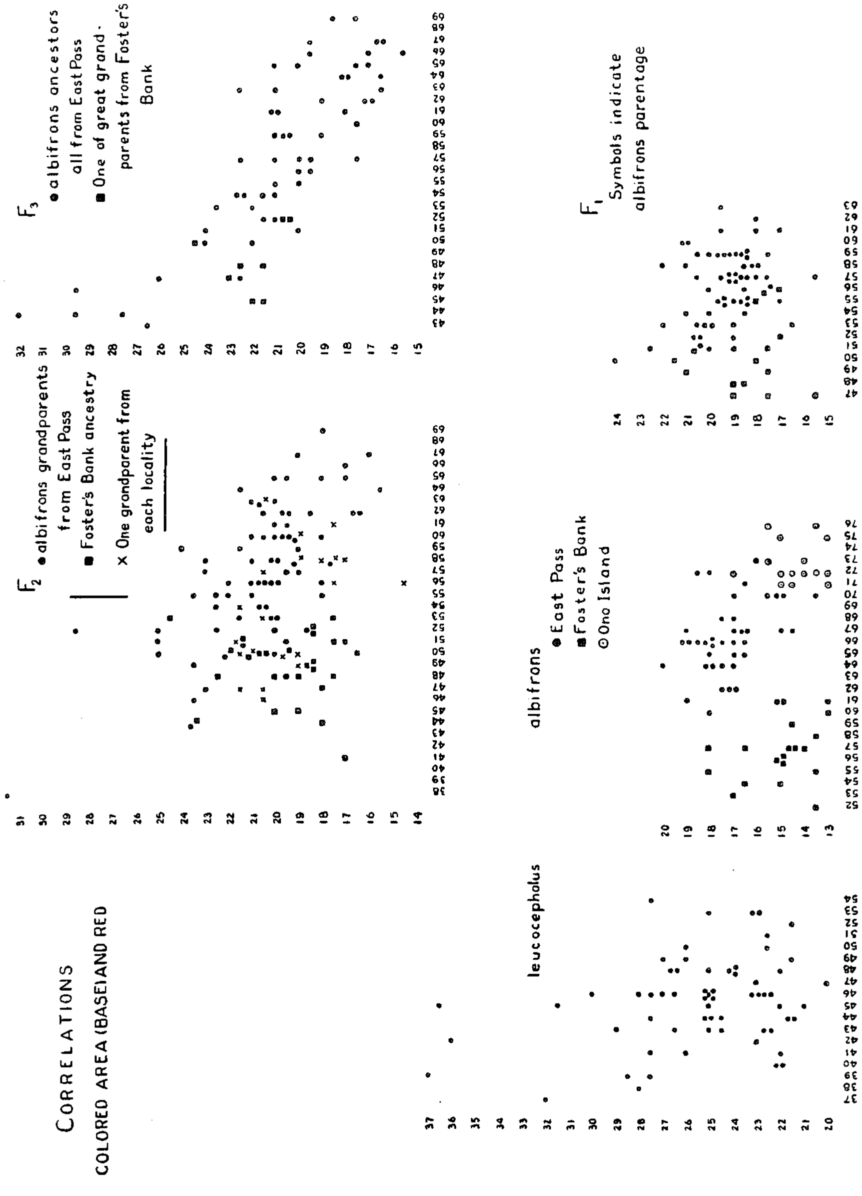
Text-fig. 8. Correlations between coloured area of pelage (abscissas) and tail stripe (ordinates) in *albifrons* (the three local collections being distinguished).

(3) An undoubted positive correlation exists between the length of the tail and foot. This is true not only of the "gross" but of the "net" correlation, *i.e.* that which remains when the influence of general body-

fourteen (the fourteen groups being the males and females of the three pure races and of the F_1 and F_2 generations of two crosses), while the weighted mean of the fourteen coefficients (based on 454 individuals) is +0·142.



Text-fig. 9. Correlations between coloured area and tail stripe in three generations of *leucocephalus-albifrons* hybrids.



Text-fig. 10. Correlations between coloured area (abscissas) and red (ordinates) in *leucocephalus*, *albifrons*, and three generations of hybrids. The influence of the different *albifrons* stocks is evident, even in the F_3 generation.

size has been eliminated[1]. Wide differences are found in the magnitude of this coefficient, according to the race, generation or sex comprised in the group under consideration. But none of these differences have any evident biological interest. Low positive correlations likewise exist in all cases between tail and ear length and in most cases between ear and foot, even when the influence of body size has been removed.

(4) Significant correlations exist, in many cases, among the various pigmental characters. These correlations are positive between tail stripe and coloured area; negative between the former and red; negative between red and coloured area.

(5) Despite single instances, no consistent correlations exist between tail length and any of the pigmental characters. As regards foot length the case appears to be different. Out of thirty-eight coefficients which have been computed for *leucocephalus*, *albifrons* and the five series of hybrids involving these two sub-species, twenty-four are of the sign which would be expected on the supposition that racial peculiarities in respect to pigmentation and foot length are genetically associated. When we consider these series of animals separately, moreover, we find that the preponderance of "expected" signs is due entirely to the F_2 and F_3 generations of hybrids, for which the twelve coefficients are all consistent with the foregoing interpretation. These are of course the generations in which such a genetic association of racial characters would be most evident. The testimony of these figures is not altogether cumulative, to be sure, since the various pigmental characters are all correlated with one another. But taken in connection with the even stronger evidence from the *leucocephalus-polionotus* cross, it can hardly be regarded as due to random sampling. These facts will be discussed more fully in relation to the cross next to be considered.

(6) The correlations within the single groups, which have been recorded under (4) and (5), correspond exactly to the manner in which the respective races differ from one another. Thus, *leucocephalus*, *albifrons* and *polionotus* form a series of increasing depth of shade (decreasing value of "red"), and also a series of *increasing* value of coloured area, tail stripe and foot pigmentation[2]. Likewise, *leucocephalus* differs from *albifrons* in having a significantly greater foot length.

(7) These correlations, for the most part, are greater in the F_2 than

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[1] I have called attention to this correlation in several previous papers.

[2] In recent papers (1929, 1929 *a*), I have shown that these same inter-racial correlations in pigmental characters held when we made a series of collections along a geographic gradient, through the range of *albifrons* into that of *polionotus*.

in the F_1 generation. In the majority of cases, they are largest of all in the F_3 generation, derived from selected F_2 parents (p. 282). Thus the correlation between coloured area and red is $-0{\cdot}326$ in the F_1, rising to $-0{\cdot}682$ in the F_2 and $-0{\cdot}788$ in the F_3. It is significant, though of moderate magnitude, in both *leucocephalus* and *albifrons*.

(8) Correlations between the index of saturation $\frac{R-V}{R}$ and the other pigmental characters are less easy to generalise. In *leucocephalus*, the correlation with red is negative, but in *albifrons* it is strongly positive, as is the case with the F_1, F_2 and F_3 generations of hybrids. In the back-crosses (3/4 *leucocephalus*), on the other hand, the coefficient is practically 0, while in the grades (7/8 *leucocephalus*) it is negative. Thus, with an increasing proportion of *leucocephalus* "blood," we have an approach to the relation found in the latter race[1]. Correlations between this index and coloured area have, in general, an opposite sign to correlations with red, though this is not true in all cases. It must be repeated that the genetic relations of this character are more obscure than those of the other pigmental characters here discussed.

The facts considered under (6) and (7) make it plain that the various colour characters therein considered are either manifestations of identical genetic factors, or at least are dependent upon closely linked factors. This subject will be discussed after the other crosses have been considered.

Regarding the correlations between length of tail stripe and other pigmental characters, it must be said that the calculation of coefficients, according to the customary procedure, is not strictly legitimate, owing to the extreme asymmetry of the distributions (Text-fig. 2). The reality and magnitude of these correlations will, however, be realised by reference to Text-figs. 8 and 9. An interesting example of this intimate relation between the extent of the coloured area and the degree of development of the tail stripe is found in plotting the correlation between the values of coloured area in the *leucocephalus* parents and of tail stripe length in their F_1 offspring (Text-fig. 3). A distinct positive correlation seems to be manifested, despite the fact that the tail stripe is always wholly lacking in *leucocephalus*[2].

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[1] The negative correlation in *leucocephalus* is probably due, in part at least, to a detail of procedure. Pelages in which the dorsal coloured area is small allow of the inclusion of considerable margins of the whitish lateral region within the rectangular area from which the instrumental reading is taken. The latter is of constant size for all pelages.

[2] This relation is even better shown in the *leucocephalus-polionotus* cross, next to be considered.

(*b*) *The* leucocephalus-polionotus *series.*

(Text-figs. 11–24; Plates VIII, IX, XI.)

Tables II and IV give the mean values and standard deviations for the parent races and hybrid generations here concerned. As already implied in the preliminary account of these sub-species (pp. 279–81), *polionotus* differs much more widely from *leucocephalus* than does *albifrons*. There are significant differences in both tail length and foot length, the latter being particularly striking in proportion to the variability of this member. There is, however, a considerable amount of overlapping in the frequency polygons for tail length in the two races, though this is almost entirely lacking in the case of foot length, at least when corrected values are considered. As regards degree of pigmentation, on the other hand, none of the measured characters based upon this show any overlapping whatever. In other words, the palest *polionotus* is more deeply and extensively pigmented than is the darkest *leucocephalus*. This is well shown in the graphs (Text-figs. 14, 17, 18). There are also certain differences which are absolute ones rather than differences of degree. Thus in *polionotus* (at least in the population here considered) the tail stripe invariably extends from base to tip, and is otherwise well developed, while the soles of the feet of the great majority of individuals are more or less heavily pigmented. In *leucocephalus*, both tail stripe and foot pigmentation are entirely lacking[1]. Likewise, in *polionotus*, the ventral and lateral parts of the pelage consist of hairs which are pigmented throughout the basal half or more of their extent, while in *leucocephalus* the hairs of most of this area of the body are entirely white.

Hence more of interest might reasonably be expected from the cross between *leucocephalus* and *polionotus* than from that between *leucocephalus* and *albifrons*. We may add to this the fact that there are larger numbers of comparable individuals in the present series, since the *polionotus* stock was obtained in one locality, and there is thus no necessity for subdividing the hybrid generations according to ancestry. The various measured characters will now be considered in order, as before.

Body length and *weight*. Here, as before, there are probably no significant differences between the two sub-species in size. Nor is there any real evidence of heterosis in the F_1 hybrids.

Tail length. As before stated, this appendage is longer in *leuco-*

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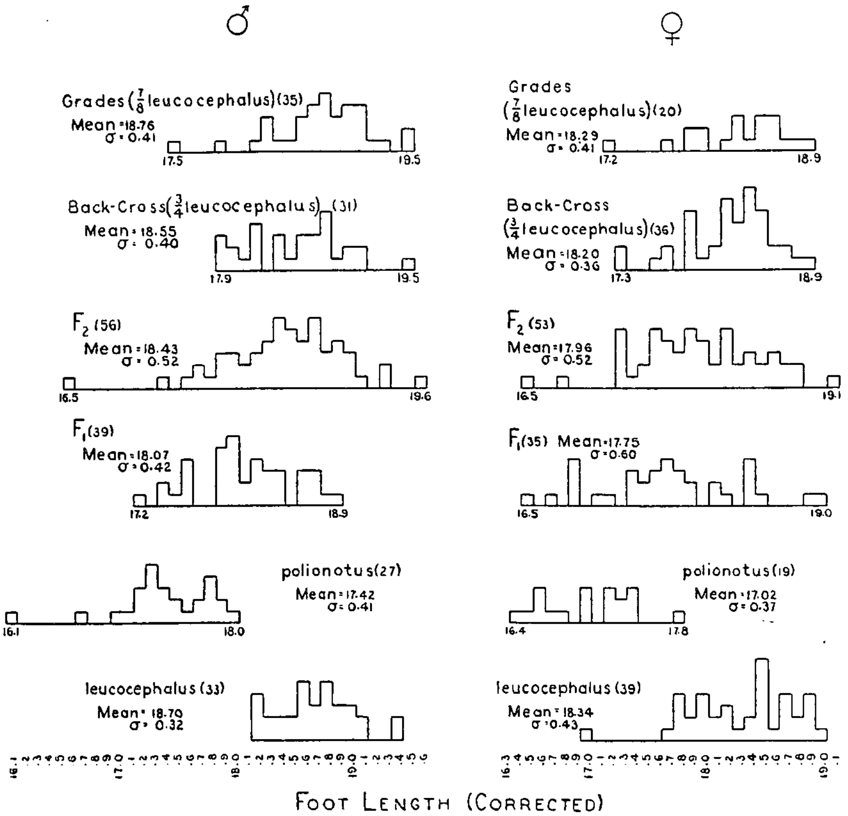
[1] In a few C_1 individuals faint traces are recorded, but this may be due to my having adopted a slightly more exacting standard for the 0 grade in my later determinations.

cephalus, the mean difference being nearly 3 mm. The condition in both hybrid generations is intermediate.

Foot length. This, as above stated, is distinctly greater in *leucocephalus*, the mean difference being about 1·2 mm. Here again, the first and second hybrid generations are intermediate, though the males of the F_2 generation for some reason show an appreciably greater foot length than those of the F_1 (Text-fig. 11). As regards the relative variability of these two generations, the two sexes show opposite relations, the standard deviation for the females being lower in the second than the first. Capricious results are not surprising in the case of foot length, in view of the sensitiveness of this member to nutritional and other environmental conditions, and to the large proportion of non-



Text-fig. 11. Length of foot in *leucocephalus*, *polionotus* and hybrids. The values for this character have been corrected for a standard body length of 80 mm. Males and females are dealt with separately, owing to marked sexual differences.

genetic variability, as shown by parent-offspring correlations. The weighted mean of the correlations between the parent and C_1 generations of *leucocephalus* and of *polionotus*, and those between the F_1 and F_2 generations of hybrids, based upon more than 200 offspring, is + 0·148[1]. The corresponding figure for coloured area is + 0·384.

The successive back-crosses with *leucocephalus*, as might have been expected, show an approach to the greater foot length of the latter sub-species.

Ear length. This is slightly greater in *polionotus* and the difference is perhaps significant. In the males, though not in the females, the condition is intermediate in both F_1 and F_2 generations. The standard deviation, in each sex, is larger in the F_2 generation, though in neither case is the difference significant.

Considering the *skeletal characters*, *polionotus* gives a slightly higher average number of caudal vertebrae than *leucocephalus*, and in both sexes a slightly longer pelvis, but shorter femur and shorter skull. Some of these differences have a fairly high statistical significance, and thus may represent actual differences between the races concerned. As regards the relative variability in the two hybrid generations, we find no general consistency, the sexes, in some cases, giving contradictory results.

Reviewing these six linear measurements (tail, foot, ear, pelvis, femur, skull length), and considering the sexes separately, we find that in nine cases the F_2 generation presents a higher standard deviation, and in three cases a lower one. This preponderant increase in variability may possibly be due to the segregation of multiple size factors, or it may be purely accidental.

Of far greater interest are the pigmental characters, in respect to which the sub-specific differences are much more pronounced.

Tail stripe length. As already stated, all specimens of *polionotus* here considered give a 100 per cent. value for this character, while all specimens of *leucocephalus* give a 0 value. As in the case of the *leucocephalus-albifrons* cross, we have a partial dominance of the stripeless condition, the mean in the F_1 generation being 18·29, instead of 50. Likewise, we have, as in the latter cross, a decided increase in the mean value in the F_2 generation (26·05), as compared with the F_1, *i.e.* a shifting of the mean in the direction of the recessive character. That this higher value in the F_2 generation is not due to any accidental choice of F_1 parents having more fully developed tail stripes is shown by the fact that

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[1] For reasons which need not be discussed here, comparison is restricted to these generations.

these F_1 parents give a weighted mean of 18·81, which is fairly close to that of the F_1 generation as a whole.

It is, as previously stated, hardly legitimate to compute standard deviations for a character with such asymmetrical distribution. These figures are, nevertheless, given in the tables. But it is much more profitable to compare graphically the behaviour of this character in the various hybrid generations (Text-fig. 12). In both the F_1 and F_2 we have values ranging from 0 to 100. But whereas in the F_1 the percentage of extreme cases (0 and 100) is in each instance 5·2, in the F_2 the percentage of these extremes is 11 and 12·8 respectively. There is, furthermore, a considerable increase in the proportion of the larger values in the F_2 generation, a fact which is responsible for the higher mean.

Back-crosses with *leucocephalus* give a mean value of 2·04, while 55 per cent. are of the 0 grade, and the highest value is 13. In the small group of back-crosses between F_1 hybrids and *polionotus*, the mean is 45·19, while none reach the 0 grade, and three reach the grade of 100.

In the group of grades (7/8 *leucocephalus*), the mean is 1·49, while 71 per cent. are of the 0 grade. In this case, the highest single value is 14, which is slightly higher than that in the first (3/4) back-cross.

In successive crosses with *leucocephalus* there is no consistency in the degree of dominance of the stripeless condition over its presence, complete or partial.

It has been seen that the hybrids between *polionotus* and *leucocephalus* agree with the "pure" race *albifrons* in possessing a commonly incomplete as well as a highly variable tail stripe. In the former case, as in the latter, it is a matter of interest to determine to what extent, if any, these individual differences are hereditary.

Considering first the F_1 generation, we cannot of course correlate differences of tail stripe here with corresponding differences in their parents, since, in every case, one parent possesses a complete stripe, while the other lacks it altogether. But we obtain highly interesting correlations between the magnitude of the coloured area in the parents of each race and that of the tail stripe in the hybrid offspring (Text-fig. 13)[1]. It is of interest that a higher correlation is shown here with the *leucocephalus* parents than with the *polionotus* ones, although the former race lacks the tail stripe altogether. These relations furnish additional evidence for the common genetic basis (or at least close linkage) of tail stripe and coloured area (see p. 291).

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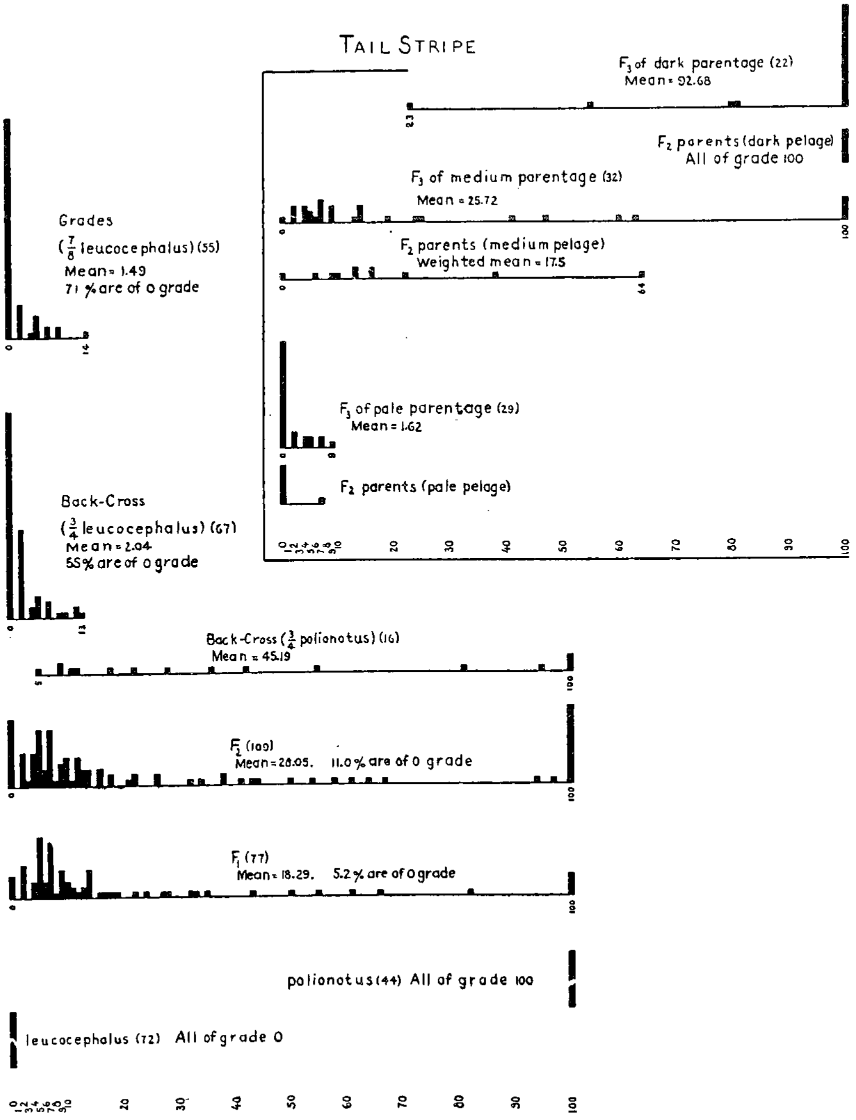
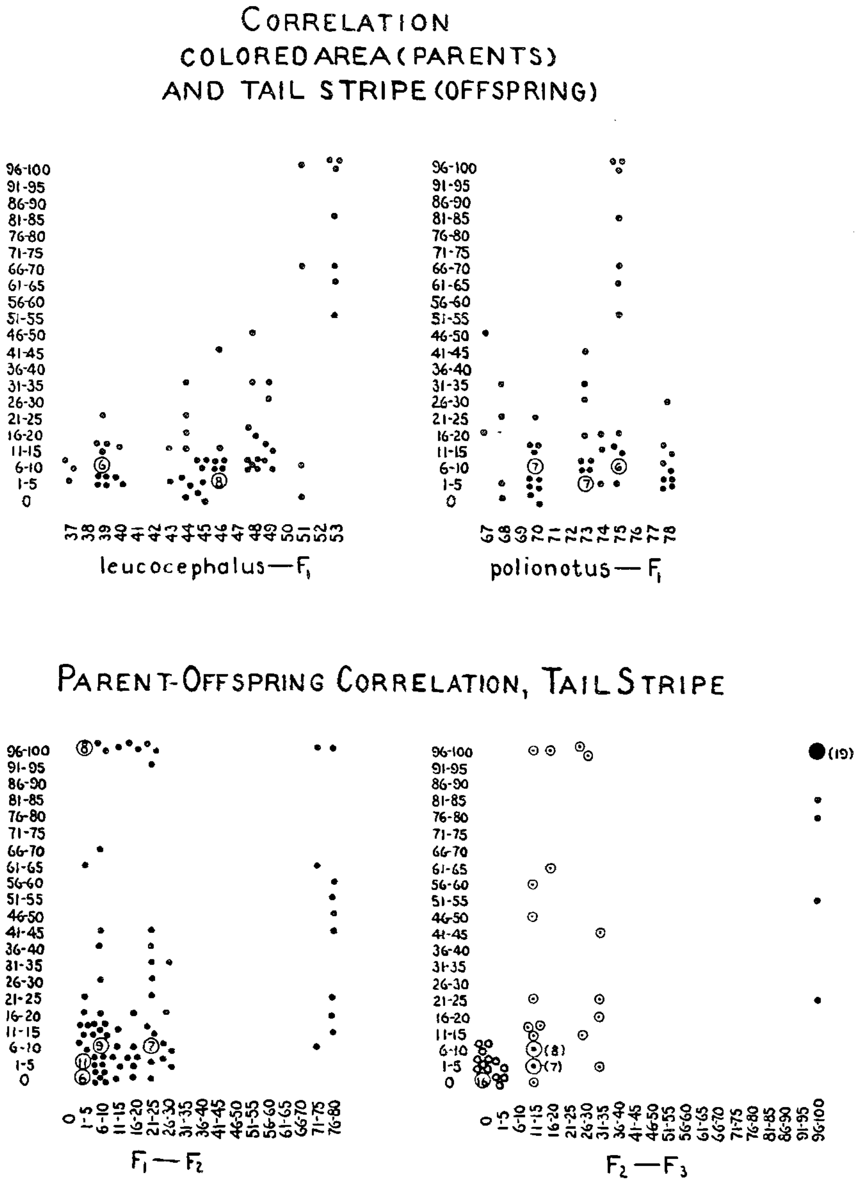
[1] Coefficients of parent-offspring correlation cannot profitably be computed for tail stripe length, for reasons already indicated.

Correlation between the magnitude of the tail stripe in the F_1 and the F_2 generations is largely concealed by the high degree of genetic



Text-fig. 12. Genetic behaviour of tail stripe in the *leucocephalus-polionotus* cross.

segregation in the latter generation (Text-fig. 13). But such correlation is strikingly shown between the selected F_2 parents and their F_3 off-



Text-fig. 13. Correlations between tail stripe (parents) and tail stripe (offspring), and between coloured area (parents) and tail stripe (offspring), in the *leucocephalus-polionotus* cross. The symbols employed for the F_2–F_3 series denote offspring of the "pale," "medium" and "dark" groups of selected F_2 parents respectively (see Text-fig. 20). Of greatest interest is the undoubted correlation between the coloured area of both parent races, particularly *leucocephalus*, and the tail stripe of the F_1 offspring. This despite the total lack of tail stripe in *leucocephalus*.

spring[1]. The mean values of tail stripe length for the "pale," "medium" and "dark" groups are 1·6, 25·7 and 92·7 respectively. The weighted means of the F_2 parents of these groups are 0·6, 17·5 and 100 respectively (Text-fig. 12).

It is interesting that the high correlation between these two generations is due chiefly to the presence of the "dark" and "pale" groups. Within the largely heterozygous "medium" group, little or no parent-offspring correlation is to be detected, just as was the case when we dealt with the offspring of the F_1 generation. It is thus plain that the "pale" and "dark" groups, both in the F_2 and F_3 generations, represent stocks which differ rather widely from one another genetically. They result from a partial segregation, in the gamete formation of the F_1 generation, of colour factors derived from *leucocephalus* and *polionotus* respectively.

It should be evident by this time that the differences between average members of any two of our races are wholly genetic, while differences among individuals of the same race are only partly genetic, and in some cases may be preponderantly non-genetic.

Foot pigmentation. The mean value of this character for the parent generation of *polionotus* is 1·47, that for *leucocephalus* being 0. The figures for the F_1 and F_2 generations are 1·06 and 0·83, respectively, both of these being above the mean for the parent races. The successive back-crosses give 0·48 and 0·31 respectively[2]. The variability of the F_1 and F_2 generations is nearly equal.

That individual differences in the degree of foot pigmentation are in part genetic has been shown for other species (Sumner, 1923*a*; Sumner and Huestis, 1925). In the present case, the weighted mean of the coefficients of parent-offspring correlation for pure *polionotus* and for the successive generations of *leucocephalus-polionotus* hybrids is + 0·295.

Coloured area of the pelage. It is impossible to make an exact comparison between the mean values of the parent races for coloured area, since different measurements have been taken in the two cases. The

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[1] See p. 291. It is probable that in this case the extent of the tail stripe was one of the factors which influenced my selection of the individuals as "pale," "medium" or "dark." This circumstance would of course tend to increase the correlation.

[2] It is questionable whether there is any dominance here of the more highly pigmented condition. There are reasons for believing either that the degree of foot pigmentation is somewhat affected by the conditions of captivity or that a slightly different standard was employed with the later series of animals than with the original stocks. Thus, the C_1 generation of *P. p. polionotus* gives a mean value of 1·97. All of the sub-species of *Peromyscus polionotus* have relatively low grades of foot pigmentation, as compared with *P. maniculatus*, and the task of grading is correspondingly difficult.

only one which can be determined accurately in the case of *leucocephalus* is the area of hairs pigmented at the base (A_b). In *polionotus*, on the other hand, this area would comprise practically the entire pelage. The coloured area of the latter, therefore, is the region of hair which is pigmented to the tips, *i.e.* the area of coloured hair which is visible when the skin is viewed from the outside (A_t). It has seemed desirable, nevertheless, to obtain approximate values for A_t in *leucocephalus* and A_b in *polionotus* in order to render possible crude comparisons between these two races. Ten skins of the former sub-species (five of each sex) gave a mean value for A_t of 33·6; ten skins of the latter a mean value for A_b of 93·3.

For the F_1 and F_2 generations of hybrids both of these measurements were made. In the case of the back-crosses and grades, however, A_b only was determined as in *leucocephalus*.

