Ann. Hum. Genet., Lond. (1964), **28**, 27
Printed in Great Britain

Studies on the inheritance of human skin colour

BY G. AINSWORTH HARRISON AND J. J. T. OWEN
Anthropology Laboratory, Department of Human Anatomy, University of Oxford

INTRODUCTION

Variation in human skin colour is remarkable in that the variation between different populations is often very great by comparison with that within populations. The nature of the between population differences has therefore seemed to be particularly open to analysis, although the character shows quantitative variation in hybrid groups.

A number of studies have been made, particularly on the differences between Africans and Europeans (Davenport & Danielson, 1913; Gates, 1949; Stern, 1953), but these have tended to suffer from the inadequacy of the methods previously available for measuring skin colour and the diversity of relationships in the populations studied. Recently, reflectance spectrophotometry has provided an objective method of measuring pigmentation (Weiner, 1951; Lasker, 1954; Harrison & Owen, 1956; Barnicot, 1958; Walsh, 1963) and in various parts of Britain, hybrid populations between Africans and Europeans have been forming in which it is often possible to trace the relationship of individuals back to the original miscegenation. The present analysis is based upon such a population studied in Liverpool during the past 10 years.

MATERIALS AND METHODS

A portable E.E.L.* reflectance spectrophotometer was used in the study. This instrument is fitted with nine different filters which 'sample' the whole of the visual spectrum. Typically, at least three of these filters were used in measuring subjects, viz. filter 601 with a dominant wavelength (d.w.l.) of 425 mμ; filter 605, d.w.l. 545 mμ; and filter 609, d.w.l. 685 mμ; but, in a few instances, and especially in the case of one large group of West African seamen, it was only possible to take readings with one filter. In these cases the 609 filter was chosen. On the other hand, readings on about a half of the subjects