The mean values and standard deviations for these measurements in the F_1 and F_2 generations are as follows:

	A_b		A_t	
	Mean	σ	Mean	σ
F_1	68·33	6·46	54·46	4·89
F_2	69·12	13·87	54·34	9·02

Thus, while the mean values in these two generations agree fairly closely, there is a very great increase of variability in the second hybrid generation.

Text-fig. 14, which gives the distributions of A_b and A_t for the parent races and certain hybrid generations, reveals in a striking way the extent of this increased "spread" in the F_2 generation, as well as various other features of interest. It will be seen that whereas no single F_1 individual falls within the range of *leucocephalus* for A_b, sixteen individuals, or about 15 per cent. of the F_2 generation, fall within these limits. Of these, two individuals fall below the mean value for *leucocephalus*.

At the opposite extreme, there are no individuals which reach the approximate mean (93) which was derived from the measurement of ten *polionotus* skins (see above), although there is a considerable group which approach this value. There results from this last circumstance a distinct bimodal appearance in our frequency polygon, with a secondary mode not far below the *polionotus* mean. That this appearance is not, however, due to any simple segregation, relating to a single pair of allelomorphs, is probable from the following considerations. (1) These exceptionally high values are due to the presence of basally pigmented hairs throughout virtually the whole of the ventral pelage, as in *polionotus*. In many other pelages pigmentation is likewise present in the ventral hair, but it is so faint as to be invisible or nearly so when the skin is viewed by transmitted light and measured with a planimeter. Only when this pigmentation becomes very distinct is it comprised within the A_b, as here measured, and in such cases the entire area, to the periphery of the skin, is commonly included; hence the relative discontinuity in the distribution of values. On the other hand, even in the individuals comprised in this secondary mode, the pigmentation is usually less intense than in that of most *polionotus*[1]. (2) When we take the other measurement of coloured area, A_t (Text-fig. 14, upper part), we find no such appearance of a bimodal distribution. Yet these two characters are closely correlated (+ 0·891, in the F_2), and probably depend to a large extent upon identical factors.

From the figure it appears that three individuals of the back-cross with *leucocephalus* fall below the mean of the latter race for coloured area, while twenty-eight individuals among the grades, or 51 per cent., fall below that mean.

The small group of back-crosses between F_1 and *polionotus* (not figured) give an unexpectedly low value (58·07) for A_t. This might be intelligible if the values of the individual parents were considered.

Considering the graphs for the other measurement of coloured area (A_t), we find five F_1 individuals which fall within the range of *polionotus*, but none which approach at all closely the mean of the latter. In the F_2 generation, however, fourteen individuals, or 13 per cent., fall within the limits of *polionotus*, while two surpass the mean value of the latter. At the opposite extreme three individuals nearly or quite reach the approximate mean which was determined for *leucocephalus*.

When we compare each individual with its own *leucocephalus* ancestor (or the mean of these, where more than one is concerned), instead of comparing it with the mean for the entire *leucocephalus* population, we have the following situation. In the F_2 generation, we find one individual, out of 108, which gives a value for A_b equal to that of its *leucocephalus* grandparent, and one individual which gives a value for A_t which probably exceeds that of its *polionotus* grandparent[2]. If these

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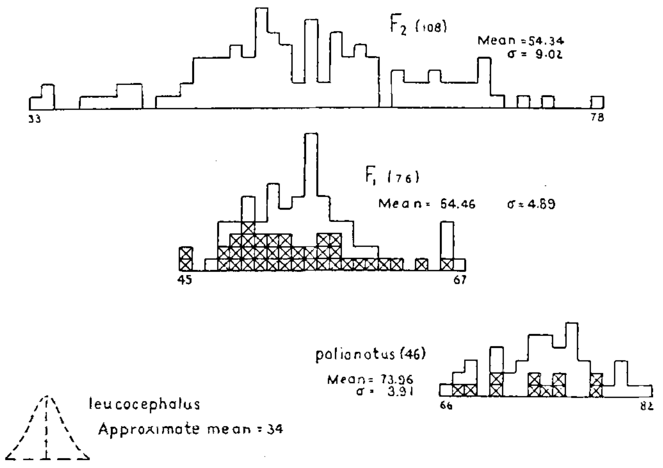
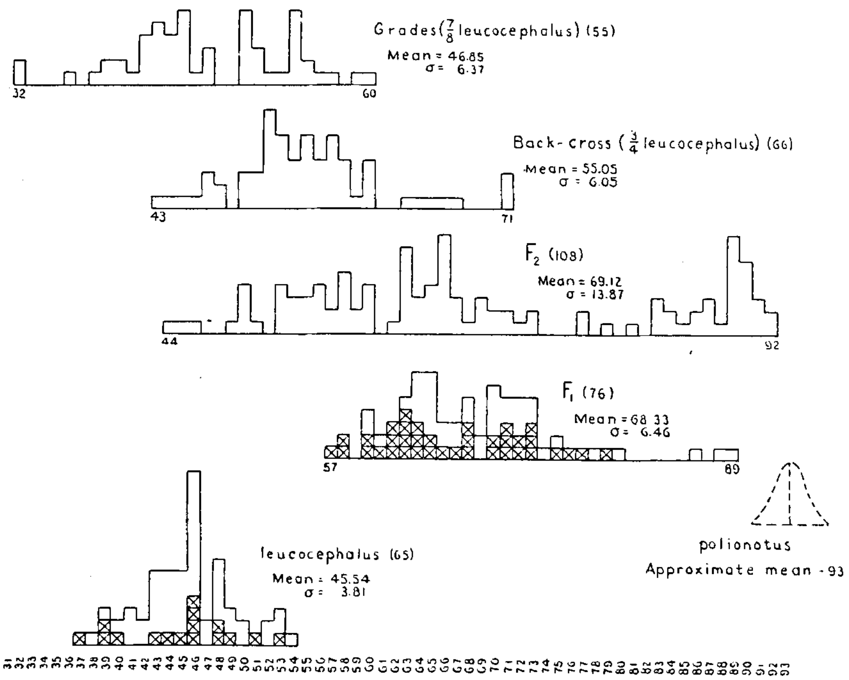
[1] An endeavour to divide the material into classes, with and without an obvious amount of pigment in the ventral hair, proved to be entirely futile. Nor has it proved worth while to grade these pelages according to "pigmentation of ventral hair," as was done for local collections of wild material in a recent paper (Sumner, 1929). Inspection has revealed no instructive relations here.

[2] The pelage of this *polionotus* ancestor is not available, owing to premature death, but the value for this particular F_2 pelage is equal to that of the highest known *polionotus* used for breeding.

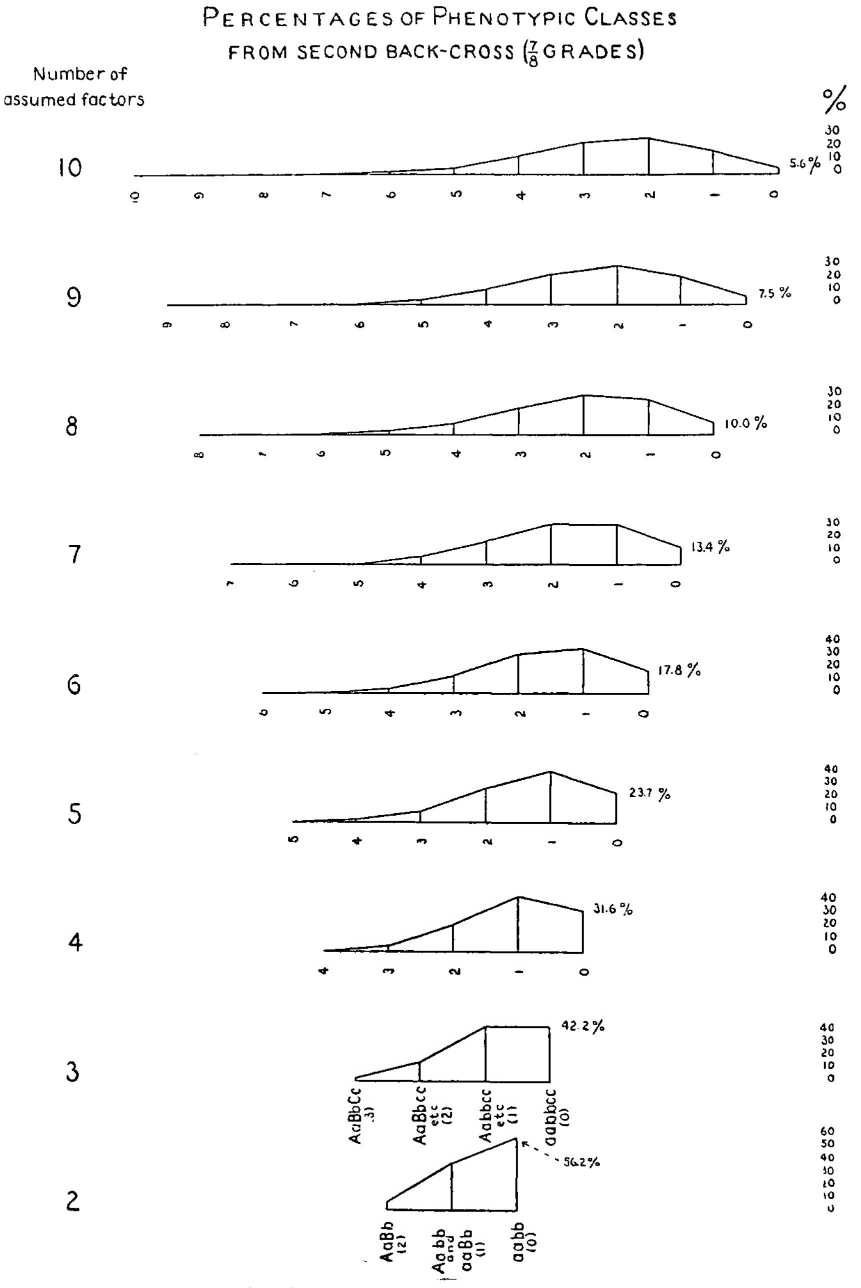


COLORED AREA (TIPS)



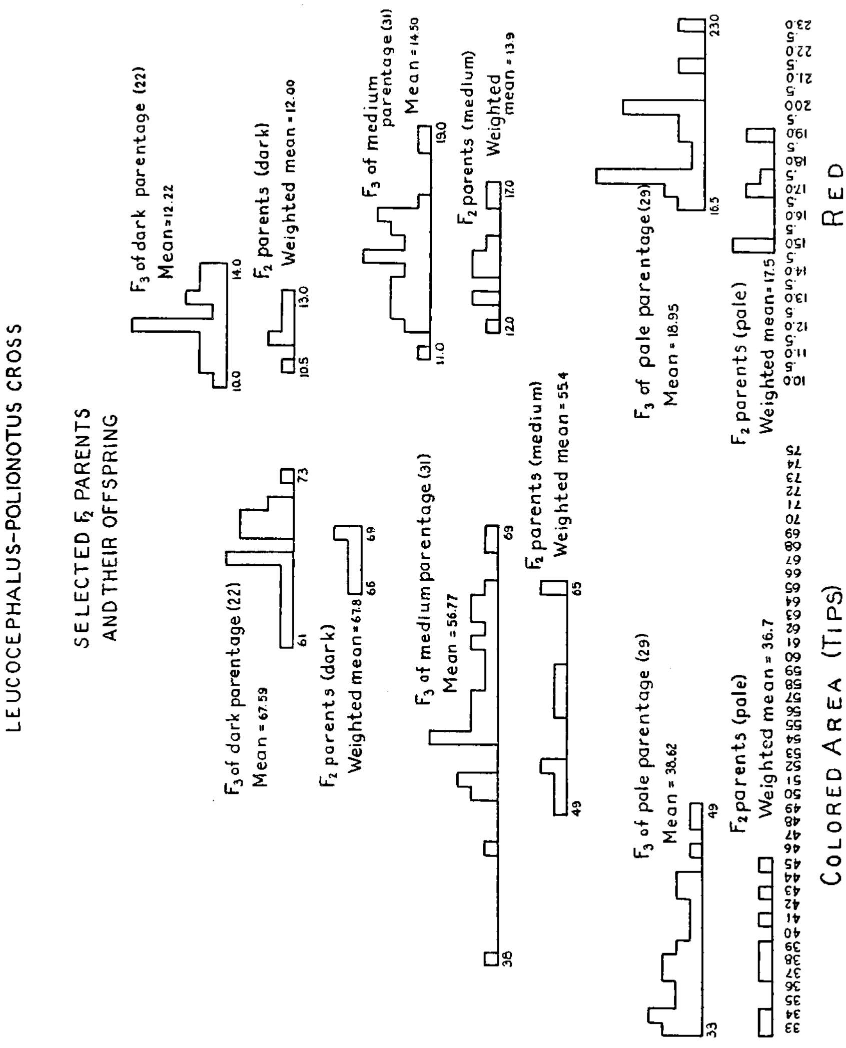
COLORED AREA (BASE)

Text-fig. 14. Genetic behaviour of the coloured area of the pelage (both determinations) in the *leucocephalus-polionotus* cross. Parents designated by cross-hatched squares, as before.



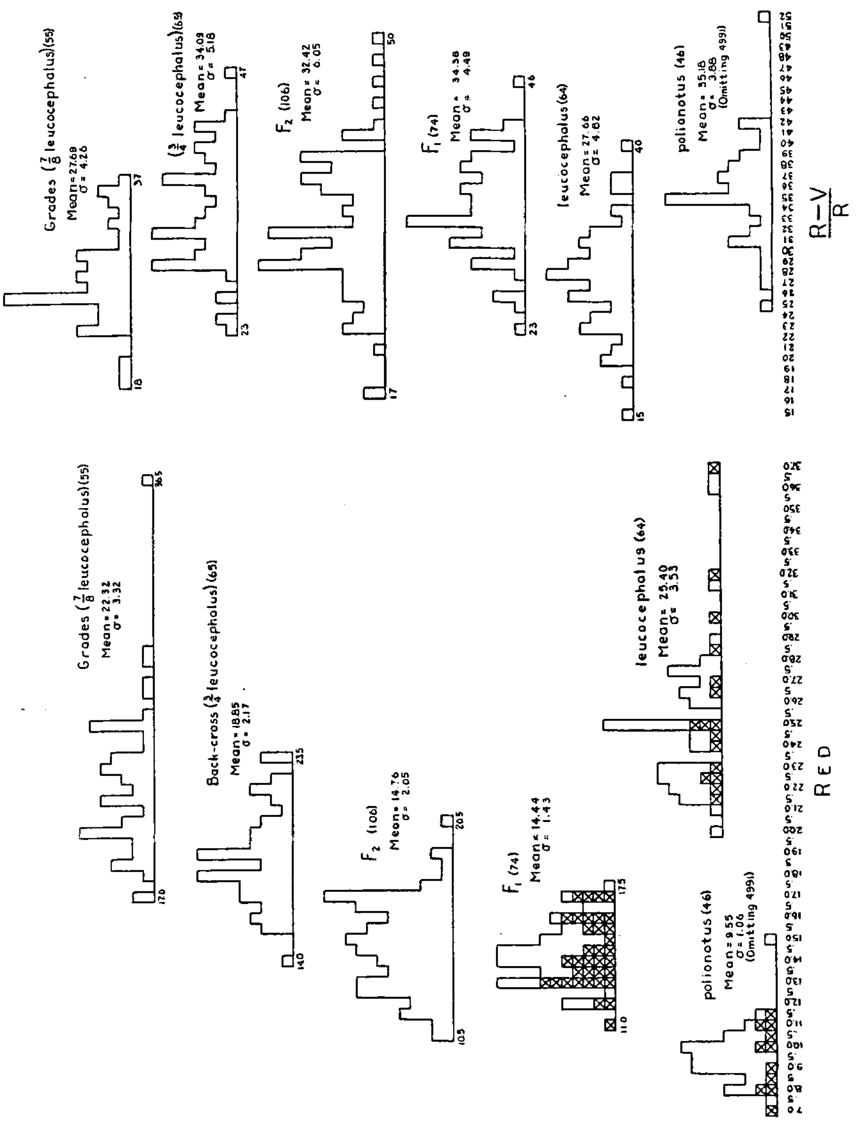
Text-fig. 15. Theoretical distributions of the various phenotypic classes in a second back-cross to one of the parent stocks, following a cross between two races (see footnote on p. 296).

two were regarded as "pure" segregants, the number would be between the expected proportions for three and four factors respectively. Among the back-crosses (3/4 *leucocephalus*) are four out of sixty-six which fall below the mean of their own *leucocephalus* ancestors. This is almost exactly the proportion for four factor differences. Finally, among the grades (7/8 *leucocephalus*), we have twenty-four individuals out of fifty-five which equal or fall below their *leucocephalus* ancestors. This is



Text-fig. 16. Two pelage characters in selected F_2 parents and their F_3 offspring (*leucocephalus-polionotus* cross).

44 per cent., a value very close to the expected proportion (42·2) for three factors.



Text-fig. 17. Values of red and the index of saturation for the parent races and hybrids of the *leucocephalus-polionotus* cross.

Thus far, the results are reasonably consistent, the indicated number of factors (according to the criterion adopted provisionally) being three or four. On the other hand, little or no tendency is to be noted toward a massing of the values on the left-hand side of the polygon for the "grades" (Text-fig. 14), as would be expected were so few factors concerned (Text-fig. 15). I shall return to this subject later.

It is desirable, as before, to determine to what extent individual differences in the values for this character are hereditary. The weighted mean of the various coefficients of correlation between the generations of the pure races (*leucocephalus* and *polionotus*), and of the hybrids (exclusive of that between F_2 and F_3) is + 0·294. This is considerably lower than the similar figure for the *leucocephalus-albifrons* series (+ 0·375). The difference is perhaps due to the heterogeneous nature of the *albifrons* stock, included in the earlier computations. On the other hand, the correlation between the selected pairs of F_2 parents and their F_3 offspring is + 0·917.

Graphs showing the distribution of values among these F_3 animals are instructive (Text-fig. 16). Of significance is the much greater range of the "medium" group, as compared with either of the others; also the reversed unilateral arrangement of the other two groups. The first of these relations may be noted in the case of the *leucocephalus-albifrons* cross (Text-fig. 6, coloured area, but not red). It is probably due, at least in part, to the greater heterozygosity of F_2 individuals of intermediate shade, as compared with the more extreme types.

This greater spread of the F_3 "medium" group is even more conspicuous in the case of the A_b values, but the unilateral arrangement of the "pale" and "dark" groups is much less evident (not figured).

Red. It will be seen (Table II and Text-fig. 17) that the mean values for this character are far apart, being 25·4 and 9·55 for *leucocephalus* and *polionotus* respectively. Moreover, the extreme values do not approach one another at all closely, despite the high variability of *leucocephalus*. The mean value in the F_1 generation represents a much darker shade than the mid-point between the parental means, being 14·44 instead of 17·5. There is thus a tendency toward dominance on the part of the *polionotus* factors which control shade. The slight, though perhaps significant, increase in the F_2 mean over the F_1 is in the expected direction (see p. 300)[1].

Of more certain significance is the increase of variability in the F_2 generation as compared with the F_1 (2·05 and 1·43 respectively). In comparison with the *leucocephalus-albifrons* cross, however, this increase

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[1] It is possible that some of the differences between successive hybrid generations, in respect to this character, are due to non-genetic agencies. Cage-bred *polionotus* appear to be slightly paler (*i.e.* have a higher mean value for red) than their "wild" parents.

in variability is considerably less evident. Only a single F_2 individual falls within the range of *leucocephalus*, while none even approach the mean value of the latter. On the other hand, nine individuals fall within the range of *polionotus*[1], although none reach the mean of this race.

In the first back-cross generation (3/4 *leucocephalus*), twenty individuals out of sixty-seven fall within the range of *leucocephalus*, although not one of these reaches the mean of the latter. Among the grades (7/8 *leucocephalus*), four-fifths of the individuals fall within the range of the latter, while twelve out of fifty-five reach or surpass the mean.

Comparing these animals individually, as before, with their own *leucocephalus* ancestors, we find that not one of the F_2 generation closely approaches its *leucocephalus* grandparent. On the other hand, a single individual falls below (is darker than) its *polionotus* grandparent. Of the sixty-five back-crosses (3/4 *leucocephalus*), one equals and one exceeds the mean value of its *leucocephalus* ancestors. If these two were regarded as pure *leucocephalus* segregants, the proportion would be very close to the expected one where five factor differences are concerned. Of the fifty-five grades, seven (12·7) equal or exceed the mean values of their *leucocephalus* ancestors. On the same assumption as before, we have approximately the expected proportion for seven pairs of factors. Likewise, the distribution of values in this generation (Text-fig. 17) seems inconsistent with any number less than six or seven.

The weighted mean of the parent-offspring correlation coefficients for this character in the present series of animals (excluding that between F_2 and F_3) is + 0·237. This is somewhat smaller than the corresponding figure for coloured area. It is likewise smaller than the coefficient for red in the cross previously considered.

The mean of the four coefficients of correlation between the selected F_2 parents and their F_3 offspring is here + 0·837. This is also lower than the corresponding figure for coloured area.

$\frac{A_b}{R}$. *Leucocephalus*, as already stated, gives a mean value for this fraction of 1·82. A comparable figure for *polionotus* cannot be given with equal precision for reasons already discussed. An approximate figure would be 9·8. The mean value for F_1 is 4·79, this being somewhat nearer to the value for *leucocephalus* than to that for *polionotus*. The mean for F_2 (4·88) is not significantly different from that for F_1. The corresponding figures for $\frac{A_t}{R}$ are 3·83 (F_1) and 3·82 (F_2). The variability, on the other hand, has increased enormously, the range $\left(\text{for } \frac{A_b}{R}\right)$ having

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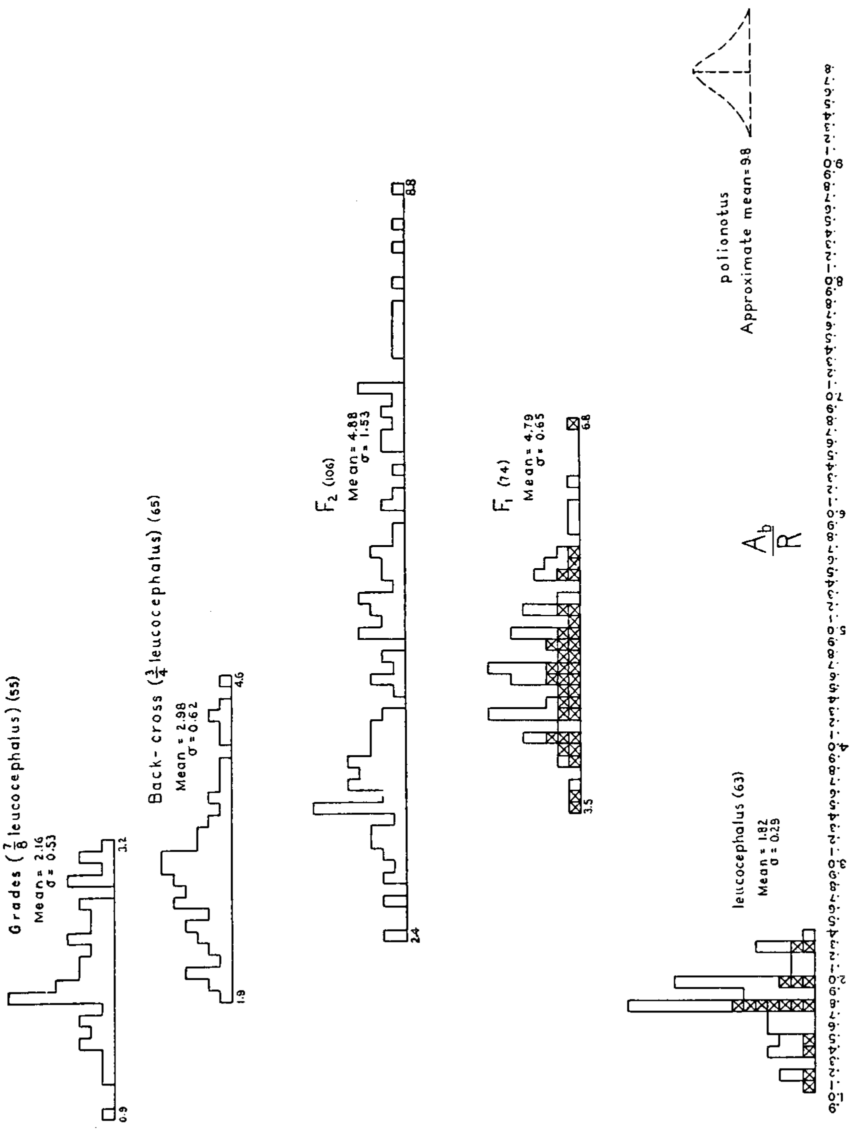
[1] One F_1 individual falls within the range of *polionotus*.

risen from 3·5 to 6·8 in the F_1, to 2·4 to 8·8 in the F_2. The standard deviations are 0·65 and 1·53 respectively. Despite this great increase in variability, however, it will be seen that even the lowest value in the F_2 generation barely falls within the range of *leucocephalus* (Text-fig. 18).



Text-fig. 18. The values here plotted are obtained by dividing the value for coloured area (base) by that for red. They are roughly proportional to the total amount of dark pigment in the pelage.

The first and second back-crosses with *leucocephalus* show a progressive shift of the mean toward that of the latter race, while the variability is equal to or less than that of the F_1 generation. In the first back-cross, thirteen individuals fall within the range of *leucocephalus*, although none reach the mean of the latter. In the second back-cross ("grades") thirty-nine, or 71 per cent., fall within the range of *leucocephalus*, while thirteen, or 24 per cent., equal or fall below the mean of the latter. Indeed, one individual gives a lower value than any *leucocephalus*.

Comparing the extreme individuals, as before, with their own pure-race ancestors, we find that not one F_2 individual falls below its *leucocephalus* grandparent, although one gives a higher value than its *polionotus* grandparent. Two back-cross individuals out of sixty-five equal or fall below the mean of their *leucocephalus* ancestors, while among the grades fourteen reach this level. If the individuals in these last two series were counted as pure *leucocephalus* segregants (at least for colour factors), the numbers are in each case such as might be expected for a cross involving five factor differences.

Reference to the histogram for the grades (Text-fig. 18) shows that we have no certain tendency toward a massing of the individuals on the left-hand side of the area. That the asymmetry which is undoubtedly present here has no special significance is probable from the fact that such asymmetry is even more evident in the case of the F_2 and back-cross generations, where it was not to be expected.

$\frac{R-V}{R}$. In respect to this ratio, which represents the richness of colour (or conversely the greyness) of the pelage, *polionotus* does not differ so widely from *leucocephalus*, as does *albifrons*, despite the vastly greater difference in depth of shade, in the former case. The figures for the two former are 35·18 and 27·66 respectively. Furthermore, there is a much broader overlap between the two, some specimens of *polionotus* actually giving lower values than the average *leucocephalus* (Text-fig. 17). It is interesting that the F_1, F_2 and back-cross groups show a mean value for this character considerably higher than the mean of the parental means. This is in keeping with the observed fact that even the palest among these pelages tend toward a richer brown than is commonly met with in *leucocephalus*[1]. In the generation of grades (7/8 *leucocephalus*), however, the mean index of saturation is about the same as in *leucocephalus*.

The usual increase of variability is to be seen here, in passing from

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[1] See p. 308.

the F_1 to the F_2 generation. The standard deviation, in this case, rises from 4·49 to 6·05.

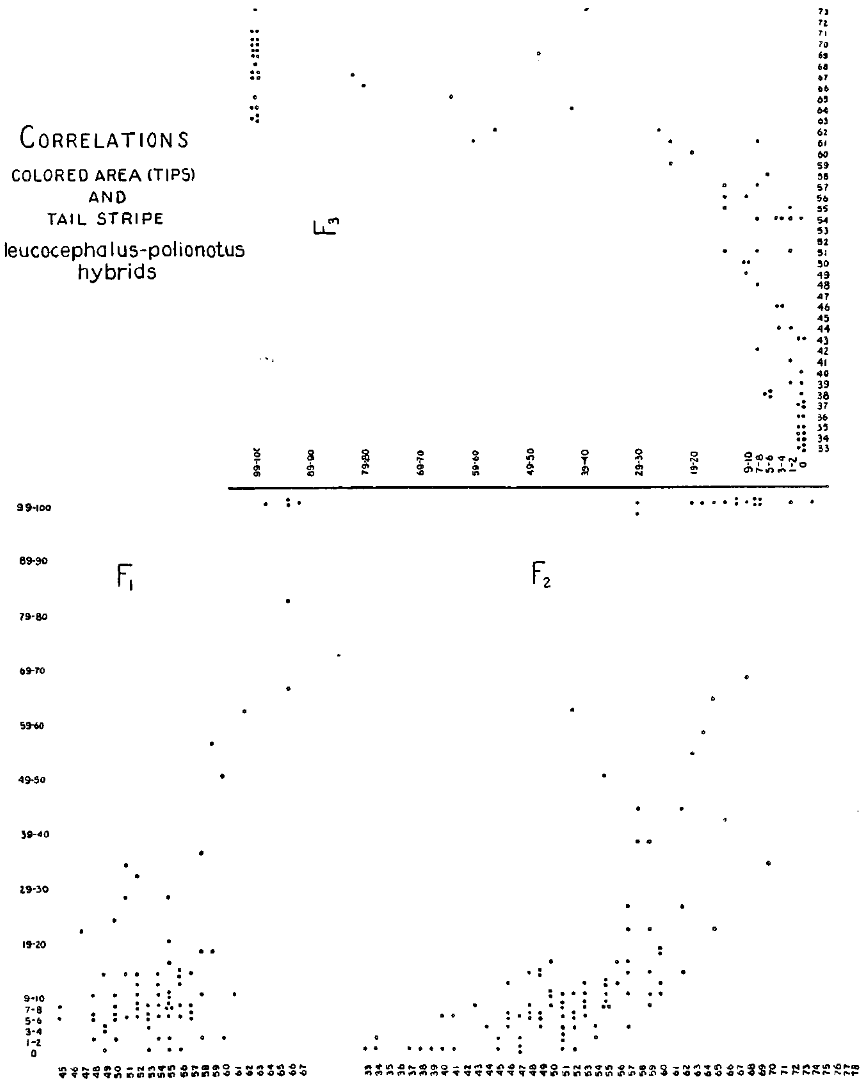
Segregants showing aggregate "pure-race" pelage characters. Let us consider, as before, the number of individuals in each of these generations which measure up to the standards of an average *leucocephalus*, in respect to all of the colour characters taken collectively. For this purpose, I have adopted the same procedure as was done for the preceding cross, namely, choosing such limiting values for each of three characters that approximately half of a population of pure *leucocephalus* would be included (see pp. 306–7). As judged by this standard, not a single specimen among the 106 F_2 pelages can fairly be regarded as average *leucocephalus*. In only three cases does the coloured area fall within the prescribed limits. All three of these individuals are excluded, however, both by reason of too low values for red and too high values for the index of saturation. One of them, likewise, has a trace of tail stripe, and two have foot pigmentation of about the average grade for *polionotus*.

Among the F_3 offspring of selected F_2 parents, thirteen individuals out of eighty-two fall within the prescribed limits in respect to coloured area (A_b). But all of these individuals have too low values for red, and all but one too high values for $\frac{R-V}{R}$, to allow of their inclusion as "average" *leucocephalus*. Half of them likewise show a low grade of foot pigmentation, and two have vestiges of tail stripes.

Among the sixty-five individuals derived from the first back-cross with *leucocephalus*, nine fall within the limits for coloured area, but all of these must be excluded by reason of their values for red or $\frac{R-V}{R}$ or both. In addition to this, the majority display a low grade of foot pigmentation, and one possesses the trace of tail stripe. It may be recalled that, in the *leucocephalus-albifrons* cross, five individuals out of fifty-eight conformed to the requirements for all of the pigmental characters.

It is only when we pass to the grades (7/8 *leucocephalus*) that we meet with specimens which measure up to the standards prescribed for an average *leucocephalus*. Here we have eleven cases out of fifty-five which fall within the limits in respect to all of the pigmented characters. Thirty-two cases would be included, if only the coloured area were concerned, but twenty-one of these fail to conform in respect to one or more of the other characters.

Here, as previously, it is a matter of interest to know whether those individuals which fall within the limits of an "average" *leucocephalus* in respect to colour characters do so likewise in respect to other racial differences, such as tail and foot length. It has not been regarded as desirable, for these characters, to apply standards of the sort which



Text-fig. 19. Correlations between coloured area (abscissas) and tail stripe (ordinates) in three generations of *leucocephalus-polionotus* hybrids.

were employed for colour characters. However, it may be said that none of these eleven individuals which reach or surpass the "average" condition (as earlier defined) in respect to colour characters fall appreciably below the mean of *leucocephalus* for tail length, and that seven of the eleven reach or surpass the mean for foot length[1]. All lie well within the limits of variation of the latter race.

Returning to the F_2 generation, we may now enquire whether any of these measure up to the standard set for an average *polionotus*[2]. There are only four individuals which fall within the limits in respect to the value for coloured area. None of these, however, conform to our requirements as regards the other characters. All show too high a value for red, all but one too low a value for the index of saturation, and all but one too low a value for foot pigmentation. In addition, two of the four possess incomplete tail stripes, whereas all of the parent stock of *polionotus* have complete ones.

Correlations. The first four paragraphs in the summarised statement under the *leucocephalus-albifrons* series hold, with but slight modifications, for the present one. As regards the second of these we must note a possible exception in the case of foot pigmentation, which is negatively correlated with body length (− 0·205 to − 0·225) in *polionotus* and in three of the hybrid generations for which this has been determined (0, however, in the fourth of these, as well as in the crosses next to be considered).

With respect to the fourth item (Text-figs. 19, 20, 21), the present series furnishes a greater number of illustrative cases than the former series, since certain coefficients were computed here which were not computed for the others. Thus, there appear to be significant correlations (having the "expected" sign) between foot pigmentation and the other pigmental characters. This had been regarded as questionable in my earlier studies of other species (Sumner, 1923, 1925; Sumner and Huestis, 1925).

Passing to the fifth of the items previously discussed, we have in the F_3 generation five coefficients of correlation between tail length and pigmental characters, all of which are of the sign which would be expected if there were a tendency for the original racial combinations to reappear. In view of the low value of most of these coefficients, and the fact that

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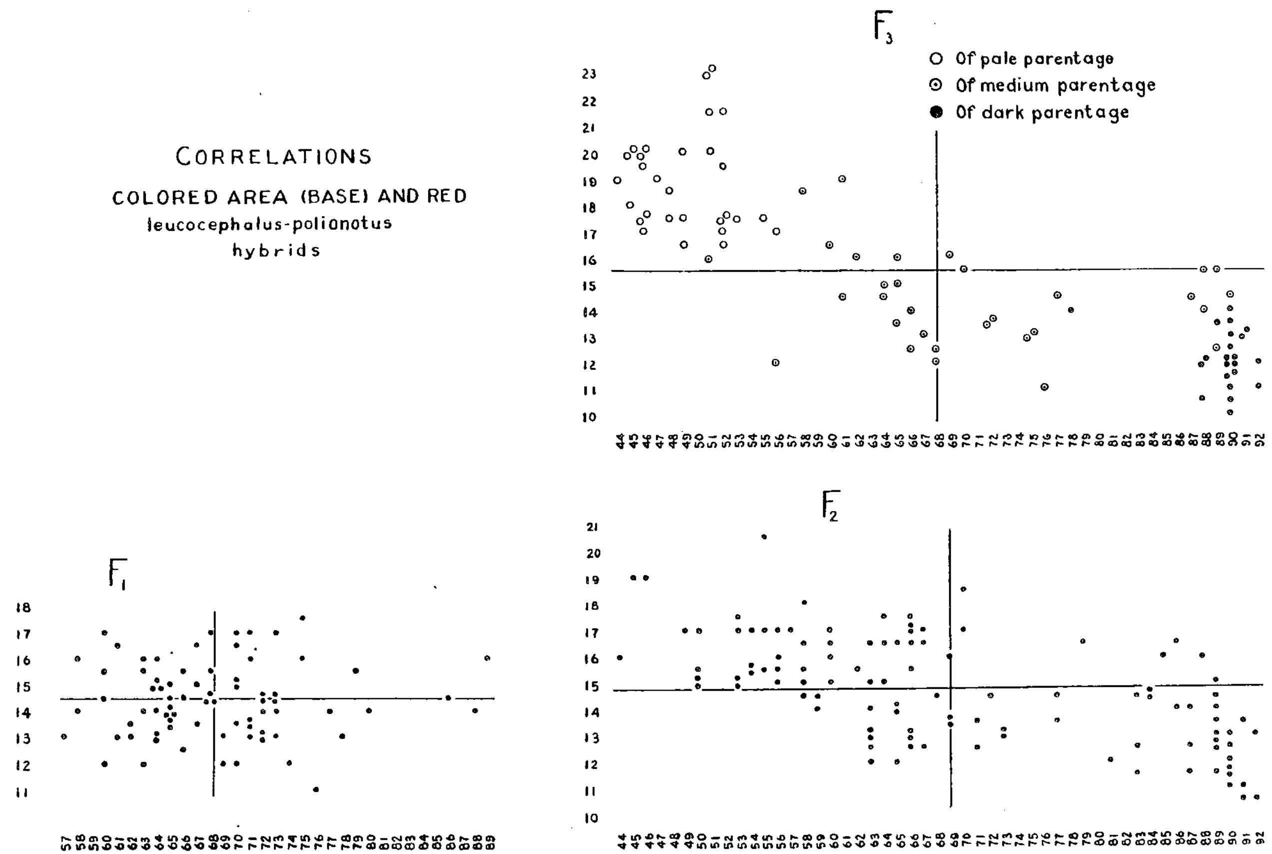
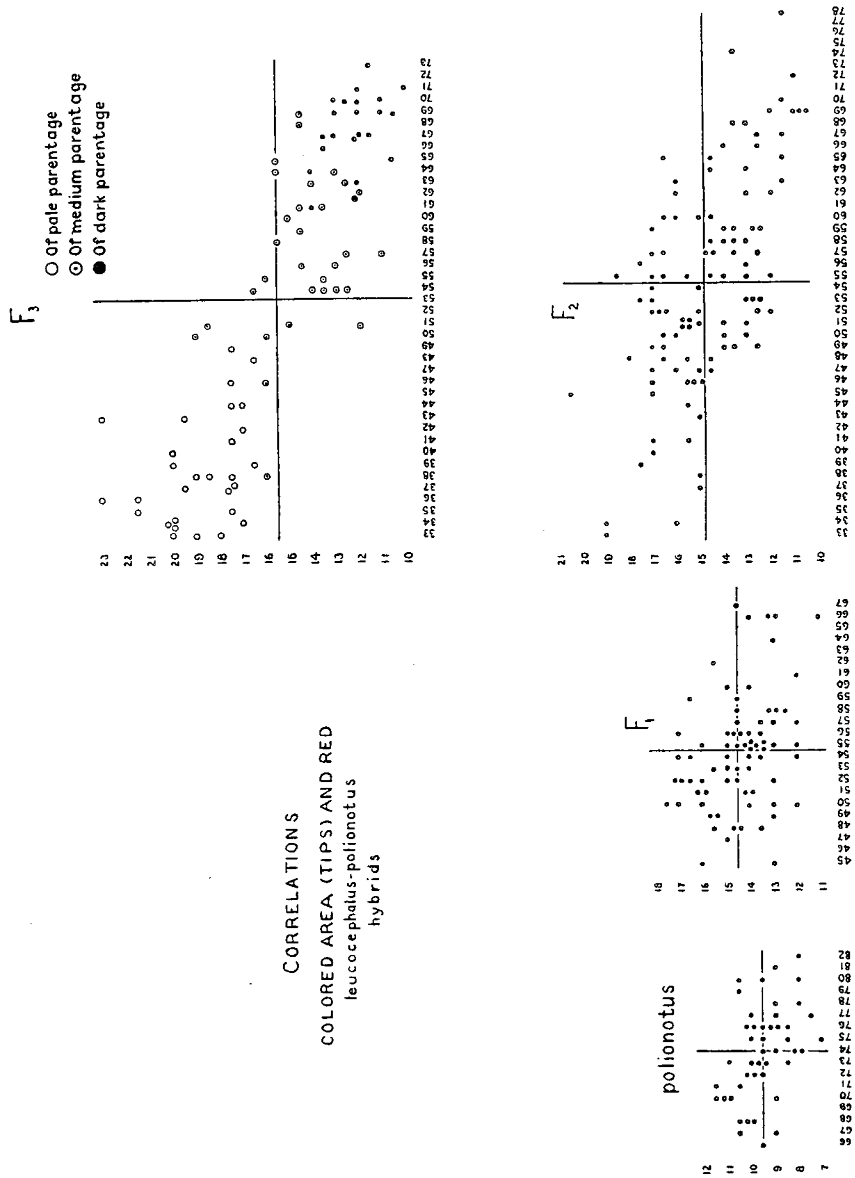
[1] They thus conform, in reality, to a much more exacting standard than was employed for the colour characters.

[2] By setting such limits for each of four characters (A_t, red, $\frac{R-V}{R}$, foot pigmentation) as would include 5/6 of the *polionotus* population, if applied singly, it was found that approximately half (47 per cent.) of the specimens of this race fell within these limits in respect to all four characters. The included values, for each character, were naturally those which tended in the direction away from *leucocephalus*.



Text-fig. 20. Correlations between pelage area pigmented at base (abscissas) and red (ordinates) in three generations of *leucocephalus-polionotus* hybrids.



Text-fig. 21. Same as Text-fig. 20, but for area pigmented to tips.

no such tendency is evident in the larger F_2 series, these might be dismissed as chance results were it not for the similar situation in the cross next to be considered.

As regards foot length, however, the relations are such that it is difficult to attribute them to chance. Of the forty-four coefficients which express the degree of correlation between this character and the various pigmental characters, in the two parent races and five series of hybrids (the sexes being treated separately), the signs of thirty-three are such as to favour the hypothesis of genetic association. Moreover, this preponderance of "expected" signs is due chiefly to the F_2 and F_3 generations, in which we have nineteen out of twenty cases of this sort[1]. A closely similar situation, it will be recalled, was encountered in the *leucocephalus-albifrons* cross.

I have referred to these signs as being the "expected" ones, merely in the sense that they accord with a particular interpretation of the facts. In reality they were quite *unexpected*, on the basis of earlier work. As has been stated previously (Sumner, 1926), I have hitherto found no evidence of a correlation between any pigmental character and the length of any bodily member, although two characters belonging to either of these classes might be strongly correlated with one another.

Owing to the interest which attaches to these correlations between foot length and pigmental characters, if they are real, it is of importance to exclude any possible source of error. Let us enquire, therefore, whether these correlations may not be spurious ones, so far, at least, as any significant biological relationship between these characters is concerned.

The possibility of obtaining by random sampling thirty-one coefficients out of thirty-two[2], having the "expected" sign, would appear to be so remote that any thought of this being a chance result seems absurd. It must be repeated, however, that the evidence is far from being wholly cumulative, owing to the fact that the various pigmental characters here considered are for the most part rather strongly correlated with one another, especially in the F_2 and F_3 generations. It might be suggested that we had here a purely accidental correlation between foot length and *pigmental characters in general*. Accordingly, it has seemed worth while to determine by the method of partial correlation whether, for

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[1] Of the parent races, *leucocephalus* shows no tendency of this sort, whereas all of the coefficients computed for *polionotus* are in the "expected" direction. For the hybrid generations (excluding the F_2 and F_3) the results are about equally balanced.

[2] These are the numbers in the F_2 and F_3 generations of both crosses, previously considered. The situation in the *polionotus-albifrons* cross, discussed below, further strengthens this evidence.

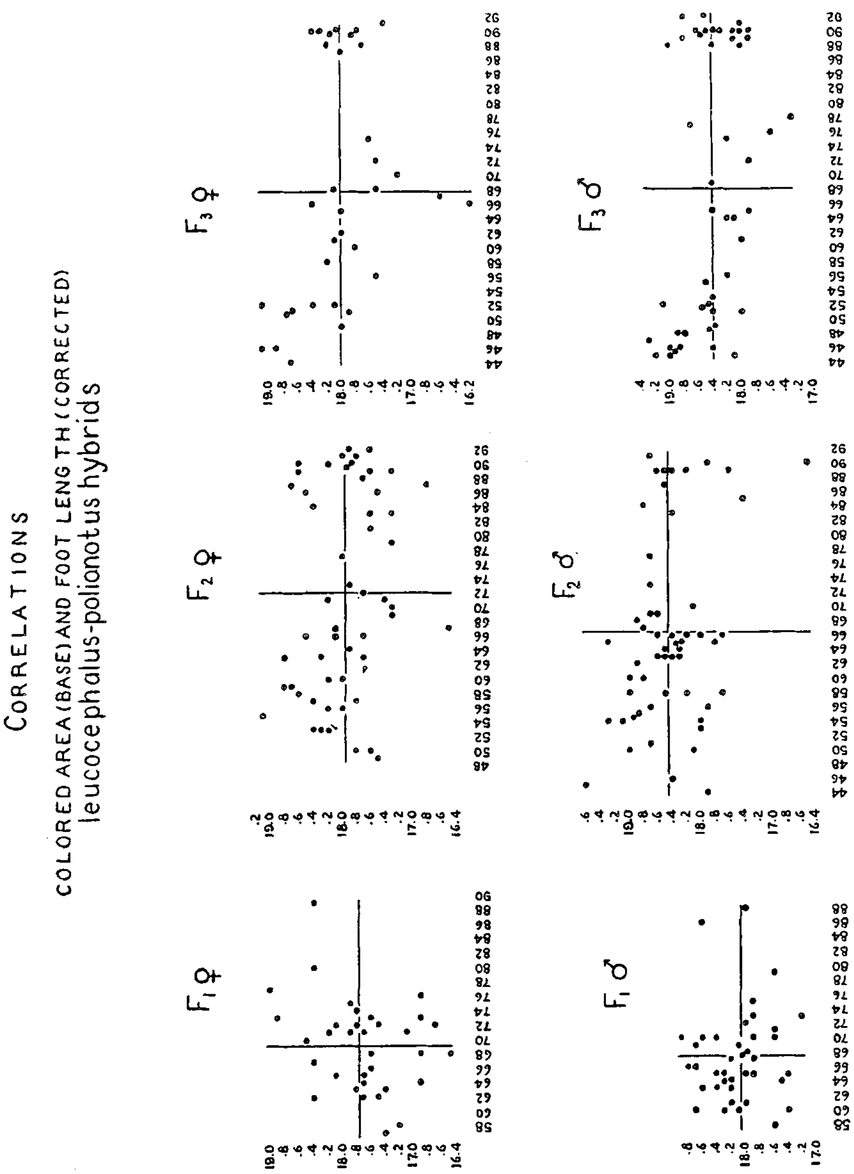
example, any correlation is manifested between foot length and coloured area, independently of the correlation between the former and red, and conversely, whether the correlation with red is to any extent independent of that with coloured area. In the first case (eliminating the influence of red), our four coefficients (F_2 and F_3, male and female) retain the same signs as previously, though in all cases but one they are so reduced in value as to be statistically non-significant when taken singly. In the second case (eliminating the influence of A_t) three of our four coefficients, while greatly reduced, retain the same signs as previously, while the sign of one (previously low) is now reversed.

It thus appears that while much of this correlation between foot length and the various pigmental characters results from a rather close correlation among the latter, there is none the less evidence for an independent correlation between the first-named character and certain of the latter ones, taken separately.

But even if all of the pigmental characters were completely correlated, the probability of such a series of coincidences would be very low, since we are dealing with two generations of two crosses, and in each case the sexes have been treated separately. We should thus have eight independent cases, all giving the "expected" sign, a situation against which the odds would be 255 to 1.

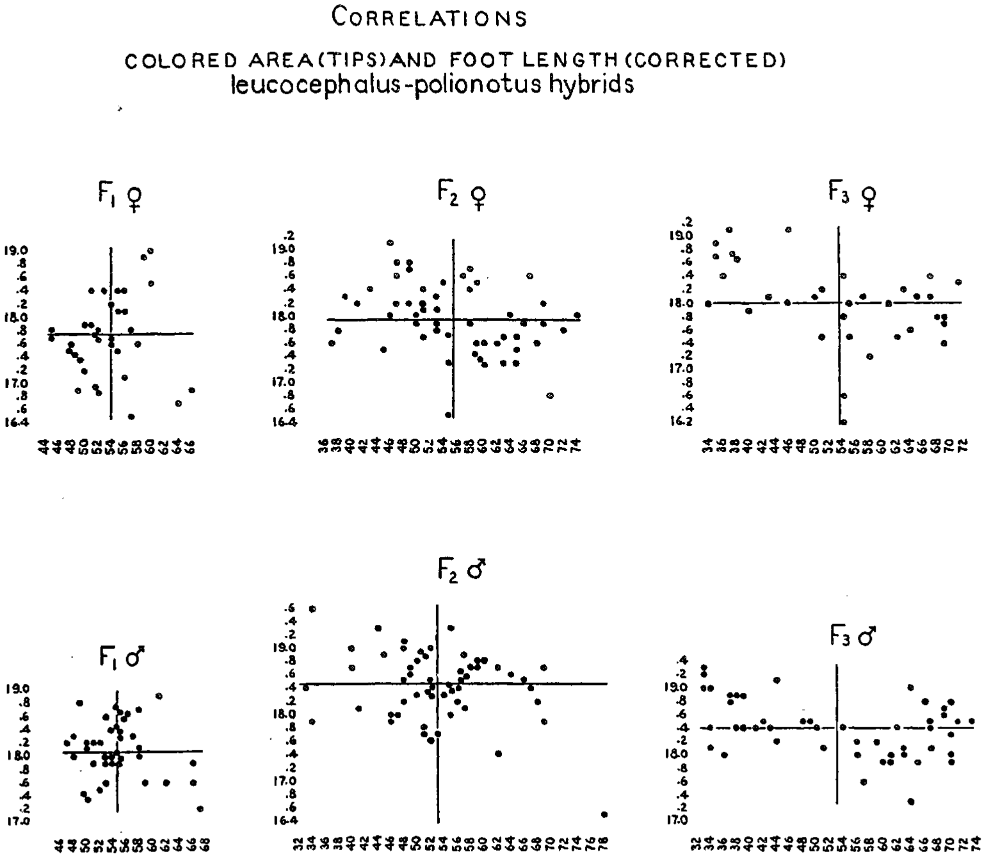
If it be objected that the F_3 generations merely reproduce selected samples of the F_2, and consequently do not furnish evidence independent of the latter, it is sufficient to point out that the parent-offspring correlations between these generations in respect to foot length are low, being 0·114 for the *leucocephalus-albifrons* cross and 0·298 for the *leucocephalus-polionotus* one. Without resorting to the laborious process of computing the partial correlation between foot length and each pigmental character in the F_3 generations (the effects of correlation between these in the F_2 being eliminated), it is clear that no considerable part of the correlation in the former generation can be due to the accidental choice of F_2 parents having this particular combination of characters.

Another circumstance which doubtless favours the existence of correlations between foot length and pigmental characters, in certain cases, is the fact that both may be correlated with general size (body length). In the case of foot length, this correlation with body length is universal, and the coefficients are usually high. With pigmental characters, on the other hand, while coefficients of fair magnitude are sometimes found, the relations are so inconsistent that the influence of size cannot be definitely affirmed except possibly in the case of foot pigmentation.



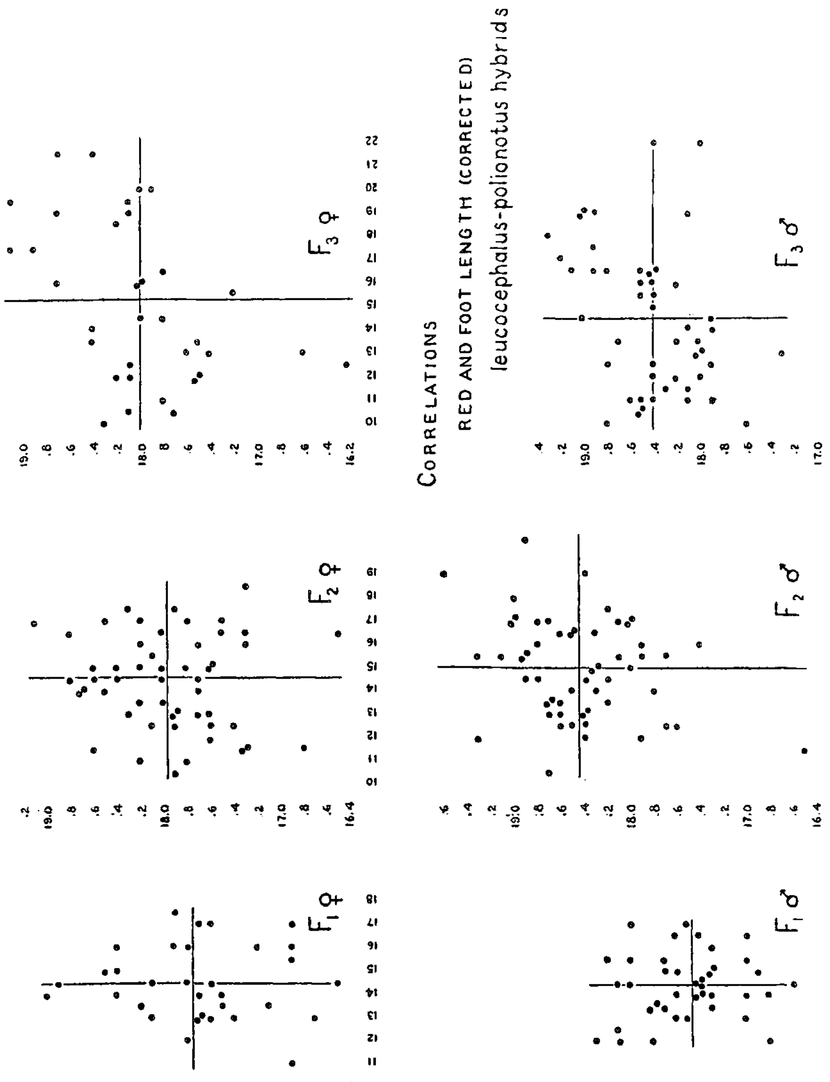
Text-fig. 22. Apparent negative correlation between pelage area pigmented at base (abscissas) and corrected foot length (ordinates) in the F_2 and F_3 generations of the *leucocephalus-polionotus* cross. (No trace of this in F_1.)

It seems worth while, however, to determine the degree of correlation between foot length and foot pigmentation, after excluding the influence of body length. I shall confine myself to the F_3 generation of the *leucocephalus-polionotus* cross, since the F_2 coefficients are both very low, one indeed furnishing the only instance in either F_2 or F_3 generations of a coefficient with the "wrong" sign. Applying the method of partial correlation, we find that the coefficient for the males is reduced from − 0·307 ± 0·09 to − 0·234 ± 0·09, while that for the females is reduced from − 0·390 ± 0·10 to − 0·327 ± 0·10. Thus these two coefficients, involving the only pigmental character which gives any appearance of being influenced by size, retain a considerable degree of



Text-fig. 23. Apparent correlations as in Text-fig. 22, except that coloured area (tips) has been plotted.

probability after this influence has been eliminated. In certain other cases, moreover, partial correlation computations would materially *increase* the coefficients. Reference to the graphs (Text-figs. 22, 23, 24) shows that we have a distinct, though feeble, appearance of correlation when the foot lengths have been "corrected" for size, *i.e.* reduced to a common body length of 80 mm.



Text-fig. 24. Apparent correlations between red (abscissas) and foot length (ordinates). In the present case, the correlation is positive, instead of negative, as for coloured area.

After making allowance, therefore, for all these qualifying circumstances, it still seems probable that we have a correlation, which is not purely accidental, between foot length and the various pigmental characters with which we have dealt, in the F_2 and F_3 generations of both of the crosses thus far considered. The evidence above presented is strongly reinforced by that derived from the *polionotus-albifrons* cross next to be considered.

The sixth paragraph of the summarised statements concerning correlations in the previous cross applies, *mutatis mutandis*, to the present one. The correlations between the various pigmental characters are in nearly all cases of the "expected" sign; that is, we meet with a tendency toward the same association of colour characters within the single populations that is encountered when we compare one geographic race with another (*e.g.* darker individuals, as well as darker races, tend to have more complete tail stripes, etc.). That the correlations between foot length and pigmental characters, in the F_2 and F_3 generations, correspond to the manner in which these characters are combined in the parent races has already been pointed out. Such an apparent genetic association is perhaps surprising in the crosses involving *albifrons*, since in this sub-species foot length may undergo marked local variation, to a large degree independently of pelage colour (see footnote on p. 281).

The statements regarding the relative magnitude of the correlation coefficients in the F_1, F_2 and F_3 generations (paragraph 7) likewise hold with even greater force for the present cross[1]. Except for cases involving the index of saturation, the correlations among the pigmental characters for these three generations form a series of increasing magnitude. The most striking instance of this, in the present case, relates to the correlation between the two measurements of coloured area (A_b and A_t). These rise from $+ 0{\cdot}458$ in the F_1 to $+ 0{\cdot}891$ in the F_2 and $+ 0{\cdot}951$ in the F_3. As has already been stated, consistent correlations between foot length and pigmental characters are met with only in the F_2 and F_3 generations. In the present cross, these coefficients are with a single exception higher in the F_3 generation than in the F_2.

Finally, the facts regarding correlation between the index of saturation and other pigmental characters may be expressed in much the same language as for the preceding cross. The meaning of some of the differences in the value of the coefficients is not clear, but the fall of the correlation with red from $+ 0{\cdot}700$ in the F_1 to $+ 0{\cdot}364$ in the

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[1] Huestis (1925, p. 464) reports several instances of increased correlation between hair characters in the F_2 generation.

back-crosses with *leucocephalus*, and to – 0·177 in the grades (7/8 *leucocephalus*), is in accordance with expectation, and agrees with the trend shown in the *leucocephalus-albifrons* cross (p. 314).

(*c*) *The* polionotus-albifrons *series.*

(Text-figs. 25–27.)

The results from this series are less satisfactory in a number of ways than those from the two previously discussed. (1) Only two hybrid generations were reared, there being an F_1 generation, and back-crosses with each of the parent races. (2) *Albifrons* of both the East Pass and the Foster's Bank collections, and ones of mixed descent, were used indiscriminately, and it has not been practicable to separate the derivatives of the two sub-races, as has been done in the case of the *leucocephalus-albifrons* cross[1]. There are, nevertheless, various points of considerable interest to be noted in connection with this series of hybrids.

It is not worth while to consider the behaviour of all of the various characters in turn, as has been done for the two preceding crosses. I shall accordingly pass over the linear measurements of bodily parts and proceed directly to the discussion of pigmental characters.

The mean value of the tail stripe in the F_1 generation (63·95) is about midway between those of the parent races (100 and 31·31)[2]. This is in striking contrast with the results of crossing either of these races with *leucocephalus*. It will be recalled that the stripeless condition of the latter sub-species is dominant, though incompletely so, over the condition found in either *albifrons* or *polionotus*. Back-crosses with the two parent races give mean values of 44·04 (*albifrons*) and 85·45 (*polionotus*) respectively. It will be seen from the graphs that there is an enormous range of variability within each series (Text-fig. 25).

The behaviour of *foot pigmentation* is less intelligible. Whereas the mean values in the wild *polionotus* and *albifrons* respectively are 1·47 and 0·07 (1·97 and 0·25 in the C_1 generations), we have a value of 1·44 in the F_1 generation, and 1·75 and 0·98 respectively in the back-crosses with *polionotus* and *albifrons*. Attention has already been called to the deeper foot pigmentation of cage-bred series of these mice (p. 321). This fact, together with a partial dominance of the deeper pigmentation, would explain the results fairly well.

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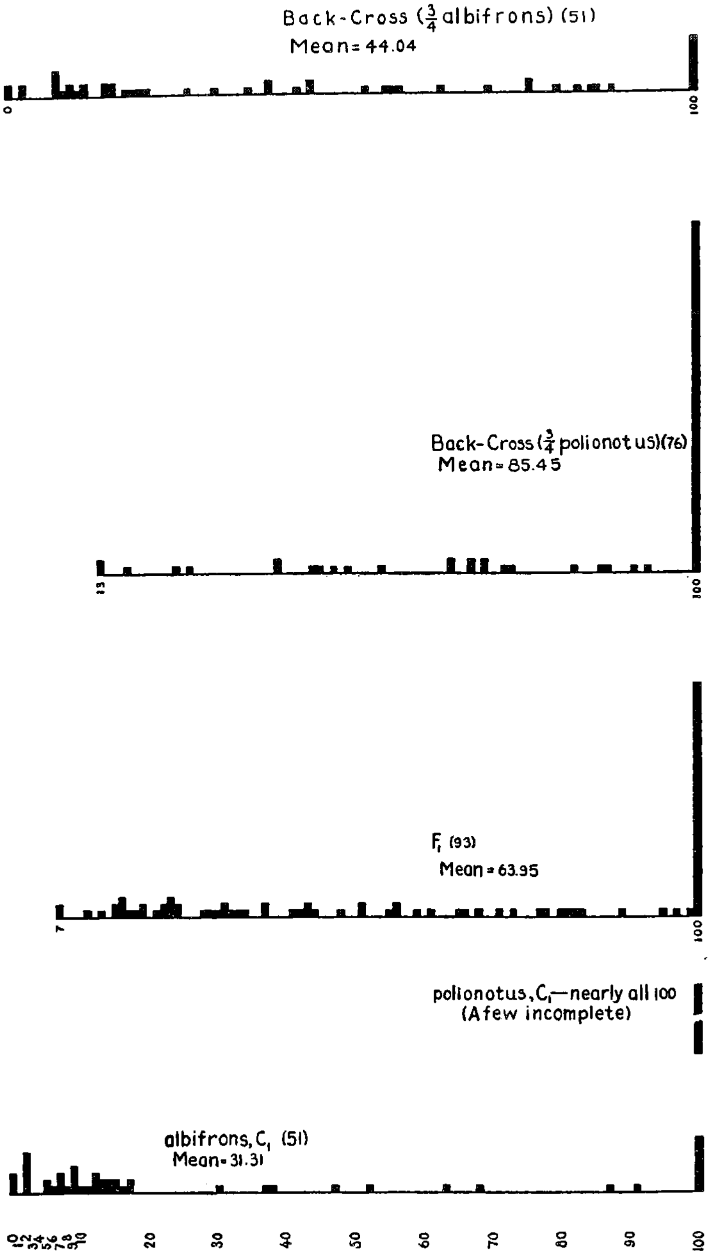
[1] Likewise, no skeletons have been prepared of the *polionotus-albifrons* series.

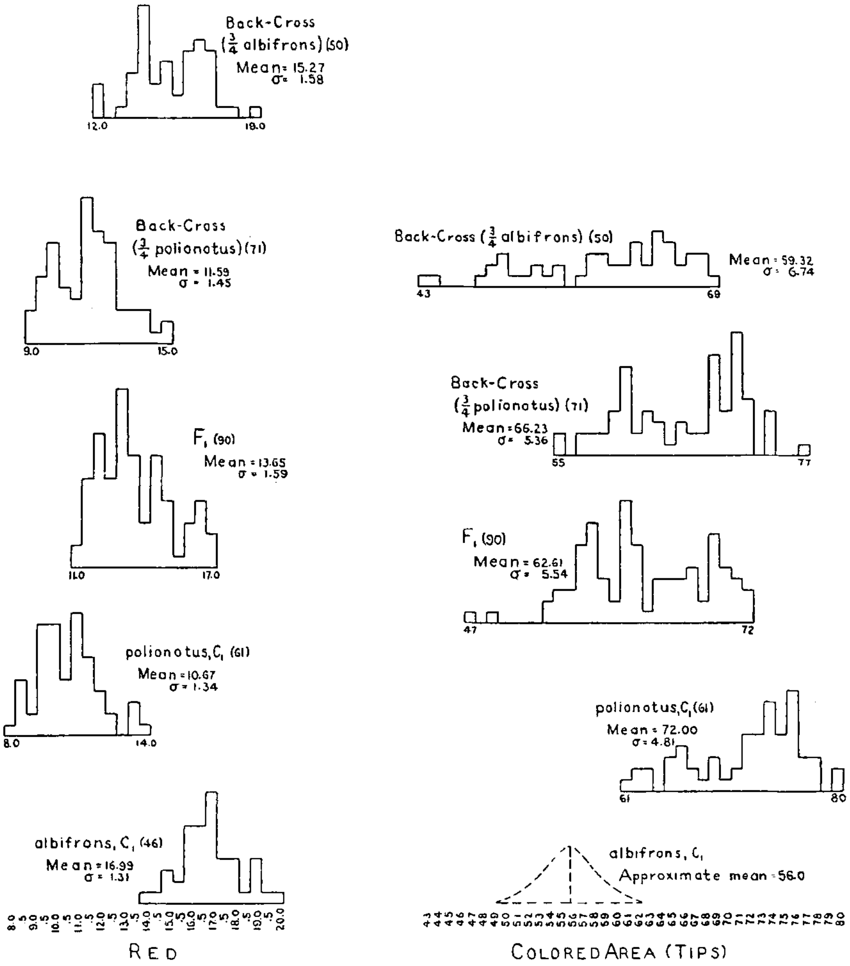
[2] C_1 (cage-bred) animals were here used as parents both of the F_1 and the back-cross generations. But the data for many of the C_1 series of *albifrons* are unfortunately incomplete, to such an extent that the mean values for actual parents cannot be profitably computed.



TAIL STRIPE

Text-fig. 25. Tail stripe in the *polionotus-albifrons* cross.

As regards the value for *red*, the F_1 generation is likewise about midway between the parent races. A fair comparison cannot be made in the case of *coloured area*, since figures for the C_1 lot of *albifrons*, which were the ones used in the present cross, are available only for A_b, while measurements of A_t alone were made for these hybrids (Text-fig. 26).



Text-fig. 26. Red and coloured area (here the area occupied by hairs pigmented to their tips) in the *polionotus-albifrons* cross.

It may be recalled that *polionotus* and *albifrons* (at least the coast representatives of the latter) present one absolute point of difference, the presence and absence of basal pigmentation in the ventral hair[1]. Such being the case, interesting relations might have been expected with regard to this character. But nothing very instructive is to be observed. In the F_1 generation it is probable that all individuals display at least a trace of such pigmentation, while most of them display much more than this. In the back-cross with *polionotus* the hairs of the ventral region, in practically all specimens, are plainly pigmented at the base. An enumeration of the 3/4 *albifrons* specimens, on the other hand, shows that twenty-five belong to the 0 grade, while the remaining twenty-six display conditions ranging from "trace" to "pronounced." Here we might be disposed to find an excellent case of a 50 : 50 ratio. But the significance of such an interpretation is largely nullified by the existence of a very strong fraternal correlation for this character. Thus, within the single fraternities, there is very little evidence of "splitting."

In the present cross, no general increase in variability is evident in the back-cross series, as compared with the F_1. This is curious, in view of the evidence for segregation in the back-cross generation which will be offered shortly.

Of the sixty-seven individuals resulting from the back-cross with *polionotus*, eight have values for coloured area which equal or exceed those of the means of their own *polionotus* ancestors. This would be almost one in eight. However, the significance of this fact is rendered uncertain by the circumstance that four out of eighty-two individuals in the F_1 generation have values which equal or exceed those of their *polionotus* ancestors. I have not looked up individual pedigrees for the values of red.

The back-cross with *albifrons* will not be considered here, owing to the fact that comparable measurements are not available (see above)[2].

Parent-offspring correlations between certain generations have been determined, but only for foot pigmentation and coloured area. In conformity with my earlier procedure, I have computed the weighted mean of the correlations between "wild" and C_1 generations of the parent races, between the parent races and the F_1 generation, and between the latter and the back-cross generations. The first-named character gives a mean value of $+ 0{\cdot}116$, the second $+ 0{\cdot}422$.

All of those correlations between various characters which were found to be indubitably present in the two preceding crosses are manifested in

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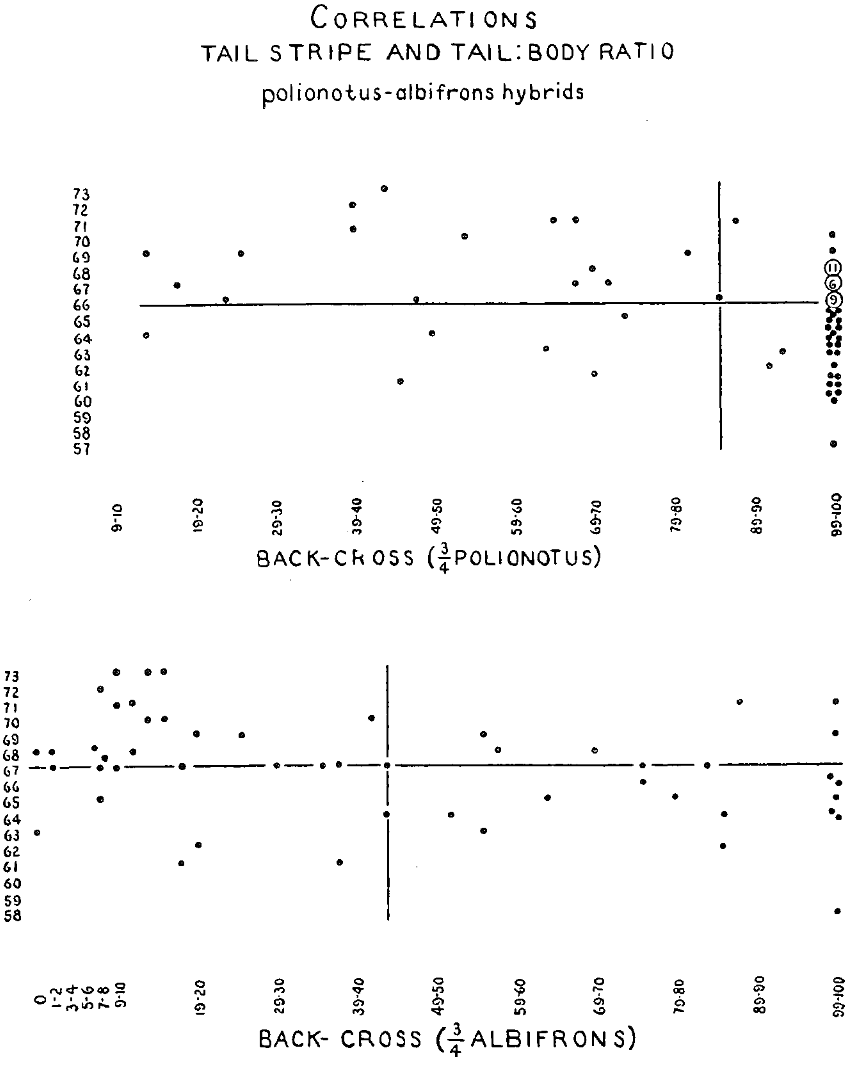
[1] Sumner (1929).

[2] It likewise happens that half of the *albifrons* ancestors of this series died prematurely, so that measurements of these characters were not obtained.

the present series. In both of the back-cross series, aggregating 127 individuals, there is a consistent correlation between the length of tail and foot



Text-fig. 27. Apparent correlations between tail stripe (abscissas) and relative tail length (ordinates) in *polionotus-albifrons* cross. Where the number at a given locus is too great to be represented by individual dots, this is indicated by the figure in the circle.

and the various pigmented characters. Coefficients were computed for the correlation between the length of each of these members and the four pigmental characters—tail stripe, foot pigmentation, coloured area (A_t)

and red. For the correlations involving foot length the sexes were dealt with separately. There are thus twenty-four coefficients. It will be noted that in every case but one (this being non-significant), these coefficients are of the sign which would be expected on the assumption that racial differences in these two classes of characters tend to segregate together. Thus tail and foot length are negatively correlated with tail stripe, foot pigmentation and coloured area, but are positively correlated with red. The latter value, it will be recalled, is a measure of the degree of pallor, *i.e.* of the *absence* of dark pigment.

It is curious that this preponderance of "expected" signs occurs among the back-crosses, in the *polionotus-albifrons* series of hybrids, whereas, in the two preceding series, it was displayed only by the F_2 and F_3 generations, not being evident in the back-crosses. Also, it is as evident here in the case of tail length as in that of foot length, which was not true of the previous crosses (see Text-fig. 27).

One qualifying circumstance must here be mentioned. Examination of individual pedigrees reveals the fact that a certain proportion of this correlation is due to the employment of two different strains of *albifrons*, as parents of these back-cross generations. Thus, as stated earlier, the East Pass strain possesses shorter feet and more extensive coloured area and tail stripe than the Foster's Bank strain, and these differences persist in their descendants, whether pure or hybrid. But it is likewise clear that this circumstance is responsible for only part of the correlations here considered, and that it has no effect, or even a reverse one, in some of the cases. The statistical force of this array of coefficients is thus somewhat weakened, but it is by no means destroyed[1].

Aside from the facts just considered, it must be repeated that these twenty-three coefficients do not have an altogether cumulative value, since tail and foot length are correlated with one another, on the one hand, and all of the pigmental characters are correlated on the other.

(*d*) *An interspecific cross.*

As stated above, one F_1 female was derived from a cross between *P. maniculatus sonoriensis* and *P. polionotus leucocephalus*. This female was successfully mated with a male *leucocephalus* and with a male *P. maniculatus gambelii*. The former back-cross yielded two offspring, the latter thirteen.

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[1] The circumstance here referred to does not, of course, affect either of the crosses previously considered. Only the East Pass derivatives have been considered in dealing with the *leucocephalus-albifrons* cross.

Certain facts relating to these hybrids are of considerable interest, despite the small numbers of animals concerned. The single F_1 female plainly displays characteristics derived from both of the species which entered the cross. In body length, it is at least equal to an average adult female *sonoriensis*, *i.e.* to the larger race[1]. In tail and foot length, on the other hand, it is intermediate, but in the former character it stands much nearer the average for the shorter-tailed *leucocephalus*. Tail stripe is almost completely lacking, having a value of about 3 per cent. of the exposed part of the tail. Here, as in the crosses previously considered, lack of tail stripe is dominant, though imperfectly, over its presence. It is always complete in normal specimens of *sonoriensis*. The coloured area is paler than in any except the palest *sonoriensis*[2], and its extent is greatly reduced, in comparison with the latter race, both on the head and the body. The influence of *leucocephalus* is further manifested in the presence of an extensive ventral area having hair which is white throughout its entire length. This condition is not present in any member of the *maniculatus* series, so far as I am aware. As in the case of *leucocephalus*, *albifrons* and the majority of hybrids considered in the foregoing pages, there is a region of hairs which are pigmented only at their basal zone, lying between the externally visible coloured area and the area of pure white hairs.

Passing to the thirteen offspring resulting from back-crossing with *maniculatus*, the coat colour of the majority would be matched very closely in a collection of *sonoriensis* skins, though the shade of the darker individuals lies closer to *gambelii*[3]. The ventrolateral whitish areas of most of them are, however, paler and more extended than in any specimens of the latter race. But, in every case, this area consists of hairs which are pigmented fairly heavily at the base. The most interesting feature of these back-cross animals relates, however, to the tail stripe. Of these thirteen individuals, six have a complete and normal tail stripe, though in one case this is not very intense, as not infrequently happens even in pure *maniculatus*[4]. Seven individuals, on the other hand, have very incomplete tail stripes. Five of these terminate short of the middle

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[1] The *maniculatus* group, as a whole, comprises mice of much larger size than the *polionotus* group.

[2] It may be closely matched in shade by many *albifrons*.

[3] *Gambelii* and *sonoriensis* overlap rather broadly in respect to general shade. Data are not at present available for satisfactory quantitative comparisons between the latter races and these hybrids.

[4] No measurements of the width of the stripe were taken. It appears, to the eye, to be slightly narrower than in *gambelii*.

of the tail, while in all cases the stripe is very faint, and consists of scattered black hairs. To the eye the tail stripes here comprised thus fall into two quite distinct classes, and the ratio is as near the traditional 50 : 50 as is possible with these numbers. If this case stood alone, we might easily recognise here a rather clear case of the segregation of a character difference dependent upon a single pair of Mendelian factors. But the lack of any such simple segregation in crosses between the much more closely related races previously considered renders this interpretation highly questionable.

The two specimens derived from the back-cross with *leucocephalus*, as might be expected, resemble the latter race much more closely. They were skinned when less than 3 months old, so that the pelage is not fully mature. That of one may be matched fairly well by some of the darkest specimens of *leucocephalus*; in the other, the coloured area is much too extended to allow of such comparison. It is of possible significance that the member of this brood (both are males) which resembles *leucocephalus* closely is also much smaller than the one which is less like the latter. Likewise, the length of both tail and foot in this smaller specimen is considerably less, both relatively and absolutely, thus approaching rather closely, in these respects, the means for *leucocephalus*. It is unfortunate that circumstances prevented the rearing of further hybrids between these species.

V. SUMMARY AND GENERAL DISCUSSION.

It is possible that the reader who has examined the foregoing data may have been more impressed by the inconsistency and inconclusiveness of some parts of the evidence than with the decisiveness of other parts. The criticism may be brought with some justice that we are dealing throughout with too many variables. It would of course have been far preferable, had this been possible, to maintain the same environmental conditions, including food, as are normal for these animals in a state of nature. Likewise, for the purposes of the hybridisation experiments, at least, it would have been far preferable to deal with genetically homogeneous stocks. However, these things were not practicable, though I realise their desirability as much as any critic. Let us, then, make the most of what we have.

Before proceeding to discuss some of the broader problems here involved, I shall introduce an itemised summary of the results presented in the foregoing pages.

(1) The geographic races of mice, chiefly here considered, differ from

one another rather strikingly in the quantity and distribution of pigments in the hair and skin, and also differ, though less strikingly, in certain details of bodily proportions. In total size, these races are approximately equal. In the case of the single interspecific cross, the two species differ considerably in general size, as well as displaying, in an even higher degree, all of the other classes of differences just mentioned.

(2) The pigmental characters of the geographic races bear definite relations to certain environmental gradients. The linear measurements of body parts, while exhibiting local differences, show no such constant relations.

(3) The mean racial differences in both linear and colorimetric characters are entirely genetic. Stocks of different races fail to converge when reared for a number of generations in a common environment.

(4) Individual differences within a single race are partly genetic, as appears from coefficients of correlation between parents and offspring, or between other groups of related individuals. These individual differences relate to the same bodily "characters" as do the racial differences.

(5) Individual differences are, however, to a considerable extent non-genetic, as is shown by the relatively low values of most of these parent-offspring correlations, and by the observed fact that some characters, particularly the length of certain members, are demonstrably affected by environmental conditions.

(6) As regards the degree of distinctness which is shown by two races subjected to hybridisation, the characters herein dealt with fall under three heads: (*a*) characters which are invariably present in full measure in one race and invariably absent in another (*e.g.* tail stripe and pigmentation at base of ventral hair in the *leucocephalus-polionotus* cross; pigmentation of ventral hair in the *polionotus-albifrons* cross); (*b*) characters which are present in both races, but which vary so widely in degree that there is no overlapping of the distribution "polygons" for the various values (*e.g.* red and coloured area in all three of the racial crosses); (*c*) characters in which the two races differ in respect to the mean values shown, but in which there is a more or less broad overlap of the individual values (*e.g.* the index of saturation, tail and foot length and bone measurements, in all three crosses).

(7) In respect to all of these racial differences, both linear and colorimetric, the first as well as the later hybrid generations show an intermediate condition. For most characters, the mean value in the F_1 and F_2 generations is approximately midway between the parental means, *i.e.* there is no appreciable dominance.

(8) Dominance is strikingly shown, however, in the case of one character, tail stripe. Lack of tail stripe is dominant, though incompletely so, over its presence, this phenomenon being clearly illustrated in two inter-racial crosses, and in one inter-specific cross. This dominance is of the "fluctuating" type, there being an enormous range of variability in the first hybrid generation (at least in the sub-specific crosses).

(9) Dominance is less strikingly shown in the case of another pigmental character, relative pallor or darkness of the pelage, represented by the value for "red" (R) in the preceding pages. A dark pelage (indicated by a low value for R) is incompletely dominant over a paler one. There also appears to be a tendency toward dominance of a richer coloration of the pelage over a greyer one, as indicated by values of the fraction $\frac{R-V}{R}$.

(10) The facts cited in the two preceding paragraphs are rather unexpected, inasmuch as the degree of development of the tail stripe is negatively correlated with "red" (*i.e. positively* correlated with depth of pigmentation). Yet presence of tail stripe is recessive, while depth of pigmentation tends to be dominant.

(11) In the case of the first two of these characters which display a partial dominance, there is a shifting of the mean in the recessive direction in the F_2 generation, as compared with the F_1.

(12) In no case does our evidence indicate that a racial difference in respect to any distinguishable character is dependent upon a single pair of Mendelian allelomorphs. This is evident from an inspection of the graphs. In the one instance in which we have the appearance of a secondary mode in the F_2 generation (Text-fig. 14) it was shown that a one-factor interpretation was quite improbable. Likewise, the seeming presence of a single factor having visible effects upon the tail stripe, in the inter-specific cross (p. 350), is very doubtfully open to such an interpretation.

(13) That genetic segregation occurs, none the less, in respect to one important class of characters at least, is conspicuously shown by the graphs for the various measurements of the intensity and extensity of pigmentation, as well as by the relative magnitudes of the standard deviations for the F_1 and F_2 hybrid generations, as shown in the tables. It is most conspicuous in the widest of these crosses (*leucocephalus-polionotus*), though quite pronounced in the *leucocephalus-albifrons* cross. The two back-cross generations show rather erratic relations in this respect.

(14) As regards the linear measurements of body parts, there is, on

the contrary, little or no evidence of segregation. The standard deviations of the F_1 and F_2 generations have been compared for seven sets of linear measurements (tail, foot, ear, certain bones), considered separately for the two sexes. In the *leucocephalus-albifrons* cross the F_2 figure is actually more often smaller than larger. This is true both for the "actual" and the "corrected" values. In the *leucocephalus-polionotus* cross, on the other hand, in which the differences between the parent races are much more pronounced, the F_2 figure ("actual") is larger than the F_1 in eleven cases out of fourteen, though this proportion falls to nine out of twelve, when "corrected" values are considered[1]. In both of these crosses the standard deviations for number of caudal vertebrae are greater in the F_2 than in the F_1 generation. It must be said, however, that the differences, taken singly, are in most of these cases trivial.

(15) The number of genetic factors commonly concerned in any single character difference is probably considerable. Various estimates of these numbers are obtained by various methods of calculation. It is likely that the lowest of these are erroneous.

(16) In the narrower *leucocephalus-albifrons* cross several individuals in an F_2 generation of seventy-four reach or surpass the mean of one or the other parent race in respect to the value of coloured area or of red. Even in the wider *leucocephalus-polionotus* cross two or three individuals out of 106 reach the mean of each parent race in respect to the value of coloured area, though not of red. One individual, however, reaches the value of red of its own *polionotus* grandparent.

(17) If we provisionally consider those individuals which reach or surpass the mean of one parent race, with respect to a given character, as "pure" segregants for that character, and base our computations upon the F_2, and the first and second back-cross generations of the *leucocephalus-albifrons* and *leucocephalus-polionotus* crosses, respectively, we reach the following estimates. The difference between *leucocephalus* and *albifrons*, in respect to the magnitude of the coloured area, is determined by about four factors (two to six), the difference in their values for red being determined by two to three factors. On the other hand, the relative magnitudes of coloured area in *leucocephalus* and *polionotus* would seem to depend, according to this method of computation, upon between three and four factor differences, while the relative magnitudes of red would depend upon three to five factor differences. Similar estimates are obtained if we rank as a "pure" segregant any individual

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[1] The latter are not given for skull breadth, hence the difference in total number.

which reaches or surpasses its own particular ancestor (or ancestors) of one or another race, in respect to a given character.

(18) That most of the estimates above given, aside from their manifest inconsistencies, are too small would seem to be indicated by a comparison of the histograms for the "grades" (7/8 *leucocephalus*) with the theoretical distribution of values in a generation of this composition (Text-fig. 15).

(19) In the *leucocephalus-albifrons* cross 15 and 18 per cent. respectively of the F_2 individuals fall within the extreme range of one or the other parent race in regard to all of the pigmental characters here considered, taken collectively. About two-thirds as great a proportion, however, fall within these limits, even in the F_1 generation. In the wider *leucocephalus-polionotus* cross, on the other hand, not a single individual in either of these generations falls within the limits of *leucocephalus* for all of the pigmental characters, although three F_2 individuals fall within the limits of *polionotus*.

(20) If we seek for individuals which measure up to the "average" condition of one or another of our pure races in respect to the ensemble of pigmental characters (*i.e.* a standard which would include half of the population of a given pure race) we do not find a single such case in the F_2 generation of either of our two principal crosses. A number are excluded from one or the other class in the *leucocephalus-albifrons* cross, only because they fail to conform to the standard set for the index of saturation. Thus, the richness of coloration has been found to be inherited to a considerable degree independently of either the depth or the extensity of pigmentation. Five out of fifty-eight back-cross individuals, and nine out of forty-one, among the grades, in the *leucocephalus-albifrons* cross, conform, however, to the standards set for an "average" *leucocephalus*. In the *leucocephalus-polionotus* cross we do not meet with any cases of this sort until we reach the grades, among which we find eleven out of fifty-five which may be rated as "average" *leucocephalus*.

(21) In both pure races and hybrids the length of certain members (tail, foot, ear) is found to be positively correlated, even when the influence of general body size has been eliminated by the method of partial correlation. Longer tailed individuals, like longer tailed races, tend to have longer feet[1]. There are, however, no significant differences between the hybrid generations in respect to the magnitude of these correlations.

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[1] Such inter-racial correlations do not hold, to be sure, for ear length.

(22) The various pigmental characters are likewise correlated with one another, both in the pure races and the hybrids, and here again intra-racial correlations are of the same sign as inter-racial ones (*e.g.* coloured area and red are negatively correlated, within each population, just as the race having the most extended coloured area has the lowest value for red, and *vice-versa*).

(23) The last named correlations are commonly lowest for the pure races and F_1 hybrids (lowest of all, frequently, in the latter); higher for the F_2 generation, and highest of all in the F_3 generation, derived from selected F_2 parents. The coefficients for the back-crosses are variable, though much more often higher than lower, in comparison with those for the F_1.

(24) These relations are, for the most part, such as might be expected, on the supposition that the characters concerned are in some way genetically connected, and that they therefore tend to segregate together. Reasons will be advanced below for believing that these correlations are due to the diverse effects of the same genetic factors, rather than to separate factors bound together by linkage.

(25) This common genetic basis for all the various pigmental characters is not, however, absolute. There is a considerable degree of independent variability among these characters, and it may be shown that a large fraction of this independent variability is genetic. Thus, two pigmental characters may be supposed to have certain factors in common and certain ones peculiar to themselves.

(26) There is some evidence for the existence of correlations between the bodily appendages (tail and foot) and the pigmental characters, in certain of the segregating generations of hybrids, in all three crosses. The coefficients are preponderantly of the "expected" sign, on the assumption that the character differences of a sub-species should segregate together. While the considerable series of coincidences here displayed can hardly be credited to random sampling, there are circumstances which render the foregoing interpretation somewhat questionable.

In the ensuing discussion I shall consider in succession three chief topics: (1) the possibility of determining the approximate number of genetic factors concerned in these racial differences; (2) the significance of the correlations which exist between certain characters, particularly in the segregating generations of hybrids; (3) the bearing of the present data upon our conceptions of evolution.

To those who accept the view that one species or race differs from another by a definite number of mutational steps, it is, of course, a matter of considerable interest to determine, if possible, the approximate number of such steps which separate one given form from another. It was, at the outset, my hope that some of the "presence-or-absence" differences, belonging to the first (*a*) class of characters listed in paragraph 6 of our summary, would lend themselves to a Mendelian analysis of the characters concerned. But this did not prove to be the case. For in the F_1 generation such characters were found to have an intermediate value, and to be extraordinarily varied in their manifestation. Thus, the length of the tail stripe of the F_1 generation (heterozygous for all factors concerned) covered the whole gamut from 0 to 100 per cent. Back-crossing with the 0 grade race (*leucocephalus*) led to a great increase in the proportion of stripeless individuals, and the disappearance of all except the lower grades of tail stripe. But since it is probable that the 0 grade consisted, in this generation, largely of individuals which were heterozygous for some or all of the factors concerned, it is plain that the proportionate number of individuals which lack the stripe altogether, as contrasted with those which possess it at all, affords no clue to the genetic classes which may be present. Furthermore, it seems certain that, with each back-cross to *leucocephalus*, an increasing proportion of the partially heterozygous individuals must fall within the 0 grade, and conversely that the relative number which show some trace of a stripe must decrease. It would thus seem to be futile to conduct such a "dilution" process in the hope of arriving at any single-factor difference in a case of this character.

Accordingly, we seem limited, in our quest for the number of factor differences between any two races, to characters which differ merely in degree (*b* and *c* of the classes listed above). Now it has already been abundantly shown that the evidence in such cases is conflicting. This has not infrequently been the experience of others.

It will be recalled that Castle and Wright (Castle, 1921) developed a formula for determining the number of factor differences concerned in a cross involving quantitative characters. Their formula was:

$$n = \frac{D^2}{8(\sigma_2^2 - \sigma_1^2)},$$

in which D is the difference between the parental means, in respect to the given character, and σ_1 and σ_2 are the standard deviations in the F_1 and F_2 generations, respectively. This formula was severely criticised by Shull (1921), and has recently been dealt with more fully by Serebrovsky (1928). The chief grounds for criticism are three: (1) that a complete lack of dominance is assumed; (2) that the factors are assumed to be of equal potency; and (3) that all of the positively working factors are assumed to be on one side of the cross, and all the negatively working ones on the other. Serebrovsky works out supplementary formulae, covering varying degrees of dominance, and differing distributions of positively and negatively working factors in the two races. Philiptschenko (1929), however, finds himself led to impossible results, even with the use of Serebrovsky's modified procedure. Castle (1928) admits that he has not found the results from the use of his own formula satisfactory, and queries whether the trouble may not lie with the fundamental postulates of the multiple factor hypothesis itself.

I have applied the formula of Castle and Wright to the computation of the number of factor differences between *leucocephalus* and *albifrons*, and between *leucocephalus* and *polionotus* respectively in relation to both coloured area and red. The fact that, in these four cases, the numbers of factors indicated are 2 +, 2 −, 2 −, and 14 respectively, in itself shows that the formula is inapplicable here. Certain other methods which I have employed have likewise given impossibly small numbers of factors.

As indicating very limited numbers of factor differences, in some of these cases, we have pointed to the relatively large proportion of seemingly pure segregants for both of the chief indices of pigmentation (coloured area and red), in the *leucocephalus-albifrons* cross, and for coloured area, in the *leucocephalus-polionotus* cross. The numbers here indicated range, for the most part, from two to four.

Against such a limited number of factor differences we have, however, a much greater array of evidence. We may mention here (1) the comparatively symmetrical distribution of values in the second backcross with *leucocephalus*; (2) the occurrence, within each sub-species, of genetic differences in respect to all of the characters, each of these minor differences being dependent upon multiple factors if this theory be accepted; (3) the existence, within both *albifrons* and *polionotus*, of geographically graded differences, some of which, at least, are known to be genetic and to depend upon more than one factor.

One means of escape from this dilemma readily suggests itself. May not the differences between the distinct sub-species be due to a relatively small number of major factors, while the local differences within a sub-species, or the differences within a single population, are due to a considerable number of minor, "modifying," factors? If the "major" factors be supposed to far outweigh the "minor" ones in their quantitative effects, a segregant which was "pure" for all the major factors of one sub-species might reach or surpass the mean value of that sub-species, in respect to a given character, even though it was not pure for all the minor factors, which entered the cross.

It would be difficult, however, to account, on such a basis, for the approximately symmetrical distribution of the "7/8 *leucocephalus*" populations, already discussed at some length. If we had to do with three or four factors, capable of producing the major pelage differences between *leucocephalus* and *polionotus*, the presence of even a large number of modifying factors, of the sort which might be supposed to underly the minor individual differences, would not suffice to mask the asymmetry to be expected in a histogram based upon such material. Moreover, it would seem more probable, on the basis of the multiple factor hypothesis, that the differences between two sub-species would depend upon a greater number of factors, instead of upon more potent factors, than the difference between two individuals within a sub-species. For presumably the sub-specific differences have arisen through the accumulation of the same type of genetic differences as distinguish members of the same sub-species.

If we are to retain the multiple factor interpretation at all, it seems to me that we must attribute any one of the sub-specific differences here considered to a much greater number of factors than three or four. This means that there is something wrong with the argument based upon the number of apparently "pure" segregants. Our argument contained the implicit assumption that all of the allelomorphs tending to increase the degree of pigmentation (to raise the value of A and to lower the value of R) were contained in one of the two sub-species entering a cross, while all of the allelomorphs tending to decrease the degree of pigmentation were contained in the other. But this, of course, is not necessarily true. *Leucocephalus*, for example, might have the constitution *aabbccddeeFF*, in respect to a given character difference, while *albifrons* had the constitution *AABBCCDDEEff*. In such an event, it is plain that the chance that an F_2 individual would equal or exceed one or the other of the parent races would be very much greater than if all of the "lower case" genes were on one side, and all the "capitals" on the other. For it would not be necessary, in order to reach this level of darkness or pallor, that an individual should be homozygous for all of the factors derived from either race[1]. A marked asymmetry of distribution in the

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[1] I am here leaving out of account the part played by the phenotypic variability of each single genotype. It has been assumed above (p. 296) that the chance for an incomplete segregant to reach or exceed the mean value of a given parent race would be balanced by the chance that a pure segregant should fall below this level.

second back-cross would remain, however, even upon the foregoing assumption.

Formally, at least, we have thus reconciled our conflicting evidence by an interpretation which is quite in harmony with the multiple factor hypothesis. While such an interpretation is far from being proved, at the present time, I know of no other which fits the facts as well.

A yet more interesting problem is that of the nature of the genetic connection between certain components of the sub-specific complex of characters. I have previously called attention to the fact that high correlations among the various pigmental characters may be observed, when series of contiguous races are thrown together and treated as single populations, whereas correlations between the same pairs of characters are found to be much weaker, or even to be imperceptible, when the component collections are treated separately[1]. I have given reasons for believing that this higher degree of inter-racial correlation, as compared with intra-racial, is due to the fact that the mean differences between the local races are entirely genetic, whereas the individual differences within any single race are partly phenotypic, *i.e.* non-hereditary. That there is some sort of a close genetic bond among the various racial differences in pigmentation has already been fully shown. The non-hereditary modifications of these characters (however produced) appear, on the contrary, to be largely independent of one another. In the case of certain other characters, to be sure (*e.g.* tail and foot), environmental influences (temperature, nutrition) are known to bring about parallel modification, but there is no indication that the various pigmental characters here considered are subject to coincident changes of this sort during the individual lifetime. Unfortunately, the nature of the non-hereditary fraction of all individual variability in animals is a subject concerning which, at the present time, we are very largely in the dark.

The interesting relations narrated in paragraph 23 of the foregoing summary are open to a similar interpretation. The higher degree of correlation among these characters which is found in the F_2 generation, as compared with the F_1, is due to an increase in the proportion of the total variability which is genetic, combined with the fact that the characters are in some way bound together genetically[2].

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[1] Sumner (1929 *a*). See also Bubnoff (1919).

[2] It is probably needless to say that the larger coefficients found in the F_2 generation do not result from a mere increase in the range of variation of the correlated characters. The standard deviations are of course increased, as well as the product moments.

The still further increase in these correlations which is manifested in the F_3 generation is due to the procedure adopted in the selection and mating of the parents. The more extreme segregants which were selected as "pale" and "dark" constituted about two-thirds of those thus chosen. This circumstance, and the further fact that at least two pigmental characters were taken into account in making the choice would inevitably result in high correlations among this parent group when treated as a single population[1]. And since these latter were mated assortatively (pale with pale, etc.), a similar genetic constitution was reflected in the F_3 generation.

Regarding the nature of this genetic connection among our correlated characters, two hypotheses are possible: (1) The characters in question may be merely different manifestations of the same genetic factors (*e.g.* the extent of both tail stripe and coloured area may depend upon factors which determine the amount of pigmented hair upon the tail and trunk alike). (2) The factors underlying these characters may be more or less closely linked, due to their presence in the same chromosome. And it is of course possible that each of these explanations may be true in part. On the other hand, parallel modification, through environmental influences acting during ontogeny, could hardly account for correlations which increase as a result of segregation.

While the data thus far discussed lend themselves perhaps equally well to either of the foregoing interpretations, there is one circumstance which strongly favours the hypothesis that our correlations result from the various pigmental characters being determined in part by a genetic basis common to all of them. I refer to the frequent association between intensity and extensity of pigmentation, upon various parts of the body, and in animals belonging to widely different groups. This phenomenon is so well known to students of systematic ornithology and mammalogy that it need not be discussed here. Reference need only be made to the diminution both in the intensity and extensity of coloured areas in desert species, as compared with the denizens of more humid climates (Allen, 1906; Buxton, 1923; Görnitz, 1923; Sumner, 1925; Rensch, 1929). In connection with this class of facts, the hypotheses of linkage can hardly be invoked as an explanation. For studies of linkage thus far

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[1] As a matter of fact the correlations in these groups of selected parents were probably at least as high as in their F_3 offspring. Thus, in the *leucocephalus-albifrons* series, the correlation between A_b and R among the selected F_2 parents was $-0{\cdot}912$, that of their offspring $-0{\cdot}788$. Similar figures for the *leucocephalus-polionotus* cross (in this case, A_t and R) are $-0{\cdot}822$ and $-0{\cdot}858$ respectively. In both cases the deviations of each parent have been weighted by the number of offspring.

made have surely revealed no general tendency toward the close propinquity, within the same chromosome, of genes which bring about similar physiological or morphological conditions. On the contrary, their associations with one another are on the whole surprisingly haphazard and arbitrary.

That each of these characters, on the other hand, is partially determined by independent genetic factors will be rendered equally probable by the evidence. The fact that the correlated characters under consideration all have a considerable range of independent variability—to such a degree, indeed, that the coefficients are sometimes reduced to zero—does not, of course, prove the case as regards independent *genetic* variability. Much of the variability of all organisms is known to be "phenotypic" or "somatic"—whatever that means. At least, much of it is not transmissible, as is shown by the low values of most parent-offspring correlations.

Of more evidential value, in this connection, are certain relations which appear in comparing one race with another. Attention has already been called to a curious anomaly presented by the Foster's Bank collection of *albifrons*. This local sub-race is at once *darker* and possessed of a *smaller* coloured area and *shorter* tail stripe (reduced to 0 in most cases) than are the other representatives of *albifrons* found near the coast. Although the collection is unfortunately small (twenty specimens) the differences in these respects are so considerable and so constant that they very probably represent actual differences in the respective local populations. Moreover, the differences revealed by the sample collected prove to be genetic ones (Text-figs. 3, 10). These facts speak for the partial genetic independence of the characters concerned, despite the fact that "red" is, in general, negatively correlated with the other two characters, both within single populations, and particularly when we consider a series of such populations in geographic sequence.

Once more, identical coloured areas are associated with different values for red in different racial crosses[1]. Thus, if we compare individuals with the same value for coloured area, in the 3/4 *albifrons* and 3/4 *polionotus* series respectively of the *polionotus-albifrons* cross, we find that the value for red is much higher in the former than in the latter, *i.e.* the former are paler.

But still more important light upon this subject is derived from an application of the method of partial correlation. The correlation between

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[1] Pure races cannot be directly compared for this purpose, since there is practically no overlap in respect to the values for either of these characters.

the two measurements of the coloured area ("base" and "tips") is high in all of the groups for which both values have been determined. It approaches unity in the F_2 and F_3 generations of the *leucocephalus-polionotus* cross. It may nevertheless be shown by the method referred to that "red" is correlated to some extent with each of these determinations of coloured area, independently of the other. For East Pass *albifrons*, the mean of these two "net" coefficients is – 0·210; for the F_2 generation of *leucocephalus-polionotus* hybrids the mean is – 0·177; for the F_3 generation it is – 0·235. All of these six values are of the same sign. The aggregate number of individuals on which they are based is 230. In the F_1 generation of this cross, on the other hand, one net coefficient is negative and the other positive, the mean being – 0·090.

The foregoing figures do not, of course, prove that this independent variability of the two measurements of coloured area is of the genetic sort. Unfortunately, this last question cannot be tested for these two characters, owing to circumstances which need not be detailed here. But the independent genetic variability of coloured area (either "base" or "tips") and red can be readily demonstrated. For this purpose, I have computed the parent-offspring correlations in respect to each of these characters, when the influence of the other has been eliminated. I have confined my computations to those generations between which correlation was found to be highest, namely, the F_2 and F_3 generations of both the *leucocephalus-albifrons* and the *leucocephalus-polionotus* crosses. As has already been pointed out, the amount of genetic variation in these F_3 generations and in the selected groups of F_2 parents is extremely high.

	Leucocephalus-albifrons F_2–F_3				*Leucocephalus-polionotus* F_2–F_3			
Character	No. of parents*	No. of offspring	r (gross)	r (net)	No. of parents*	No. of offspring	r (gross)	r (net)
A	22	65	+0·751	+0·344	26	82	+0·917	+0·712
R	22	65	+0·743	+0·437	24	82	+0·837	+0·464

* Here and elsewhere, in computing parent-offspring correlations, each parental deviation has been repeated to correspond with the number of offspring. Each filial deviation has thus been paired off against a parental one, and the *n* of the formula has been the number of offspring, rather than that of the parents. A similar weighting process was applied in computation of means and standard deviations in these cases. This procedure has both advantages and disadvantages.

In computing the net parent-offspring correlation for coloured area, the influence of red being eliminated, the three gross coefficients used were (1) that for coloured area (parents) and coloured area (offspring),

(2) that for coloured area (parents) and red (parents), and (3) that for red (parents) and coloured area (offspring). Conversely, in computing the net parent-offspring correlation for red, the gross coefficients used were those for red (parents) and red (offspring), coloured area (parents) and red (parents), and coloured area (parents) and red (offspring). Four separate coefficients were computed for each series (fathers—sons, fathers—daughters, mothers—sons, mothers—daughters). The weighted mean of these four figures, for each cross and each character, is given above.

It will be seen that these "net" coefficients are from a half to three-quarters as great as the "gross" ones. This can only be interpreted as showing that a large proportion of the variation which each of these characters undergoes, independently of the other, in this material at least, is genetic.

It is relevant to call attention, likewise, to the relatively high values of the cross-correlations, computed at this time, as compared with the direct ones. Thus, the weighted mean of the four cross-correlations here considered (coloured area of parents with red of offspring, and *vice-versa*, in the two crosses) is – 0·767, the weighted mean of the direct correlations being + 0·819. We may also refer again to the striking correlations (Text-fig. 13) between coloured area, in the *leucocephalus* parents, and tail stripe in the F_1 generation of a cross with *polionotus*, despite the fact that tail stripe itself is totally lacking in the former race.

To sum up our conclusions from the facts discussed in the last few paragraphs, we may say that the close correlation found to exist between certain pigmental characters is probably due to their partial dependence upon common genetic factors. That the correlation is never absolute is due in part to the existence of independent factors which influence one character without affecting the other; in part to the presence of a considerable degree of non-genetic variability. It is possible that linkage likewise exists here and further complicates the situation. But it is not necessary to assume its occurrence.

This is quite a different conclusion from that of Tine Tammes (1912) in the case of flax hybrids. This author attributes the correlation of certain characters in the F_2 generation to linkage ("in the gamete formation in the F_1 particular factor combinations occur by preference"), although it is stated that these correlations are already feebly present in the F_1 and the parent races. She is led to the rather surprising conclusion "that a closer interdependence exists between the factor groups for the various characters than between the factors for the same character." Such a situation might be intelligible on the basis of polyploidy, but it is, at best, entirely hypothetical.

Whatever may be the situation in respect to flax, I regard such an explanation as much less satisfactory for *Peromyscus* than that of the multiple effects of the same genes. In this respect, my interpretation is in accord with that of Dobzhansky (1927), who adopts the hypothesis of "multiple effects," rather than that of linkage, in explaining the correlation between the pigmentation of the eye and that of the testis in *Drosophila*. In the case described by Dobzhansky, however, the correlation is absolute, and seems to depend upon a single pair of allelomorphs. Moreover, the pigmentation of certain other regions of the body is quite independent of that of the parts named. These last statements do not appear to hold for any of the sub-specific differences with which I have dealt in the case of *Peromyscus*, though they apply, one or all, to certain colour mutations which I have described in species of this genus (Sumner, 1917, 1928; Sumner and Collins, 1922).

The foregoing interpretation is offered only for the correlations between one pigmental character and another. A few further words are necessary regarding another type of correlation which has been discussed above, namely, that between foot or tail length, on the one hand, and the various pigmental characters on the other. The evidence for such correlation has been discussed in detail in connection with each of the three sub-specific crosses considered in the present paper, and it need not be repeated here. Statistically, the case is strong that this series of coincidences does not result from random sampling.

Certain circumstances have already been mentioned which considerably weaken the conclusion that the preponderant occurrence in some of the segregating generations, of coefficients having the "expected" sign, is due to any genetic bond between the two classes of characters. I refer especially to (1) the fact that the standard deviations for foot and tail length are not preponderantly greater in the F_2 generation than in the F_1; and (2) the related fact that the correlations between tail and foot length show no constant tendency to be greater in the F_2 and F_3 generations than in the F_1 hybrids and the pure races. So far as they go, these last facts are not in accord with the supposition that there is any manifest segregation of the genetic factors which underly racial differences in the length of these two members. Yet the correlations referred to in the preceding paragraph would seem to depend upon the simultaneous segregation of factors affecting the length of the latter and ones affecting pigmental characters.

Let us assume, however, that these corelation have an actual genetic basis, and that they result from a tendency of certain racial characters to segregate in their original combinations[1]. I believe that in that case the hypothesis of linkage, rather than that of multiple effects of the same genes, would be preferable. For, in the first place, the correlations are so feeble that in most instances they are statistically non-significant, when taken singly; and in the second place, the length of tail and foot bears no general relation, in this genus as a whole, to the extent or shade of the coloured area of the pelage. In a recent paper (1929) I have pointed out that while the *albifrons* of the immediate neighbourhood of the coast has a markedly longer tail and foot than *polionotus*, we meet with a type, only 20 miles inland, in which these members are no longer than in the latter race. Furthermore, on the Pacific coast, it is the *darkest* sub-species of *Peromyscus maniculatus* that have by far the *longest* tails and feet, and this reversed association holds throughout a considerable area. This last fact, as well as the exactly opposite relation of these same characters in certain members of the *P. polionotus* series[2] could both be accounted for on the basis of a rather low degree of linkage between some of the factors concerned[3].

A few words, in conclusion, relative to the bearing of these studies upon our conceptions of the process of evolution. It is evident that in no case does one of these sub-species, or even a genetically distinct subdivision of such a sub-species, appear to have arisen through a single act of mutation. Wherever investigated, such races or sub-races appear to differ by considerable numbers of Mendelian factors. Since these differences have frequently been accumulated in a fairly consistent manner, along some geographic, climatic or edaphic gradient, we can hardly regard the relationships as being entirely haphazard ones[4]. Either

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[1] These phenomena may be related to certain evidences for the coherence of specific characters which were obtained by Gates (1925) in crossing *Mus musculus* with the Japanese waltzing-mouse, and which were interpreted by him on the assumption that "the chromosomes of each species tend to segregate as a group and not at random."

[2] *Leucocephalus*, coast *albifrons*, and *polionotus* represent a series of decreasing tail and foot length, and of increasing pigmentation.

[3] However, it is worth noting that a recent examination of measurements from the F_2 generation of certain sub-specific crosses of *P. maniculatus* discussed in an earlier paper (Sumner, 1923 *a*) has revealed no consistent tendency toward correlations of the sort here considered.

[4] This subject has been discussed in an illuminating manner in two recent volumes (Robson, 1928; Rensch, 1929), while Osborn (1927 and earlier papers) has brought together much valuable material, and made this the basis of an interesting theoretical discussion. I have myself considered certain of these cases of intergradation in some detail (Sumner, 1923, 1929, 1929 *a*).

(1) there has been a selection on the basis of adaptedness (whether in respect to the visible manifestation of these factors or to some more recondite effects); or (2) the genetic changes have resulted in some more direct way, from the action of the environment. In various earlier papers I have argued for the second of these alternatives[1], and I still believe that it is the more probable one in many instances, particularly in those cases in which humidity and aridity appear to have been the controlling factors. It must be admitted, however, that the simultaneous transformation of considerable series of pigmental characters, even when these are but feebly correlated within any single population, is not, in itself, to be regarded as evidence of their parallel modification by the environment, as I formerly supposed. This becomes obvious if we accept the conclusion that these characters rest, in part, upon a common genetic basis.

In the case of the present series (*polionotus-albifrons-leucocephalus*), it seems much more likely that an important element in the situation has been a selective effect of the environment, on the basis of colour. As regards the pigmental changes, the admittedly ill-supported, though far from disproved theory of "concealing coloration" seems to fit these facts better than any other[2].

Such an interpretation does not mean, however, that the actual factorial changes or "mutations" have necessarily occurred at the time when one geographic race has arisen from another. There is much genetic diversity in every natural population, resulting presumably from factorial changes which have occurred in the past, combined with hybridisation in the broadest sense of the term. It is likely, therefore, that rather wide divergence could be brought about in such a population by continued selection, in the entire absence of new mutations. If it should turn out that suitable mutations likewise occur from time to time, and particularly if such mutations are in any way responsive to organic "needs," the process would, of course, be vastly expedited. Or appropriate crosses between different existing stocks might give rise to an adequate supply of variations, as Lotsy and others have so forcefully contended.

I trust, however, that the foregoing remarks will not be taken to imply that I regard such a "mutational" explanation of the origin of these geographic races, or of species in general, as either adequate or satisfying. It is no more adequate or satisfying than is the related notion that the entire heritage of an organism consists of an aggregation of Mendelian genes. Both conceptions, I believe, are to be viewed merely

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[1] Sumner (1920, 1923, 1925).

[2] Sumner (1929, 1929 *a*).

as highly useful provision hypotheses, which account for certain important aspects of individual and racial development, but which entirely overlook certain others. In this belief I think it likely that I am in agreement with many mutationists, though probably not with all.

REFERENCES.

ALLEN, J. A. (1906). "The influence of physical conditions in the genesis of species." *Ann. Rept. Smithsonian Inst. for* 1905 [1906], pp. 375–402. (Reprinted with additions from *Radical Review*, I, 1877.)

BUBNOFF, S. (1919). "Ueber einige grundlegende Prinzipien der paläontologischen Systematik." *Zeitschr. f. induktive Abstammungs- u. Vererbungslehre*, XXI, 158–68.

BUXTON, P. A. (1923). *Animal Life in Deserts; a Study of the Fauna in relation to the Environment.* Edward Arnold and Co., London; Longmans, Green and Co., New York.

CASTLE, W. E. (1921). "An improved method of estimating the number of genetic factors concerned in cases of blending inheritance." *Science*, N.S. LIV, 223.

—— (1924). "Does the inheritance of differences in general size depend upon general or special size factors?" *Proc. Nat. Acad. Sci.* v, 19–22.

—— (1924 *a*). "Are the various parts of the body genetically independent in size?" *Ibid.* v, 181–2.

—— (1928). "Continuation of experimental studies of heredity in small mammals." *Carnegie Inst. Year Book*, No. 27, pp. 321–4.

COLLINS, H. H. (1923). "Studies of the pelage phases and of the nature of colour variations in mice of the genus *Peromyscus*." *Journ. Exp. Zool.* XXXVIII, 45–107.

DOBZHANSKY, T. (1927). "Studies on the manifold effect of certain genes in *Drosophila melanogaster*." *Zeitschr. f. induktive Abstammungs- u. Vererbungslehre*, XLIII, 330–88.

GATES, W. H. (1925). "The Japanese waltzing mouse, its origin and genetics." *Proc. Nat. Acad. Sci.* XI, 651–3.

GÖRNITZ, K. (1923). "Ueber die Wirkung klimatischer Faktoren auf die Pigmentfarben der Vogelfedern." *Journ. f. Ornithologie*, LXXI, 456–511.

GRINNELL, J. (1922). "A geographical study of the kangaroo rats of California." *Univ. Calif. Publ. in Zool.* XXIV, 1–124.

HOWELL, A. H. (1920). "Description of a new species of beach mouse from Florida." *Journ. Mammalogy*, I, 237–40.

HUESTIS, R. R. (1925). "A description of microscopic hair characters and of their inheritance in *Peromyscus*." *Journ. Exp. Zool.* XLI, 429–70.

OSBORN, H. F. (1927). "The origin of species, V: speciation and mutation." *Amer. Naturalist*, LXI, 5–42.

OSGOOD, W. H. (1909). "Revision of the mice of the American genus *Peromyscus*." *Bureau Biol. Survey, North American Fauna*, No. 28, 285 pp.

PHILIPTSCHENKO, J. (1929). "Zur Frage nach der Berechnung der Faktorenzahl bei Vererbung quantitativer Merkmale." *Zeitschr. f. induktive Abstammungs- u. Vererbungslehre*, LI, 245–8.

RENSCH, B. (1929). *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung.* Gebrüder Borntraeger, Berlin, 206 pp.

Robson, G. C. (1928). *The Species Problem, an Introduction to the Study of Evolutionary Divergence in Natural Populations.* Oliver and Boyd, Edinburgh and London, 283 pp.

Serebrovsky, A. S. (1928). "An analysis of the inheritance of quantitative transgressive characters." *Zeitschr. f. induktive Abstammungs- u. Vererbungslehre,* xlviii, 229–43.

Shull, G. H. (1921). "Estimating the number of genetic factors concerned in blending inheritance." *Amer. Naturalist,* lv, 556–64.

Sumner, F. B. (1915). "Genetic studies of several geographic races of California deer-mice." *Amer. Naturalist,* xlix, 688–701.

—— (1917). "The rôle of isolation in the formation of a narrowly localised race of deer-mice (*Peromyscus*)." *Ibid.* li, 173–85.

—— (1917 *a*). "Several colour 'mutations' in mice of the genus *Peromyscus.*" *Genetics,* ii, 291–300.

—— (1918, 1918 *a*, 1918 *b*). "Continuous and discontinuous variations and their inheritance in *Peromyscus.*" *Amer. Naturalist,* lii, 177–208, 290–301, 439–54.

—— (1920). "Geographic variation and Mendelian inheritance." *Journ. Exper. Zool.* xxx, 369–402.

—— (1922). "Linkage in *Peromyscus.*" *Amer. Naturalist,* lvi, 412–17.

— (1923). "Some factors relevant to a discussion of the origin and inheritance of specific characters." *Ibid.* lvii, 238–54.

—— (1923 *a*). "Results of experiments in hybridising sub-species of *Peromyscus.*" *Journ. Exper. Zool.* xxxviii, 245–92.

—— (1923 *b*). "Size factors and size inheritance." *Proc. Nat. Acad. Sci.* ix, 391–7.

—— (1924). "The partial genetic independence in size of the various parts of the body." *Ibid.* x, 178–80.

—— (1924 *a*). "The stability of sub-specific characters under changed conditions of environment." *Amer. Naturalist,* lviii, 481–505.

—— (1924 *b*). "Hairless mice." *Journ. Heredity,* xv, 475–81.

—— (1925). "Some biological problems of our south-western deserts." *Ecology,* vi, 352–71.

—— (1926). "An analysis of geographic variation in mice of the *Peromyscus polionotus* group from Florida and Alabama." *Journ. Mammalogy,* vii, 149–84.

—— (1927). "Linear and colorimetric measurements of small mammals." *Ibid.* viii, 177–206.

—— (1928). "Observations on the inheritance of a multifactor colour variation in white-footed mice (*Peromyscus*)." *Amer. Naturalist,* lxii, 193–206.

—— (1928 *a*). "Continuation of ecological and genetical studies with *Peromyscus.*" *Carnegie Inst. Year Book,* No. 27, pp. 335–9.

—— (1929). "The analysis of a concrete case of intergradation between two sub-species." *Proc. Nat. Acad. Sci.* xv, 110–20.

—— (1929 *a*). "The analysis of a concrete case of intergradation between two sub-species. II. Additional data and interpretations." *Ibid.* xv, 481–93.

—— (1929 *b*). "Is evolution a continuous or discontinuous process?" *Scientific Monthly,* xxix, 72–78.

Sumner, F. B. and Collins, H. H. (1922). "Further studies of colour mutations in mice of the genus *Peromyscus.*" *Journ. Exper. Zool.* xxxvi, 289–316.

SUMNER, F. B. and HUESTIS, R. R. (1921). "Bilateral asymmetry and its relation to certain problems of genetics." *Genetics*, VI, 445–85.

—— —— (1925). "Studies of coat-colour and foot pigmentation in sub-specific hybrids of *Peromyscus eremicus*." *Biological Bull.* XLVIII, 37–55.

SUMNER, F. B. and SWARTH, H. S. (1924). "The supposed effect of the colour tone of the background upon the coat colour of mammals." *Journ. Mammalogy*, V, 81–113.

TAMMES, TINE (1912). "Einige Korrelationserscheinungen bei Bastarden." *Recueil des Travaux Botaniques Néerlandais*, IX, 69–84.

EXPLANATION OF PLATES VIII—XI.

PLATE VIII.

Fig. 1. (Upper left.) Skin of *Peromyscus polionotus leucocephalus*, close to average in respect to all pelage characters.

Fig. 2. (Centre.) Average *P. p. albifrons* (East Pass series).

Fig. 3. (Upper right.) Average *P. p. polionotus* (Autaugaville series).

Fig. 4. (Lower left.) Extreme pale segregant in F_2 generation of *leucocephalus-polionotus* (*i.e.* cross between sub-species *leucocephalus* and *polionotus*).

Fig. 5. (Lower right.) Extreme dark segregant in F_2 generation of same cross.

PLATE IX.

Figs. 6, 7, 8. Palest, mean and darkest specimens of *leucocephalus*. In choosing extremes, here and elsewhere, the values both for "coloured area" and "red" were taken into consideration, and a skin was chosen, in each case, which gave nearly or quite the extreme values for both of these characters. (The actual extreme values are not always combined in the same individual.) In choosing the means, "coloured area," "red," and the "index of saturation" were all taken into account.

Figs. 9, 10, 11. Palest, mean and darkest skins of *albifrons* (East Pass series).

Figs. 12, 13, 14. Palest, mean and darkest skins of *polionotus*.

PLATE X.

Figs. 15, 16, 17. Palest, mean and darkest specimens in F_1 generation of *leucocephalus-albifrons* cross.

Figs. 18, 19, 20. Palest, mean and darkest specimens in F_2 generation of same cross.

Fig. 21. Palest specimen in first back-cross with *leucocephalus* (3/4 *leucocephalus*).

Fig. 22. Palest specimen in second back-cross with *leucocephalus* (7/8 *leucocephalus*).

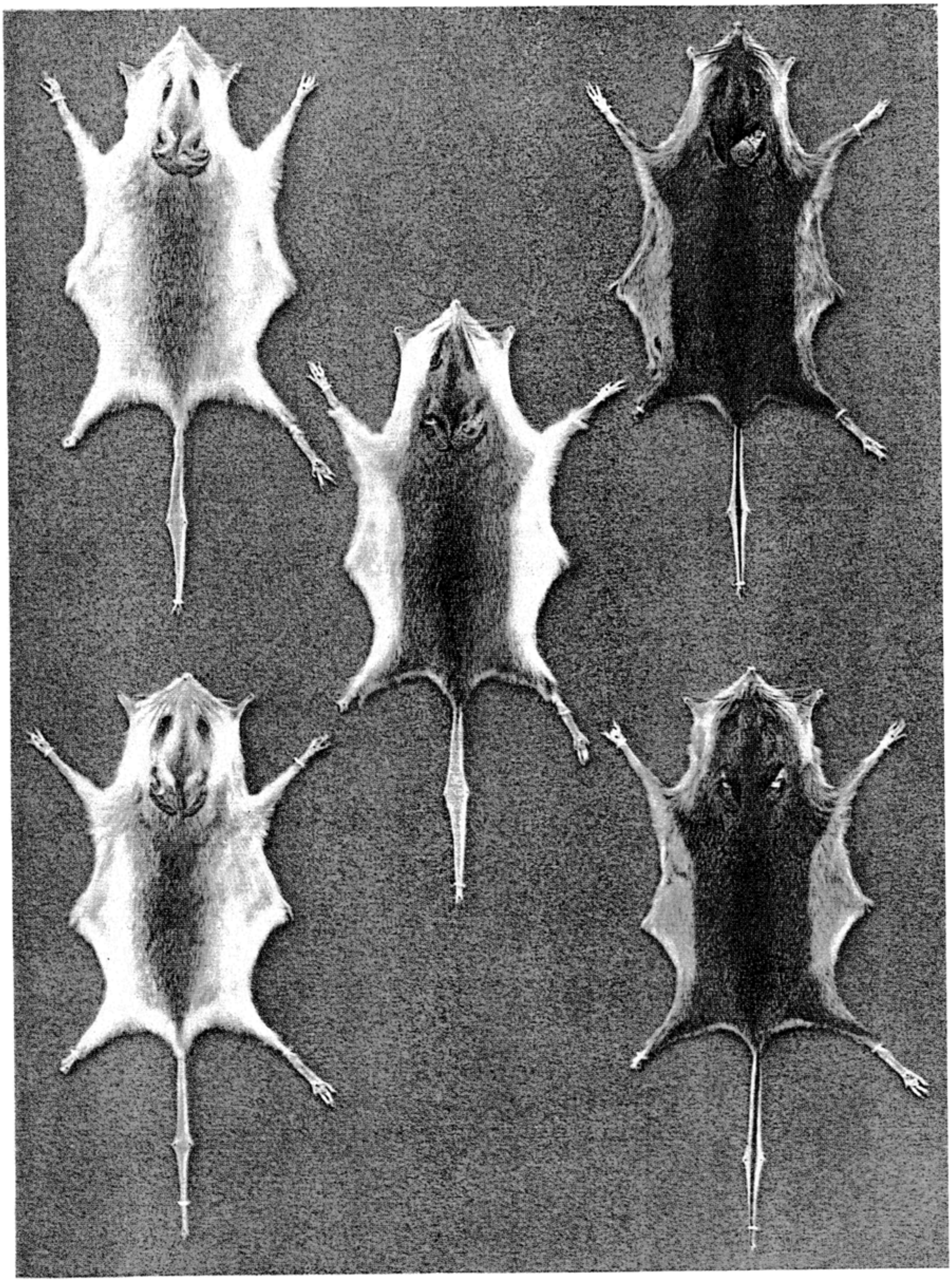
PLATE XI.

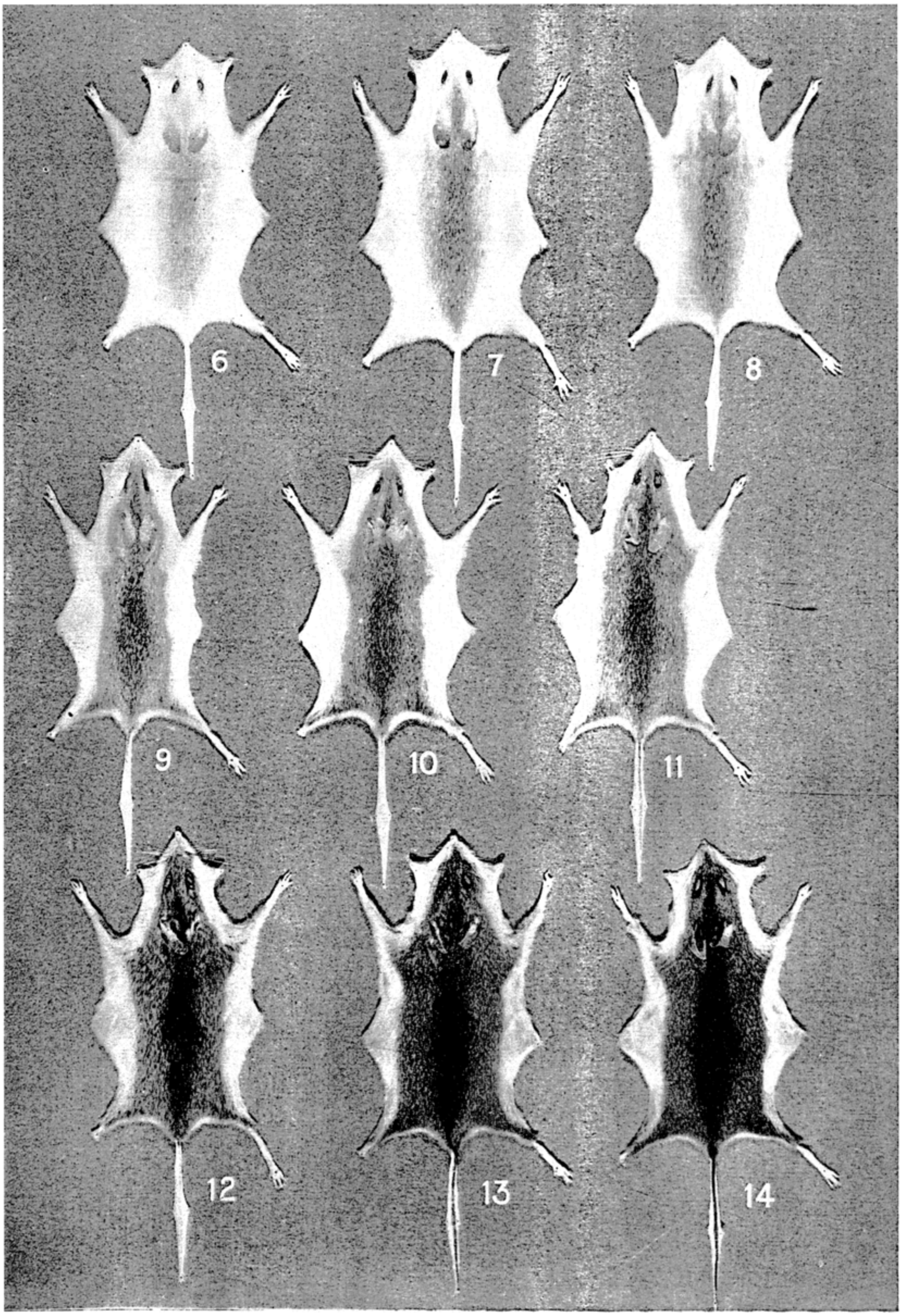
Figs. 23, 24, 25. Palest, mean and darkest specimens in F_1 generation of *leucocephalus-polionotus* cross.

Figs. 26, 27, 28. Palest, mean and darkest specimens in F_2 generation of same cross.

Fig. 29. Palest specimen in first back-cross with *leucocephalus* (3/4 *leucocephalus*).

Fig. 30. Palest specimen in second back-cross with *leucocephalus* (7/8 *leucocephalus*).

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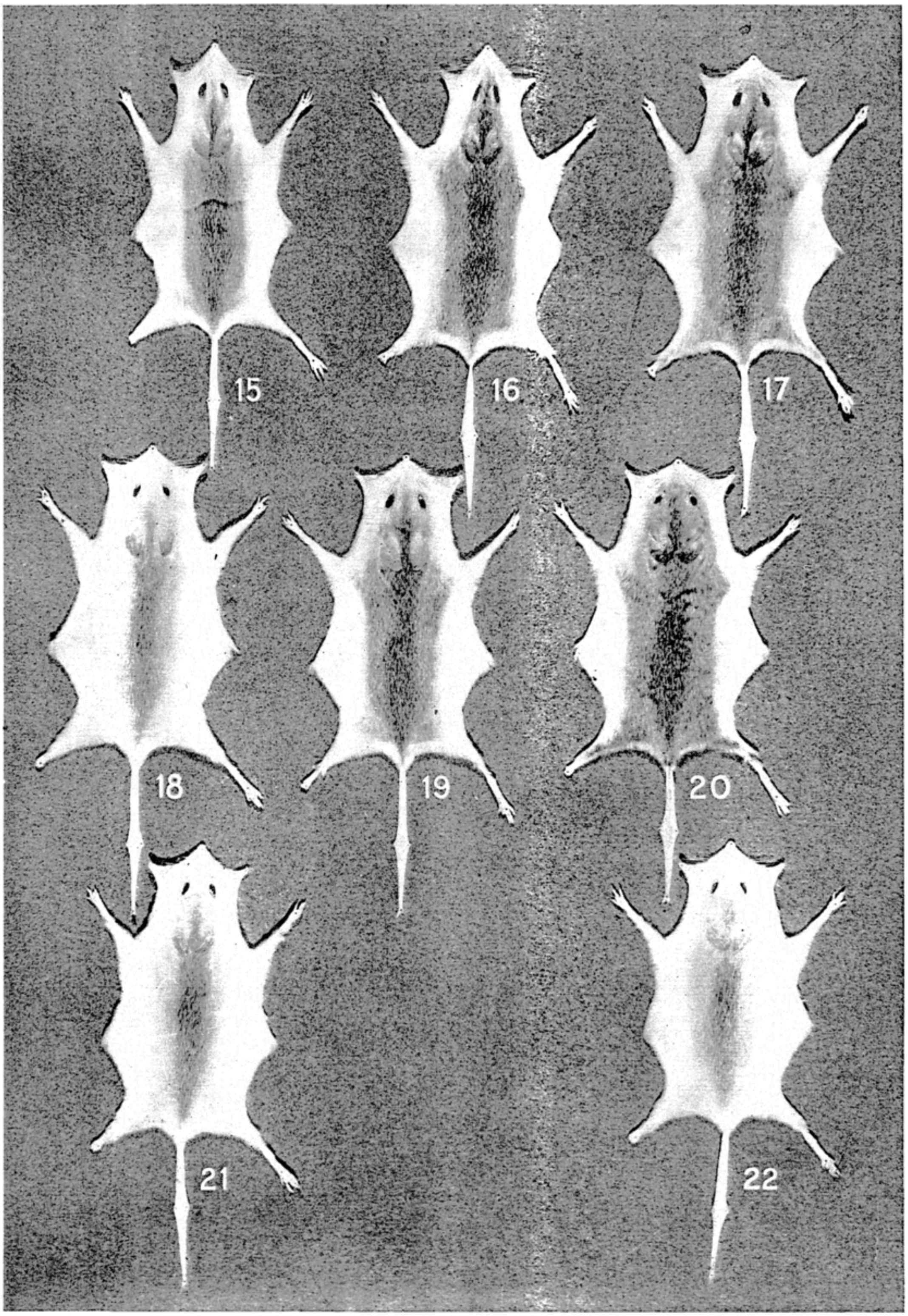
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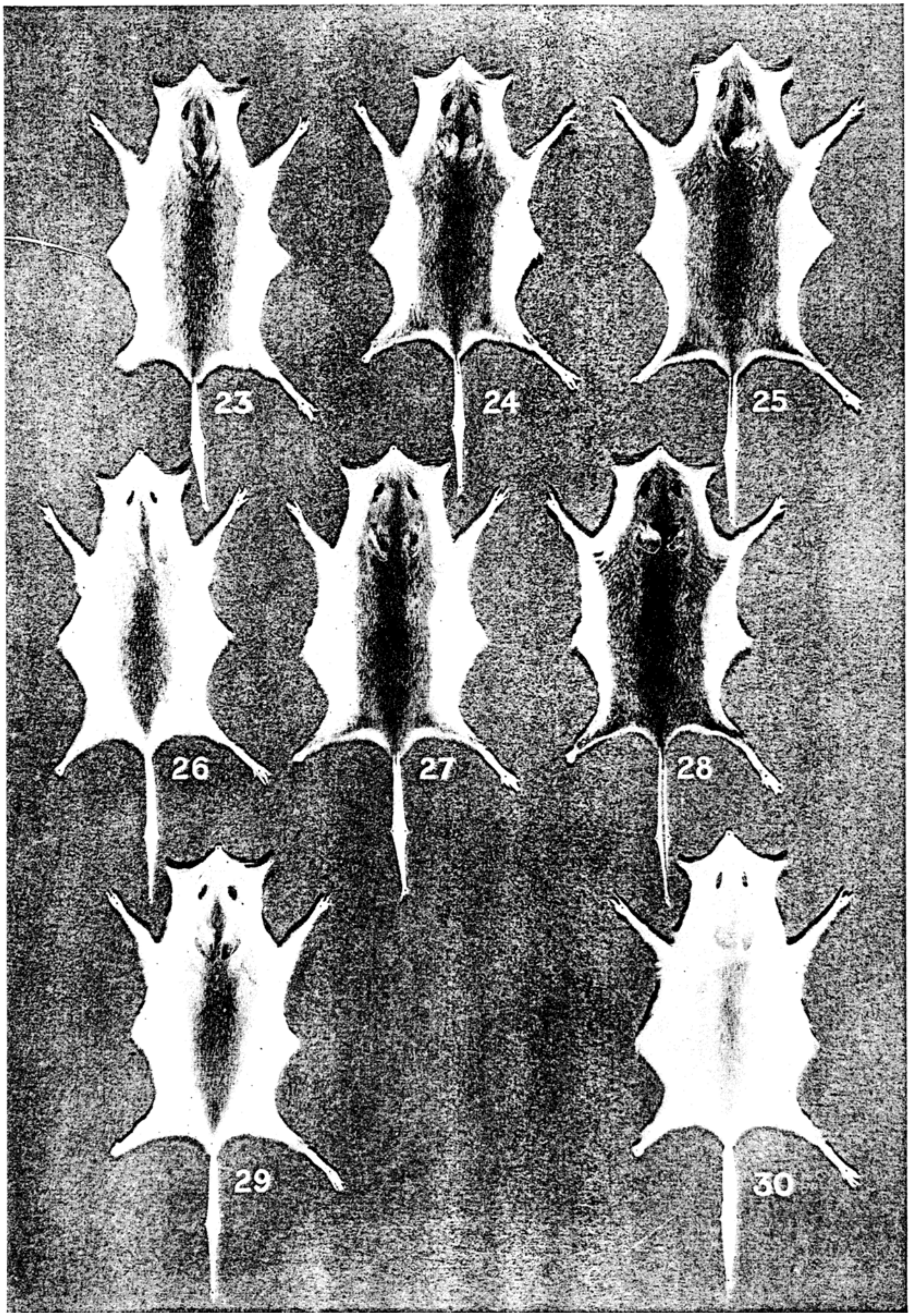
PLATE XI



TABLE

Mean values, Leucocephalus,

		Leucocephalus			*Albifrons*					F_1 (East Pass derivatives only)	
	Sex	Wild	Parents of F_1*	C_1	East Pass	Parents of F_1*	Foster's Bank	Ono Island	C_1 generation (combined)	All	Parents of F_2*
Number ...		72		46	41		21	16	50	59	
		(33♂, 39♀)		(27♂, 19♀)	(25♂, 16♀)		(16♂, 5♀)	(4♂, 12♀)	(30♂, 20♀)	(31♂, 28♀)	
Body length	♂	77·79 ±0·24	—	77·67 ±0·26	78·84 ±0·27	—	78·50	78·75	78·48 ±0·21	77·92 ±0·21	—
	♀	82·29 ±0·36	—	81·37 ±0·45	83·12 ±0·47	—	82·40	82·46	80·27 ±0·44	81·82 ±0·34	—
Tail length	Both	54·21 ±0·20	—	51·42 ±0·25	53·49 ±0·34	—	52·37	55·37	52·35 ±0·27	53·24 ±0·24	—
(actual)	♂	53·27 ±0·24	—	50·24 ±0·22	52·48 ±0·41	—	—	—	51·71 ±0·31	52·23 ±0·31	—
	♀	55·03 ±0·27	—	53·11 ±0·40	55·06 ±0·47	—	—	—	53·27 ±0·46	54·36 ±0·32	—
(corrected)†	♂	54·24	—	51·26	52·99	—	—	—	52·38	53·14	—
	♀	53·93	—	52·46	53·58	—	—	—	53·14	53·50	—
Foot length	♂	18·52 ±0·04	—	18·49 ±0·05	17·74 ±0·05	—	18·15	18·37	17·69 ±0·05	18·12 ±0·05	—
(actual)	♀	18·50 ±0·05	—	18·44 ±0·04	17·78 ±0·07	—	18·25	18·15	17·67 ±0·07	18·13 ±0·09	—
(corrected)	♂	18·70	—	18·68	17·84	—	18·21	18·43	17·82	18·29	—
	♀	18·34	—	18·34	17·56	—	18·08	17·97	17·65	18·00	—
Ear length	Both	14·50 ±0·04	—	14·04 ±0·04	14·72 ±0·06	—	14·63	14·34	14·81 ±0·06	14·47 ±0·04	—
(actual)	♂	14·27 ±0·05	—	14·01 ±0·06	14·58 ±0·07	—	—	—	14·62 ±0·07	14·45 ±0·06	—
	♀	14·68 ±0·05	—	14·08 ±0·06	14·93 ±0·08	—	—	—	15·08 ±0·10	14·50 ±0·06	—
(corrected)	♂	14·42	—	14·17	14·66	—	—	—	14·72	14·59	—
	♀	14·57	—	14·01	14·78	—	—	—	15·07	14·41	—
Weight	♂	12·72 ±0·17	—	12·64 ±0·20	13·60 ±0·19	—	—	—	12·66 ±0·19	12·80 ±0·13	—
	♀	13·00 ±0·17	—	12·54 ±0·26	12·45 ±0·17	—	—	—	11·96 ±0·26	14·03 ±0·20	—
Caudal vertebrae	Both	23·46 ±0·05	—	—	24·56 ±0·09	—	23·88	—	—	23·60 ±0·06	—
Right pelvis	♂	14·53 ±0·05	—	—	15·11 ±0·05	—	—	—	—	14·61 ±0·05	—
(actual)	♀	15·43 ±0·07	—	—	15·79 ±0·09	—	—	—	—	15·35 ±0·08	—
(corrected)	♂	14·84	—	—	15·27	—	—	—	—	14·90	—
	♀	14·99	—	—	15·19	—	—	—	—	15·00	—
Right femur	♂	14·06 ±0·04	—	—	13·99 ±0·05	—	—	—	—	13·81 ±0·04	—
(actual)	♀	14·79 ±0·06	—	—	14·82 ±0·09	—	—	—	—	14·51 ±0·07	—
(corrected)	♂	14·34	—	—	14·14	—	—	—	—	14·08	—
	♀	14·36	—	—	14·23	—	—	—	—	14·17	—
Skull length	♂	22·88 ±0·05	—	—	22·63 ±0·05	—	—	—	—	22·61 ±0·06	—
(actual)	♀	23·21 ±0·05	—	—	22·89 ±0·07	—	—	—	—	23·03 ±0·07	—
(corrected)	♂	23·24	—	—	22·82	—	—	—	—	22·94	—
	♀	22·88	—	—	22·44	—	—	—	—	22·77	—
Skull breadth	♂	10·01 ±0·02	—	—	10·05 ±0·03	—	—	—	—	9·99 ±0·02	—
(actual)	♀	10·03 ±0·02	—	—	9·99 ±0·02	—	—	—	—	10·12 ±0·02	—
Tail stripe	Both	0	—	0	41·73	40·74	0·81	38·37	31·31	3·81	4·29
Foot pigment	Both	0	—	0	0·07	—	0	0·29	—	0·23	—
Coloured area	Both	45·54 ±0·32	43·66	43·80 ±0·34	66·46 ±0·33	67·12	56·80	72·87	61·74 ±0·59	56·24 ±0·26	56·04
(base)	♂	45·21 ±0·46	—	42·96 ±0·42	66·39 ±0·42	—	—	—	61·90 ±0·83	56·09 ±0·38	—
	♀	45·81 ±0·44	—	44·81 ±0·52	66·56 ±0·53	—	—	—	61·50 ±0·76	56·41 ±0·34	—
Coloured area	Both	—	—	—	59·79 ±0·54	60·51	47·95	65·47	—	—	—
(tips)	♂	—	—	—	59·56 ±0·71	—	—	—	—	—	—
	♀	—	—	—	60·12 ±0·82	—	—	—	—	—	—
Red	Both	25·40 ±0·30	26·03	27·66 ±0·42	17·17 ±0·15	16·84	15·07	14·51	16·99 ±0·13	19·32 ±0·13	19·14
	♂	26·05 ±0·45	—	28·01 ±0·57	17·39 ±0·17	—	—	—	17·15 ±0·18	19·74 ±0·18	—
	♀	24·90 ±0·39	—	27·26 ±0·61	16·86 ±0·26	—	—	—	16·75 ±0·17	18·85 ±0·15	—
$\frac{A_b}{R}$	Both	1·82 ±0·02	1·71	1·63 ±0·03	3·90 ±0·03	3·95	3·81	5·05	3·66 ±0·05	2·93 ±0·03	2·93
$\frac{R-V}{R}$	Both	27·66 ±0·41	23·84	25·96 ±0·50	42·02 ±0·54	39·04	37·60	30·73	36·22 ±0·57	35·90 ±0·37	33·97

* Weighted by number of offspring.

I.

Albifrons *and hybrids.*

F_2 (East Pass derivatives only) 75 (35♂, 40♀)	Back-cross		Grades 7/8 *leucocephalus* (East Pass derivatives only) 41 (19♂, 22♀)	Selected parents of F_3 (weighted by number of offspring)			F_3			
	3/4 *leucocephalus* (East Pass derivatives only) 58 (35♂, 23♀)	3/4 *albifrons*		Pale	Medium	Dark	All 65 (41♂, 24♀)	Pale 17 (12♂, 5♀)	Medium 27 (17♂, 10♀)	Dark 21 (12♂, 9♀)
78·11 ±0·24	78·69 ±0·19	—	77·47 ±0·32	—	—	—	78·48 ±0·16	78·25	78·32	78·92
81·11 ±0·26	80·83 ±0·28	—	78·77 ±0·18	—	—	—	81·46 ±0·21	81·60	81·65	81·17
53·09 ±0·21	52·35 ±0·22	52·93	52·54 ±0·16	—	—	—	53·73 ±0·15	53·50	52·91	54·98
52·69 ±0·26	51·89 ±0·27	—	51·97 ±0·26	—	—	—	53·39 ±0·18	53·50	52·59	54·42
53·44 ±0·32	53·06 ±0·34	—	53·02 ±0·18	—	—	—	54·31 ±0·25	53·50	53·45	55·72
53·52	52·47	—	53·08	—	—	—	54·06	—	—	—
52·91	52·67	—	53·60	—	—	—	53·62	—	—	—
18·28 ±0·05	18·42 ±0·04	18·01	18·42 ±0·05	—	—	—	18·37 ±0·04	18·54	18·27	18·35
18·00 ±0·05	18·23 ±0·06	17·80	18·27 ±0·05	—	—	—	18·19 ±0·04	18·48	18·12	18·11
18·43	18·53	—	18·63	—	—	—	18·50	—	—	—
17·93	18·17	—	18·36	—	—	—	18·09	—	—	—
14·41 ±0·03	14·35 ±0·03	14·42	14·20 ±0·04	—	—	—	14·48 ±0·04	—	—	—
14·43 ±0·05	14·41 ±0·04	—	14·20 ±0·05	—	—	—	14·50 ±0·05	—	—	—
14·39 ±0·04	14·27 ±0·05	—	14·20 ±0·07	—	—	—	14·47 ±0·07	—	—	—
14·56	14·50	—	14·37	—	—	—	14·60	—	—	—
14·33	14·23	—	14·26	—	—	—	14·40	—	—	—
12·73 ±0·15	13·10 ±0·17	—	12·40 ±0·23	—	—	—	12·67 ±0·18	11·37	12·91	13·63
13·32 ±0·16	12·49 ±0·15	—	12·18 ±0·19	—	—	—	12·67 ±0·17	12·14	12·57	13·09
23·67 ±0·07	—	—	—	—	—	—	—	—	—	—
14·49 ±0·05	—	—	—	—	—	—	—	—	—	—
15·16 ±0·06	—	—	—	—	—	—	—	—	—	—
14·75		—	—	—	—	—	—	—	—	—
14·95	—	—	—	—	—	—	—	—	—	—
13·74 ±0·05	—	—	—	—	—	—	—	—	—	—
14·29 ±0·06	—	—	—	—	—	—	—	—	—	
13·98	—	—	—	—	—	—	—	—	—	—
14·08	—	—	—	—	—	—	—	—	—	—
22·70 ±0·05	—	—	—	—	—	—	—	—	—	—
22·86 ±0·05	—	—	—	—	—	—	—	—	—	—
23·00	—	—	—	—	—	—	—	—	—	—
22·70	—	—	—	—	—	—	—	—	—	—
9·98 ±0·02	—	—	—	—	—	—	—	—	—	—
10·03 ±0·02	—	—	—	—	—	—	—	—	—	—
9·33	1·22	14·33	0·05	0	2·33	42·31	21·23	0·82	8·48	54·14
0·28	0·22	0·80	0·12	—	—	—	0·15	—	—	—
57·18 ±0·45	51·64 ±0·41	61·27	48·00 ±0·45	46·91	55·80	63·02	56·62 ±0·61	47·82	56·81	63·48
57·11 ±0·56	51·51 ±0·59	—	48·21 ±0·57	—	—	—	55·95 ±0·78	47·67	57·06	62·67
57·23 ±0·70	51·83 ±0·52	—	47·82 ±0·68	—	—	—	57·75 ±0·99	48·20	56·40	64·56
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
20·66 ±0·20	23·40 ±0·26	19·07	25·17 ±0·33	24·70	20·63	16·73	20·95 ±0·28	24·66	20·67	18·31
20·93 ±0·26	23·60 ±0·34	—	24·98 ±0·45	—	—	—	21·48 ±0·37	25·16	21·01	18·46
20·41 ±0·31	23·10 ±0·42	—	25·34 ±0·47	—	—	—	20·06 ±0·37	23·48	20·11	18·11
2·82 ±0·04	2·25 ±0·04	—	1·93 ±0·03	1·96	2·71	3·78	2·80 ±0·06	2·01	2·78	3·50
35·94 ±0·47	33·60 ±0·39	38·53	30·85 ±0·53	40·24	35·06	29·74	33·58 ±0·55	40·94	31·59	30·19

† "Corrected" means are the "actual" ones, reduced to a standard body length of 80 mm.

TABLE

Mean values, Leucocephalus,

		Leucocephalus		*Polionotus*			F_1			Back-cross	
	Sex	Wild (all)	Parents of F_1*	Wild (all)	Parents of F_1*	C_1	All	Parents of F_2*	F_2 All	3/4 *leucocephalus*	3/4 *polionotus*
Number ...		72 (33♂, 39♀)		46 (27♂, 19♀)		60 (39♂, 21♀)	74 (39♂, 35♀)		109 (56♂, 53♀)	67 (31♂, 36♀)	16 (10♂, 6♀)
Body length	♂	77·79 ±0·24	—	78·59 ±0·23	—	79·63 ±0·22	78·05 ±0·19	—	78·77 ±0·21	78·97 ±0·28	79·85
	♀	82·29 ±0·36	—	83·18 ±0·58	—	83·83 ±0·44	83·33 ±0·35	—	81·42 ±0·27	81·71 ±0·33	81·00
Tail length	Both	54·21 ±0·20	—	51·33 ±0·32	—	51·64 ±0·23	52·43 ±0·23	—	52·84 ±0·18	53·49 ±0·18	51·93
(actual)	♂	53·27 ±0·24	—	49·98 ±0·31	—	50·71 ±0·24	51·04 ±0·25	—	52·11 ±0·22	53·13 ±0·24	51·80
	♀	55·03 ±0·27	—	53·28 ±0·49	—	53·31 ±0·39	53·97 ±0·32	—	53·61 ±0·28	53·81 ±0·25	52·20
(corrected)†	♂	54·24	—	50·60	—	50·87	51·90	—	52·65	53·58	—
	♀	53·93	—	51·77	—	51·50	52·39	—	52·94	53·00	—
Foot length	♂	18·52 ±0·04	—	17·31 ±0·06	—	17·33 ±0·04	17·95 ±0·05	—	18·33 ±0·05	18·46 ±0·05	18·25
(actual)	♀	18·50 ±0·05	—	17·25 ±0·08	—	17·55 ±0·07	17·94 ±0·07	—	18·06 ±0·05	18·32 ±0·04	18·11
(corrected)	♂	18·70	—	17·42	—	17·36	18·11	—	18·43	18·55	—
	♀	18·34	—	17·03	—	17·28	17·70	—	17·96	18·20	—
Ear length	Both	14·50 ±0·04	—	15·01 ±0·07	—	14·99 ±0·04	14·61 ±0·04	—	14·67 ±0·03	14·53 ±0·03	15·07
(actual)	♂	14·27 ±0·05	—	14·93 ±0·09	—	14·92 ±0·05	14·60 ±0·05	—	14·72 ±0·05	14·41 ±0·04	15·05
	♀	14·68 ±0·05	—	15·12 ±0·10	—	15·13 ±0·07	14·63 ±0·05	—	14·60 ±0·05	14·63 ±0·04	15·09
(corrected)	♂	14·42	—	15·02	—	14·94	14·73	—	14·80	14·48	—
	♀	14·57	—	14·97	—	14·94	14·46	—	14·54	14·54	—
Weight	♂	12·72 ±0·17	—	12·33 ±0·18	—	12·20 ±0·20	12·21 ±0·18	—	13·19 ±0·16	13·32 ±0·21	—
	♀	13·00 ±0·17	—	13·61 ±0·38	—	14·15 ±0·43	14·05 ±0·25	—	13·33 ±0·16	13·16 ±0·20	—
Caudal vertebrae	Both	23·46 ±0·05	—	23·77 ±0·08	—	—	23·51 ±0·05	—	23·86 ±0·05	—	—
Right pelvis	♂	14·53 ±0·05	—	14·89 ±0·07	—	—	14·57 ±0·04	—	14·76 ±0·05	—	—
(actual)	♀	15·43 ±0·07	—	15·65 ±0·09	—	—	15·41 ±0·08	—	15·28 ±0·06	—	—
(corrected)	♂	14·84	—	15·09	—	—	14·84	—	14·93	—	—
	♀	14·99	—	15·04	—	—	14·77	—	15·01	—	—
Right femur	♂	14·06 ±0·04	—	13·43 ±0·07	—	—	13·64 ±0·04	—	13·76 ±0·04	—	—
(actual)	♀	14·79 ±0·06	—	14·18 ±0·12	—	—	14·27 ±0·10	—	14·28 ±0·05	—	—
(corrected)	♂	14·34	—	13·61	—	—	13·89	—	13·92	—	—
	♀	14·36	—	13·58	—	—	13·64	—	14·01	—	—
Skull length	♂	22·88 ±0·05	—	22·70 ±0·06	—	—	22·79 ±0·05	—	22·87 ±0·05	—	—
(actual)	♀	23·21 ±0·05	—	23·04 ±0·10	—	—	23·13 ±0·07	—	23·03 ±0·07	—	—
(corrected)	♂	23·24	—	22·93	—	—	23·10	—	23·07	—	—
	♀	22·88	—	22·58	—	—	22·65	—	22·82	—	—
Skull breadth	♂	10·01 ±0·02	—	9·91 ±0·03	—	—	9·98 ±0·02	—	10·04 ±0·02	—	—
(actual)	♀	10·03 ±0·02	—	9·97 ±0·05	—	—	10·05 ±0·02	—	10·02 ±0·02	—	—
Tail stripe	Both	0	—	100·00	—	—	18·29	18·81	26·05	2·04	45·19
Foot pigment	Both	0	—	1·47 ±0·08	—	1·97 ±0·07	1·06 ±0·07	—	0·83 ±0·05	0·48 ±0·05	1·75
Coloured area	Both	45·54 ±0·32	44·99	—	—	—	68·33 ±0·50	65·95	69·12 ±0·90	55·05 ±0·50	—
(base)	♂	45·21 ±0·46	—	—	—	—	67·42 ±0·68	—	66·45 ±1·20	53·77 ±0·59	—
	♀	45·81 ±0·44	—	—	—	—	69·33 ±0·73	—	71·89 ±1·30	56·17 ±0·77	—
Coloured area	Both	—	—	73·96 ±0·39	72·99	72·00 ±0·42	54·46 ±0·38	53·09	54·34 ±0·59	—	58·07
(tips)	♂	—	—	74·67 ±0·49	—	71·95 ±0·52	54·82	—	53·11 ±0·81	—	—
	♀	—	—	72·95 ±0·60	—	72·09 ±0·68	54·06	—	55·62 ±0·83	—	—
Red	Both	25·40 ±0·30	26·00	9·55 ±0·11	9·74	10·67 ±0·12	14·44 ±0·11	14·49	14·76 ±0·13	18·85 ±0·18	13·12
	♂	26·05 ±0·45	—	9·62 ±0·14	—	10·59 ±0·15	14·38 ±0·15	—	15·00 ±0·19	19·07 ±0·22	—
	♀	24·90 ±0·39	—	9·44 ±0·16	—	10·80 ±0·18	14·51 ±0·17	—	14·67 ±0·19	18·67 ±0·28	—
$\frac{A_b}{R}$	Both	1·82 ±0·02	1·77	—	—	—	4·79 ±0·05	—	4·88 ±0·10	2·98 ±0·05	—
$\frac{A_t}{R}$	Both	—	—	7·86 ±0·11	7·69	6·89 ±0·10	3·83 ±0·05	3·73	3·82 ±0·07	—	—
$\frac{R-V}{R}$	Both	27·66 ±0·41	25·89	35·18 ±0·39	34·51	31·03 ±0·46	34·38 ±0·35	33·84	32·42 ±0·40	34·09 ±0·43	36·14

* Weighted by number of offspring.

II.

Polionotus *and hybrids.*

Grades 7/8 *leucocephalus* 55 (35♂, 20♀)	Selected parents of F_3*			F_3				*Polionotus-albifrons* cross		
	Pale	Medium	Dark	All 82 (48♂, 34♀)	Pale 29	Medium 31	Dark 22	F_1 95 (57♂, 38♀)	Back-cross	
									3/4 *polionotus* 76 (38♂, 38♀)	3/4 *albifrons* 51 (21♂, 30♀)
78·17 ± 0·20	—	—	—	78·86 ± 0·23	—	—	—	79·18 ± 0·19	79·76 ± 0·24	80·10 ± 0·30
80·75 ± 0·34	—	—	—	81·49 ± 0·32	—	—	—	82·64 ± 0·28	81·00 ± 0·26	80·97 ± 0·27
53·50 ± 0·21	—	—	—	53·10 ± 0·19	53·83	52·62	52·80	53·44 ± 0·16	52·89 ± 0·21	53·96 ± 0·22
53·51 ± 0·25	—	—	—	53·02 ± 0·24	—	—	—	52·74 ± 0·20	52·74 ± 0·32	53·24 ± 0·30
53·47 ± 0·37	—	—	—	53·21 ± 0·29	—	—	—	54·53 ± 0·22	53·04 ± 0·27	54·47 ± 0·31
54·31	—	—	—	53·52	—	—	—	53·10	52·85	53·20
53·11	—	—	—	52·50	—	—	—	53·28	52·57	54·01
18·61 ± 0·04	—	—	—	18·31 ± 0·05	18·56	18·13	18·14	18·14 ± 0·04	17·89 ± 0·05	18·06 ± 0·07
18·34 ± 0·06	—	—	—	18·11 ± 0·08	18·77	17·79	18·06	18·10 ± 0·05	17·79 ± 0·05	18·10 ± 0·05
18·76	—	—	—	18·41	18·65	18·17	18·30	18·21	17·91	18·05
18·29	—	—	—	18·01	18·55	17·71	18·02	17·91	17·72	18·03
14·33 ± 0·03	—	—	—	14·67 ± 0·03	14·81	14·55	14·65	15·10 ± 0·03	15·20 ± 0·03	14·98 ± 0·05
14·32 ± 0·04	—	—	—	14·69 ± 0·04	—	—	—	15·02 ± 0·05	15·18 ± 0·05	14·99 ± 0·08
14·35 ± 0·04	—	—	—	14·64 ± 0·05	—	—	—	15·20 ± 0·05	15·21 ± 0·05	14·97 ± 0·06
14·45	—	—	—	14·77	—	—	—	15·08	15·20	14·98
14·31	—	—	—	14·56	—	—	—	15·07	15·16	14·93
12·31 ± 0·15	—	—	—	13·15 ± 0·19	—	—	—	12·22 ± 0·14	12·72 ± 0·12	13·57 ± 0·21
12·15 ± 0·25	—	—	—	13·06 ± 0·21	—	—	—	12·96 ± 0·15	12·42 ± 0·20	12·48 ± 0·16
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—
1·49	0·60	17·45	100·00	35·05	1·62	25·72	92·68	63·95	85·45	44·04
0·31	—	—	—	0·64 ± 0·05	—	—	—	1·44 ± 0·05	1·75 ± 0·05	0·98 ± 0·07
46·85 ± 0·58	48·57	68·69	90·07	68·00 ± 1·29	49·14	70·45	89·41	—	—	—
46·20 ± 0·75	—	—	—	68·21 ± 1·77	—	—	—	—	—	—
48·00 ± 0·89	—	—	—	67·71 ± 1·84	—	—	—	—	—	—
—	36·71	55·37	67·82	53·26 ± 0·95	38·62	56·77	67·59	62·61 ± 0·39	66·23 ± 0·43	59·32 ± 0·64
—	—	—	—	53·15 ± 1·30	—	—	—	62·82 ± 0·50	64·72 ± 0·56	58·65 ± 0·99
—	—	—	—	53·41 ± 1·35	—	—	—	62·29 ± 0·64	67·77 ± 0·60	59·77 ± 0·84
22·32 ± 0·30	17·55	13·93	11·98	15·46 ± 0·24	18·95	14·50	12·22	13·65 ± 0·11	11·59 ± 0·12	15·27 ± 0·15
22·53 ± 0·42	—	—	—	15·56 ± 0·30	—	—	—	13·60 ± 0·14	11·83 ± 0·16	15·42 ± 0·21
21·96 ± 0·38	—	—	—	15·33 ± 0·39	—	—	—	13·72 ± 0·18	11·34 ± 0·16	15·16 ± 0·21
2·16 ± 0·05	2·80	5·01	7·56	4·79 ± 0·15	—	—	—	—	—	—
—	—	—	—	—	—	—	—	4·68 ± 0·06	5·85 ± 0·09	3·94 ± 0·07
27·69 ± 0·39	36·03	29·60	30·41	34·34 ± 0·48	39·24	31·71	31·59	35·30 ± 0·34	34·73 ± 0·40	39·40 ± 0·48

† "Corrected" means are the "actual" ones, reduced to a standard body length of 80 mm.

TABLE III.

Standard deviations—Leucocephalus, Albifrons *and hybrids.*

		Leucocephalus		*Albifrons*						
	Sex	Wild	C_1	East Pass	C_1 generation (combined)	F_1 (East Pass derivatives only)	F_2 (East Pass derivatives only)	Back-cross 3/4 *Leucocephalus*	Grades 7/8 *Leucocephalus*	F_3
Number ...		72	46	41	50	59	75	58	41	65
		(33 ♂, 39 ♀)	(27 ♂, 19 ♀)	(25 ♂, 16 ♀)	(30 ♂, 20 ♀)	(31 ♂, 28 ♀)	(35 ♂, 40 ♀)	(35 ♂, 23 ♀)	(19 ♂, 22 ♀)	(41 ♂, 24 ♀)
Body length	♂	2·08 ±0·17	2·00 ±0·18	2·01 ±0·19	1·71 ±0·15	1·75 ±0·15	2·14 ±0·17	1·65 ±0·13	2·09 ±0·23	1·51 ±0·11
	♀	3·37 ±0·26	2·90 ±0·32	2·80 ±0·33	2·93 ±0·31	2·69 ±0·24	2·44 ±0·18	1·97 ±0·20	1·25 ±0·13	1·52 ±0·15
Tail length	Both	2·49 ±0·14	2·54 ±0·18	3·20 ±0·24	2·85 ±0·19	2·73 ±0·17	2·68 ±0·15	2·44 ±0·15	1·54 ±0·11	1·81 ±0·11
(actual)	♂	2·08 ±0·17	1·68 ±0·15	3·02 ±0·29	2·48 ±0·22	2·53 ±0·22	2·24 ±0·18	2·33 ±0·19	1·67 ±0·18	1·73 ±0·13
	♀	2·53 ±0·19	2·60 ±0·28	2·82 ±0·34	3·08 ±0·33	2·50 ±0·23	2·96 ±0·22	2·44 ±0·24	1·23 ±0·13	1·80 ±0·18
(corrected)*	♂	1·91	1·54	2·78	2·28	2·33	2·06	2·14	1·54	1·59
	♀	2·20	2·26	2·45	2·67	2·17	2·57	2·12	1·07	1·57
Foot length	♂	0·36 ±0·03	0·42 ±0·04	0·38 ±0·04	0·41 ±0·04	0·41 ±0·04	0·40 ±0·03	0·40 ±0·03	0·32 ±0·03	0·41 ±0·03
(actual)	♀	0·47 ±0·04	0·24 ±0·03	0·41 ±0·05	0·46 ±0·05	0·68 ±0·06	0·43 ±0·03	0·40 ±0·04	0·33 ±0·03	0·30 ±0·03
(corrected)	♂	0·33	0·38	0·35	0·38	0·38	0·37	0·37	0·30	0·38
	♀	0·43	0·22	0·38	0·42	0·62	0·39	0·37	0·30	0·28
Ear length	Both	0·48 ±0·03	0·44 ±0·03	0·54 ±0·04	0·64 ±0·04	0·46 ±0·03	0·41 ±0·02	0·38 ±0·02	0·42 ±0·03	0·47 ±0·03
(actual)	♂	0·41 ±0·03	0·47 ±0·04	0·53 ±0·05	0·57 ±0·05	0·47 ±0·04	0·43 ±0·03	0·39 ±0·03	0·35 ±0·04	0·45 ±0·03
	♀	0·45 ±0·03	0·40 ±0·04	0·50 ±0·06	0·64 ±0·07	0·45 ±0·04	0·39 ±0·03	0·34 ±0·03	0·48 ±0·05	0·51 ±0·05
(corrected)	♂	0·39	0·45	0·51	0·55	0·45	0·41	0·38	0·33	0·43
	♀	0·43	0·39	0·48	0·61	0·43	0·38	0·32	0·46	0·49
Weight	♂	1·45 ±0·12	1·57 ±0·14	1·41 ±0·13	1·55 ±0·13	1·10 ±0·09	1·35 ±0·11	1·48 ±0·12	1·51 ±0·17	1·69 ±0·13
	♀	1·58 ±0·12	1·71 ±0·19	1·00 ±0·12	1·69 ±0·18	1·56 ±0·14	1·54 ±0·12	1·10 ±0·11	1·32 ±0·13	1·25 ±0·12
Caudal vertebrae	Both	0·64 ±0·04	—	0·90 ±0·07	—	0·72 ±0·04	0·84 ±0·05	—	—	—
Right pelvis	♂	0·40 ±0·03	—	0·39 ±0·04	—	0·42 ±0·04	0·43 ±0·03	—	—	—
(actual)	♀	0·67 ±0·05	—	0·53 ±0·06	—	0·61 ±0·06	0·53 ±0·04	—	—	—
(corrected)	♂	0·31	—	0·30	—	0·32	0·33	—	—	—
	♀	0·40	—	0·32	—	0·37	0·32	—	—	—
Right femur	♂	0·36 ±0·03	—	0·36 ±0·03	—	0·31 ±0·03	0·45 ±0·04	—	—	—
(actual)	♀	0·51 ±0·04	—	0·56 ±0·07	—	0·53 ±0·05	0·56 ±0·04	—	—	—
(corrected)	♂	0·28	—	0·28	—	0·24	0·35	—	—	—
	♀	0·31	—	0·34	—	0·32	0·34	—	—	—
Skull length	♂	0·40 ±0·03	—	0·41 ±0·04	—	0·52 ±0·04	0·48 ±0·04	—	—	—
(actual)	♀	0·46 ±0·04	—	0·45 ±0·05	—	0·57 ±0·05	0·51 ±0·04	—	—	—
(corrected)	♂	0·28	—	0·29	—	0·37	0·34	—	—	—
	♀	0·35	—	0·34	—	0·43	0·39	—	—	—
Skull breadth	♂	0·19 ±0·02	—	0·21 ±0·02	—	0·18 ±0·02	0·21 ±0·02	—	—	—
(actual)	♀	0·18 ±0·01	—	0·14 ±0·02	—	0·17 ±0·02	0·18 ±0·01	—	—	—
Tail stripe	Both	—	—	30·13	36·08	5·65	16·22	4·33	—	31·79
Foot pigment	Both	—	—	—	—	—	—	—	—	—
Coloured area	Both	3·81 ±0·23	3·44 ±0·25	3·05 ±0·23	5·96 ±0·41	3·04 ±0·18	5·75 ±0·32	4·65 ±0·29	4·27 ±0·32	7·29 ±0·43
(base)	♂	3·59 ±0·32	3·13 ±0·30	3·02 ±0·30	6·60 ±0·58	3·27 ±0·27	4·88 ±0·39	5·17 ±0·42	3·66 ±0·40	7·36 ±0·55
	♀	3·94 ±0·31	3·51 ±0·37	3·14 ±0·37	4·74 ±0·53	2·74 ±0·24	6·43 ±0·49	3·71 ±0·37	4·72 ±0·48	7·19 ±0·70
Coloured area	Both	—	—	5·00 ±0·38	—	—	—	—	—	—
(tips)	♂	—	—	5·07 ±0·50	—	—	—	—	—	—
	♀	—	—	4·87 ±0·58	—	—	—	—	—	—
Red	Both	3·53 ±0·21	4·18 ±0·30	1·37 ±0·10	1·31 ±0·09	1·50 ±0·09	2·61 ±0·14	2·99 ±0·19	3·14 ±0·23	3·29 ±0·19
	♂	3·50 ±0·32	4·18 ±0·41	1·20 ±0·12	1·42 ±0·13	1·55 ±0·13	2·29 ±0·18	2·96 ±0·24	2·94 ±0·32	3·49 ±0·26
	♀	3·46 ±0·28	4·13 ±0·43	1·54 ±0·18	1·08 ±0·12	1·19 ±0·11	2·84 ±0·22	2·99 ±0·30	3·28 ±0·33	2·69 ±0·26
$\frac{A_b}{R}$	Both	0·29 ±0·02	0·30 ±0·02	0·31 ±0·02	0·48 ±0·03	0·31 ±0·02	0·55 ±0·03	0·43 ±0·03	0·29 ±0·02	0·70 ±0·04
$\frac{R-V}{R}$	Both	4·82 ±0·29	4·93 ±0·35	5·09 ±0·38	5·73 ±0·40	4·33 ±0·26	6·02 ±0·33	4·48 ±0·28	5·07 ±0·38	6·54 ±0·39

* Standard deviations for certain body parts have been "corrected" by the elimination of that part of the total variation which is due to variation in general body size. This is effected by multiplying the gross standard deviation by $\sqrt{1-r^2}$, r being the coefficient of correlation between body length and the character in question.

TABLE V

Correlations between various characters.

	Sex	*Leucocephalus* Wild		*Leucocephalus* C_1		*Albifrons* East Pass		*Polionotus* Wild		*Polionotus* C_1	
		Gross	Net*	Gross	Net	Gross	Net	Gross	Net	Gross	Net
Tail—Foot	♂	+·455 ±·093	−·356	+·388 ±·110	+·278	+·388 ±·115	+·279	+·765 ±·054	+·721	+·292 ±·099	+·165
	♀	+·597 ±·070	+·502	+·384 ±·132	+·236	+·813 ±·057	+·772	+·780 ±·061	+·731	−·604 ±·094	+·511
Tail—Ear	Both	+·404 ±·066	+·314	+·364 ±·085	+·265	+·400 ±·089	+·309	+·442 ±·080	+·360	−·329 ±·080	+·222
Tail—Tail stripe	Both	—	—	—	—	−·225 ±·100	—	—	—	—	—
Tail—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—
Tail—Coloured area, base	Both	+·239 ±·075	—	+·081 ±·099	—	−·317 ±·095	—	—	—	—	—
Tail—Coloured area, tips	Both	—	—	—	—	—	—	−·260 ±·093	—	−·052 ±·057	—
Tail—Red	Both	−·014 ±·079	—	−·085 ±·099	—	+·203 ±·101	—	+·134 ±·098	—	+·190 ±·084	—
Foot—Ear	♂	+·131 ±·126	+·020	−·277 ±·120	+·186	+·213 ±·129	+·113	+·450 ±·103	+·383	−·336 ±·096	+·253
	♀	+·405 ±·090	+·332	+·111 ±·153	−·002	+·556 ±·117	+·503	+·456 ±·123	+·390	−·357 ±·131	+·278
Foot—Tail stripe	♂	—	—	—	—	−·291 ±·123	—	—	—	—	—
	♀	—	—	—	—	+·039 ±·168	—	—	—	—	—
Foot—Coloured area, base	♂	−·023 ±·118	—	+·043 ±·129	—	−·131 ±·133	—	—	—	—	—
	♀	+·290 ±·099	—	−·377 ±·133	—	−·140 ±·155	—	—	—	—	—
Foot—Coloured area, tips	♂	—	—	—	—	—	—	−·167 ±·126	—	+·040 ±·108	—
	♀	—	—	—	—	—	—	−·120 ±·153	—	+·265 ±·137	—
Foot—Red	♂	+·175 ±·114	—	−·042 ±·129	—	+·441 ±·109	—	+·240 ±·122	—	+·149 ±·106	—
	♀	−·245 ±·102	—	−·336 ±·137	—	−·110 ±·166	—	+·366 ±·134	—	−·007 ±·147	—
Foot—Foot pigment	♂	—	—	—	—	—	—	—	—	—	—
	♀	—	—	—	—	—	—	—	—	—	—
Tail stripe—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—
Tail stripe—Coloured area, base	Both	—	—	—	—	+·464 ±·083	—	—	—	—	—
Tail stripe—Coloured area, tips	Both	—	—	—	—	—	—	—	—	—	—
Tail stripe—Red	Both	—	—	—	—	−·586 ±·069	—	—	—	—	—
Foot pigm.—Coloured area, base	Both	—	—	—	—	—	—	—	—	—	—
Foot pigm.—Coloured area, tips	Both	—	—	—	—	—	—	+·168 ±·097	—	—	—
Foot pigm.—Red	Both	—	—	—	—	—	—	—	—	—	—
Coloured area, base—Red	Both	−·310 ±·072	—	−·191 ±·096	—	−·373 ±·091	—	—	—	—	—
Coloured area, tips—Red	Both	—	—	—	—	−·446 ±·084	—	−·426 ±·081	—	−·615 ±·054	—
Coloured area, base—$\frac{R-V}{R}$	Both	+·418 ±·069	—	+·119 ±·098	—	−·220 ±·100	—	—	—	—	—
Coloured area, tips—$\frac{R-V}{R}$	Both	—	—	—	—	—	—	−·158 ±·097	—	−·647 ±·051	—
Coloured area, base-tips	Both	—	—	—	—	+·637 ±·063	—	—	—	—	—
Red—$\frac{R-V}{R}$	Both	−·309 ±·076	—	−·310 ±·090	—	−·546 ±·074	—	+·250 ±·094	—	−·803 ±·031	—

	Sex	*Leuc.-alb. F_1*		*Leuc.-alb. F_2*		*3/4 leuc.*		*7/8 leuc.*		*Leuc.-alb. F_3*	
		Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net
Tail—Foot	♂	+·731 ±·056	+·681	+·533 ±·082	+·448	−·412 ±·093	+·307	+·120 ±·15	−·038	+·282 ±·081	+·355
	♀	+·551 ±·089	+·445	+·251 ±·100	+·070	−·294 ±·128	+·124	+·027 ±·14	−·210	+·125 ±·135	−·087
Tail—Ear	Both	+·165 ±·085	+·022	+·152 ±·076	+·005	+·186 ±·056	+·048	+·512 ±·07	+·445	+·403 ±·070	+·312
Tail—Tail stripe	Both	−·009 ±·088	—	−·052 ±·078	—	−·130 ±·087	—	—	—	+·350 ±·073	—
Tail—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—
Tail—Coloured area, base	Both	+·095 ±·087	—	−·098 ±·077	—	−·161 ±·086	—	−·008 ±·10	—	+·195 ±·080	—
Tail—Coloured area, tips	Both	—	—	—	—	—	—	—	—	—	—
Tail—Red	Both	−·180 ±·085	—	−·059 ±·078	—	+·112 ±·087	—	−·111 ±·10	—	−·269 ±·075	—
Foot—Ear	♂	−·179 ±·117	+·074	+·394 ±·096	+·319	−·475 ±·089	+·412	+·068 ±·15	−·051	−·192 ±·101	+·090
	♀	+·324 ±·092	+·467	+·105 ±·106	−·009	−·335 ±·124	+·253	+·301 ±·13	+·214	−·272 ±·137	−·437
Foot—Tail stripe	♂	−·145 ±·119	—	−·209 ±·109	—	−·097 ±·113	—	—	—	−·099 ±·104	—
	♀	+·176 ±·124	—	−·252 ±·100	—	−·227 ±·133	—	—	—	−·463 ±·108	—
Foot—Coloured area, base	♂	+·064 ±·121	—	−·325 ±·103	—	+·167 ±·111	—	−·162 ±·15	—	−·156 ±·102	—
	♀	−·286 ±·119	—	−·180 ±·103	—	−·310 ±·127	—	−·339 ±·12	—	−·153 ±·134	—
Foot—Coloured area, tips	♂	—	—	—	—	—	—	—	—	—	—
	♀	—	—	—	—	—	—	—	—	—	—
Foot—Red	♂	+·037 ±·121	—	+·223 ±·108	—	−·116 ±·113	—	−·196 ±·14	—	+·092 ±·105	—
	♀	+·007 ±·128	—	+·076 ±·106	—	+·140 ±·138	—	−·096 ±·14	—	+·253 ±·129	—
Foot—Foot pigment	♂	—	—	—	—	—	—	—	—	—	—
	♀	—	—	—	—	—	—	—	—	—	—
Tail stripe—Foot pigm.	Both	—	—	—	—	—	—	—	—	—	—
Tail stripe—Coloured area, base	Both	+·649 ±·051	—	+·598 ±·050	—	+·538 ±·063	—	—	—	+·758 ±·036	—
Tail stripe—Coloured area, tips	Both	—	—	—	—	—	—	—	—	—	—
Tail stripe—Red	Both	−·190 ±·085	—	−·455 ±·062	—	−·245 ±·083	—	—	—	−·536 ±·060	—
Foot pigm.—Coloured area, base	Both	—	—	—	—	—	—	—	—	—	—
Foot pigm.—Coloured area, tips	Both	—	—	—	—	—	—	—	—	—	—
Foot pigm.—Red	Both	—	—	—	—	—	—	—	—	—	—
Coloured area, base—Red	Both	−·325 ±·077	—	−·682 ±·042	—	−·547 ±·062	—	−·117 ±·10	—	−·788 ±·032	—
Coloured area, tips—Red	Both	—	—	—	—	—	—	—	—	—	—
Coloured area, base—$\frac{R-V}{R}$	Both	−·000	—	−·299 ±·071	—	+·156 ±·086	—	−·042 ±·10	—	−·538 ±·059	—
Coloured area, tips—$\frac{R-V}{R}$	Both	—	—	—	—	—	—	—	—	—	—
Coloured area, base-tips	Both	+·778 ±·051	—	—	—	—	—	—	—	—	—
Red—$\frac{R-V}{R}$	Both	+·455 ±·070	—	+·436 ±·063	—	−·039 ±·088	—	−·210 ±·1[illegible]	—	+·729 ±·039	—

	Sex	*Leuc.-pol. F_1*		*Leuc.-pol. F_2*		*3/4 leuc.*		*7/8 leuc.*		*Leuc.-pol. F_3*		*Pol.-alb. F_1*		*3/4 pol.*		*3/4 alb.*	
		Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net	Gross	Net
Tail—Foot	♂	+·512 ±·082	+·425	+·675 ±·049	+·615	+·116 ±·119	−·042	+·192 ±·110	+·046	+·433 ±·079	+·331	+·578 ±·059	−·501	+·749 ±·048	+·702	+·735 ±·068	+·686
	♀	+·679 ±·061	+·605	+·662 ±·052	+·584	+·352 ±·098	−·199	+·302 ±·137	+·134	+·548 ±·081	+·441	+·462 ±·087	−·338	+·654 ±·063	+·574	+·367 ±·106	+·215
Tail—Ear	Both	+·473 ±·061	+·396	−·358 ±·056	+·257	+·365 ±·071	−·265	+·617 ±·056	+·573	+·380 ±·064	+·284	+·266 ±·055	+·358	+·276 ±·071	+·157	+·279 ±·087	+·161
Tail—Tail stripe	Both	+·033 ±·078	—	+·005 ±·065	—	−·165 ±·080	—	—	—	−·189 ±·072	—	+·008 ±·069	—	−·221 ±·074	—	−·2[illegible] ±·090	—
Tail—Foot pigm.	Both	—	—	−·002 ±·065	—	−·043 ±·082	—	—	—	−·289 ±·068	—	+·025 ±·069	—	−·016 ±·077	—	−·277 ±·087	—
Tail—Coloured area, base	Both	—	—	+·001 ±·065	—	−·010 ±·082	—	−·392 ±·077	—	−·154 ±·073	—	—	—	—	—	—	—
Tail—Coloured area, tips	Both	+·120 ±·077	—	−·039 ±·064	—	—	—	—	—	−·261 ±·069	—	−·134 ±·068	—	−·082 ±·077	—	−·271 ±·088	—
Tail—Red	Both	−·276 ±·072	—	−·109 ±·064	—	−·184 ±·080	—	+·281 ±·084	—	+·150 ±·073	—	+·103 ±·069	—	+·228 ±·073	—	+·017 ±·094	—
Foot—Ear	♂	+·478 ±·083	−·385	+·478 ±·070	+·415	+·273 ±·112	+·182	+·238 ±·107	+·142	+·327 ±·087	+·243	+·355 ±·078	+·275	+·473 ±·084	+·409	+·014 ±·147	−·112
	♀	+·261 ±·106	+·158	+·399 ±·078	+·325	+·440 ±·090	+·372	+·120 ±·149	+·008	+·441 ±·093	+·373	+·463 ±·086	+·398	+·196 ±·105	+·094	+·452 ±·098	+·585
Foot—Tail stripe	♂	−·433 ±·088	—	−·258 ±·084	—	−·033 ±·121	—	—	—	−·243 ±·090	—	−·038 ±·089	—	−·120 ±·108	—	−·195 ±·142	—
	♀	−·180 ±·110	—	−·118 ±·091	—	−·330 ±·100	—	—	—	−·120 ±·114	—	+·425 ±·090	—	−·040 ±·109	—	−·253 ±·098	—
Foot—Coloured area, base	♂	−·044 ±·109	—	−·247 ±·089	—	+·081 ±·120	—	+·211 ±·109	—	−·355 ±·085	—	—	—	—	—	—	—
	♀	+·154 ±·112	—	−·260 ±·086	—	−·188 ±·108	—	+·365 ±·131	—	−·374 ±·099	—	—	—	—	—	—	—
Foot—Coloured area, tips	♂	−·139 ±·107	—	−·223 ±·086	—	—	—	—	—	−·376 ±·084	—	−·049 ±·089	—	−·126 ±·108	—	−·169 ±·143	—
	♀	+·006 ±·114	—	−·329 ±·063	—	—	—	—	—	−·476 ±·089	—	+·333 ±·097	—	−·002 ±·109	—	−·382 ±·105	—
Foot—Red	♂	−·084 ±·107	—	−·225 ±·066	—	−·075 ±·120	—	+·012 ±·114	—	−·387 ±·083	—	−·050 ±·069	—	+·248 ±·103	—	+·062 ±·147	—
	♀	−·041 ±·114	—	−·068 ±·092	—	−·185 ±·108	—	−·063 ±·150	—	+·515 ±·085	—	−·381 ±·094	—	+·034 ±·109	—	+·184 ±·119	—
Foot—Foot pigment	♂	—	—	+·044 ±·090	—	—	—	—	—	−·307 ±·088	—	+·068 ±·089	—	−·300 ±·100	—	−·335 ±·131	—
	♀	—	—	−·069 ±·092	—	—	—	—	—	−·390 ±·098	—	−·003 ±·109	—	+·087 ±·109	—	−·292 ±·113	—
Tail stripe—Foot pigm.	Both	−·001 ±·078	—	−·133 ±·063	—	−·096 ±·082	—	—	—	+·157 ±·073	—	−·100 ±·065	—	+·140 ±·076	—	+·372 ±·081	—
Tail stripe—Coloured area, base	Both	+·467 ±·061	—	+·784 ±·025	—	+·637 ±·049	—	—	—	+·898 ±·014	—	—	—	—	—	—	—
Tail stripe—Coloured area, tips	Both	+·706 ±·039	—	+·755 ±·028	—	—	—	—	—	+·840 ±·022	—	−·674 ±·035	—	+·660 ±·044	—	+·763 ±·040	—
Tail stripe—Red	Both	−·133 ±·077	—	−·397 ±·042	—	−·414 ±·068	—	—	—	−·701 ±·038	—	−·420 ±·057	—	−·605 ±·051	—	−·338 ±·084	—
Foot pigm.—Coloured area, base	Both	—	—	—	—	+·154 ±·080	—	—	—	+·209 ±·071	—	—	—	—	—	—	—
Foot pigm.—Coloured area, tips	Both	−·158 ±·076	—	−·165 ±·063	—	—	—	—	—	+·207 ±·071	—	+·123 ±·068	—	+·305 ±·070	—	+·451 ±·074	—
Foot pigm.—Red	Both	−·171 ±·076	—	−·192 ±·062	—	−·165 ±·080	—	—	—	−·318 ±·067	—	−·123 ±·068	—	−·310 ±·070	—	−·157 ±·092	—
Coloured area, base—Red	Both	+·017 ±·078	—	−·627 ±·039	—	−·658 ±·043	—	−·711 ±·045	—	−·823 ±·024	—	—	—	—	—	—	—
Coloured area, tips—Red	Both	−·330 ±·070	—	−·600 ±·041	—	—	—	—	—	−·858 ±·020	—	−·526 ±·050	—	−·744 ±·034	—	−·472 ±·073	—
Coloured area, base—$\frac{R-V}{R}$	Both	—	—	—	—	−·152 ±·050	—	—	—	−·451 ±·059	—	—	—	—	—	—	—
Coloured area, tips—$\frac{R-V}{R}$	Both	−·096 ±·078	—	−·350 ±·057	—	—	—	—	—	−·545 ±·052	—	−·203 ±·066	—	−·393 ±·065	—	−·199 ±·091	—
Coloured area, base-tips	Both	+·458 ±·062	—	+·891 ±·012	—	—	—	—	—	+·951 ±·071	—	—	—	—	—	—	—
Red—$\frac{R-V}{R}$	Both	+·700 ±·040	—	−·529 ±·047	—	−·364 ±·071	—	−·177 ±·088	—	+·633 ±·045	—	+·669 ±·038	—	+·624 ±·047	—	+·702 ±·048	—

* "Net" correlations are those from which the influence of general body size has been eliminated by the use of the method of partial correlation.

TABLE IV.

Standard deviations.

		Leucocephalus and *polionotus* and hybrids								*Polionotus-albifrons* hybrids		
		Leucocephalus	*Polionotus*									
	Sex	Wild	Wild	C_1	F_1	F_2	3/4 *Leucocephalus*	7/8 *Leucocephalus*	F_3	F_1	3/4 *Polionotus*	3/4 *Albifrons*
Number ...		72 (33 ♂, 39 ♀)	46 (27 ♂, 19 ♀)	60 (39 ♂, 21 ♀)	74 (39 ♂, 35 ♀)	109 (56 ♂, 53 ♀)	67 (31 ♂, 36 ♀)	55 (35 ♂, 20 ♀)	82 (48 ♂, 34 ♀)	95 (57 ♂, 38 ♀)	76 (38 ♂, 38 ♀)	51 (21 ♂, 30 ♀)
Body length	♂	2·08 ±0·17	1·77 ±0·16	2·04 ±0·16	1·75 ±0·13	2·33 ±0·15	2·32 ±0·20	1·79 ±0·14	2·39 ±0·16	2·11 ±0·13	2·20 ±0·17	2·06 ±0·21
	♀	3·37 ±0·26	3·77 ±0·41	2·96 ±0·31	3·07 ±0·25	2·89 ±0·19	2·99 ±0·24	2·26 ±0·24	2·73 ±0·22	2·60 ±0·20	2·42 ±0·19	2·22 ±0·19
Tail length	Both	2·49 ±0·14	3·19 ±0·22	2·70 ±0·17	2·98 ±0·17	2·82 ±0·13	2·14 ±0·12	2·31 ±0·15	2·49 ±0·13	2·31 ±0·11	2·73 ±0·15	2·38 ±0·16
(actual)	♂	2·08 ±0·17	2·42 ±0·22	2·23 ±0·17	2·34 ±0·18	2·44 ±0·16	1·95 ±0·17	2·23 ±0·18	2·51 ±0·17	2·20 ±0·14	2·94 ±0·23	2·03 ±0·21
	♀	2·53 ±0·19	3·16 ±0·35	2·67 ±0·28	2·85 ±0·23	2·99 ±0·20	2·24 ±0·18	2·43 ±0·26	2·47 ±0·20	2·05 ±0·16	2·50 ±0·19	2·48 ±0·22
(corrected)*	♂	1·91	2·23	2·05	2·15	2·24	1·79	2·05	2·31	2·02	2·70	1·87
	♀	2·20	2·75	2·32	2·48	2·60	1·95	2·11	2·15	1·78	2·17	2·16
Foot length	♂	0·36 ±0·03	0·48 ±0·04	0·38 ±0·03	0·44 ±0·03	0·59 ±0·04	0·38 ±0·03	0·39 ±0·03	0·48 ±0·03	0·47 ±0·03	0·49 ±0·04	0·46 ±0·05
(actual)	♀	0·47 ±0·04	0·54 ±0·06	0·51 ±0·05	0·61 ±0·05	0·55 ±0·04	0·40 ±0·03	0·41 ±0·04	0·70 ±0·06	0·45 ±0·03	0·45 ±0·03	0·44 ±0·04
(corrected)	♂	0·33	0·44	0·35	0·41	0·54	0·35	0·36	0·41	0·43	0·45	0·42
	♀	0·43	0·50	0·47	0·56	0·51	0·37	0·38	0·64	0·42	0·41	0·40
Ear length	Both	0·48 ±0·03	0·68 ±0·05	0·48 ±0·03	0·47 ±0·03	0·54 ±0·02	0·37 ±0·02	0·36 ±0·02	0·44 ±0·02	0·49 ±0·02	0·46 ±0·02	0·50 ±0·03
(actual)	♂	0·41 ±0·03	0·68 ±0·06	0·47 ±0·04	0·45 ±0·03	0·56 ±0·04	0·33 ±0·03	0·39 ±0·03	0·45 ±0·03	0·52 ±0·03	0·47 ±0·04	0·54 ±0·06
	♀	0·45 ±0·03	0·67 ±0·07	0·47 ±0·05	0·48 ±0·04	0·52 ±0·03	0·38 ±0·03	0·29 ±0·03	0·41 ±0·03	0·44 ±0·03	0·44 ±0·03	0·48 ±0·04
(corrected)	♂	0·39	0·65	0·45	0·44	0·53	0·32	0·38	0·43	0·50	0·45	0·51
	♀	0·43	0·64	0·45	0·46	0·50	0·37	0·28	0·40	0·42	0·42	0·46
Weight	♂	1·45 ±0·12	1·42 ±0·13	1·87 ±0·14	1·62 ±0·12	1·74 ±0·11	1·75 ±0·15	1·31 ±0·11	1·97 ±0·14	1·62 ±0·10	1·14 ±0·09	1·46 ±0·15
	♀	1·58 ±0·12	2·12 ±0·23	2·93 ±0·30	2·23 ±0·18	1·77 ±0·12	1·80 ±0·14	1·68 ±0·18	1·82 ±0·15	1·38 ±0·11	1·80 ±0·14	1·28 ±0·11
Caudal vertebrae	Both	0·64 ±0·04	0·80 ±0·06	—	0·66 ±0·04	0·83 ±0·04	—	—	—	—	—	—
Right pelvis	♂	0·40 ±0·03	0·52 ±0·05	—	0·38 ±0·03	0·51 ±0·03	—	—	—	—	—	—
(actual)	♀	0·67 ±0·05	0·61 ±0·07	—	0·73 ±0·06	0·67 ±0·04	—	—	—	—	—	—
(corrected)	♂	0·31	0·40	—	0·29	0·39	—	—	—	—	—	—
	♀	0·40	0·37	—	0·44	0·40	—	—	—	—	—	—
Right femur	♂	0·36 ±0·03	0·55 ±0·05	—	0·36 ±0·03	0·47 ±0·03	—	—	—	—	—	—
(actual)	♀	0·51 ±0·04	0·77 ±0·08	—	0·92 ±0·07	0·58 ±0·04	—	—	—	—	—	—
(corrected)	♂	0·28	0·42	—	0·28	0·36	—	—	—	—	—	—
	♀	0·31	0·46	—	0·55	0·35	—	—	—	—	—	—
Skull length	♂	0·40 ±0·03	0·43 ±0·04	—	0·44 ±0·03	0·51 ±0·03	—	—	—	—	—	—
(actual)	♀	0·46 ±0·04	0·62 ±0·07	—	0·60 ±0·05	0·77 ±0·05	—	—	—	—	—	—
(corrected)	♂	0·28	0·30	—	0·31	0·36	—	—	—	—	—	—
	♀	0·35	0·47	—	0·46	0·58	—	—	—	—	—	—
Skull breadth	♂	0·19 ±0·02	0·22 ±0·02	—	0·15 ±0·01	0·22 ±0·01	—	—	—	—	—	—
(actual)	♀	0·18 ±0·01	0·32 ±0·01	—	0·20 ±0·02	0·23 ±0·02	—	—	—	—	—	—
Tail stripe	Both	—	—	—	24·70	33·72	3·23	2·94	42·42	34·18	24·96	35·31
Foot pigment	Both	—	0·83 ±0·06	0·80 ±0·05	0·85 ±0·05	0·81 ±0·04	0·61 ±0·04	—	0·67 ±0·04	0·69 ±0·03	0·63 ±0·03	0·73 ±0·05
Coloured area	Both	3·81 ±0·23	—	—	6·46 ±0·35	13·87 ±0·64	6·05 ±0·36	6·37 ±0·41	17·27 ±0·91	—	—	—
(base)	♂	3·59 ±0·32	—	—	6·37 ±0·48	13·16 ±0·85	4·85 ±0·42	6·55 ±0·53	18·17 ±1·25	—	—	—
	♀	3·94 ±0·31	—	—	6·47 ±0·51	14·05 ±0·92	6·75 ±0·54	5·87 ±0·63	15·91 ±1·30	—	—	—
Coloured area	Both	—	3·91 ±0·27	4·81 ±0·29	4·89 ±0·27	9·02 ±0·41	—	—	12·70 ±0·67	5·54 ±0·28	5·36 ±0·30	6·74 ±0·45
(tips)	♂	—	3·75 ±0·34	4·85 ±0·37	4·72	8·87 ±0·57	—	—	13·36 ±0·92	5·48 ±0·35	5·03 ±0·40	6·56 ±0·70
	♀	—	3·91 ±0·43	4·73 ±0·48	5·05	9·00 ±0·59	—	—	11·70 ±0·96	5·63 ±0·45	5·24 ±0·42	6·81 ±0·59
Red	Both	3·53 ±0·21	1·06 ±0·08	1·34 ±0·08	1·43 ±0·08	2·05 ±0·09	2·17 ±0·13	3·32 ±0·21	3·17 ±0·17	1·59 ±0·08	1·45 ±0·08	1·58 ±0·11
	♂	3·50 ±0·32	1·07 ±0·10	1·37 ±0·10	1·36 ±0·10	2·09 ±0·14	1·82 ±0·16	3·67 ±0·30	3·04 ±0·21	1·58 ±0·10	1·48 ±0·12	1·37 ±0·15
	♀	3·46 ±0·28	1·02 ±0·11	1·28 ±0·13	1·51 ±0·12	2·02 ±0·13	2·44 ±0·20	2·55 ±0·27	3·36 ±0·27	1·60 ±0·13	1·38 ±0·11	1·70 ±0·15
$\frac{A_b}{R}$	Both	0·29 ±0·02	—	—	0·65 ±0·04	1·53 ±0·07	0·62 ±0·04	0·52 ±0·03	2·01 ±0·11	—	—	—
$\frac{A_t}{R}$	Both	—	1·13 ±0·08	1·16 ±0·07	0·60 ±0·03	1·08 ±0·05	—	—	—	0·80 ±0·04	1·13 ±0·06	0·72 ±0·05
$\frac{R-V}{R}$	Both	4·82 ±0·29	3·88 ±0·28	5·33 ±0·33	4·49 ±0·25	6·05 ±0·28	5·18 ±0·31	4·26 ±0·27	6·45 ±0·34	4·84 ±0·24	5·05 ±0·29	5·05 ±0·34

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* See foot-note under Table III.

TABLE VI.

Parent-offspring correlations.

Generations	No. of parents	No. of off-spring	Foot length	Foot pigmen-tation	A_b	A_t	Red	$\frac{A}{R}$	$\frac{R-V}{R}$
Leucocephalus, P–C_1	21	46	−0·036	—	+0·303	—	+0·486	+0·500	+0·075
Albifrons, P–C_1	25	49	+0·258	—	+0·668	—	+0·201	+0·556	+0·431
Polionotus, P–C_1	21	61	+0·368	+0·195	—	+0·387	+0·463	—	—
Leucocephalus–leucocephalus-albifrons, F_1	19	72	—	—	+0·317	—	+0·296	+0·458	−0·045
Albifrons–leucocephalus-albifrons, F_1	15	73	—	—	+0·560	—	+0·016	+0·277	+0·135
Leucocephalus-albifrons, F_1–F_2	30	122	+0·041	—	+0·510	—	+0·276	+0·291	+0·046
Leucocephalus–leucocephalus-albifrons, back-cross	11	67	—	—	+0·289	—	+0·224	+0·224	−0·060
F_1–*leucocephalus-albifrons* back-cross	18	70	—	—	+0·237	—	+0·200	+0·075	+0·091
Leucocephalus–grades	4	37	—	—	+0·318	—	+0·359	+0·211	−0·283
Back-cross–grades	14	58	—	—	−0·390	—	+0·366	+0·101	+0·308
Leucocephalus-albifrons, F_2–F_3	22	65	+0·114	—	+0·751	—	+0·743	+0·762	+0·381
Leucocephalus–leucocephalus-polionotus, F_1	17	72	—	—	+0·458	—	−0·099	—	—
Polionotus–leucocephalus-polionotus, F_1	12	66	—	+0·576	—	+0·237	+0·233	—	—
Leucocephalus-polionotus, F_1–F_2	37	108	+0·110	+0·362	+0·219	+0·417	+0·092	—	—
Leucocephalus–leucocephalus-polionotus back-cross	13	65	—	—	−0·207	—	+0·094	—	—
F_1–*leucocephalus-polionotus* back-cross	13	66	—	+0·076	+0·122	—	+0·253	—	—
Leucocephalus–grades	10	42	—	—	+0·300	—	+0·481	—	—
Back-cross–grades	10	55	—	—	+0·616	—	+0·343	—	—
Leucocephalus-polionotus, F_2–F_3	26	82	+0·298	+0·250	—	+0·917	+0·837	—	—
Polionotus–polionotus-albifrons, F_1	13	85	—	+0·271	—	+0·402	—	—	—
Albifrons–polionotus-albifrons, F_1	6	49	—	—	—	+0·601	—	—	—
Polionotus–back-cross (3/4 *polionotus*)	12	73	—	−0·378	—	+0·249	—	—	—
F_1–back-cross (3/4 *polionotus*)	14	69	—	+0·184	—	+0·216	—	—	—
Albifrons–back-cross (3/4 *albifrons*)	4	25	—	—	—	+0·521	—	—	—
F_1–back-cross (3/4 *albifrons*)	11	48	—	+0·473	—	+0·734	—	—	—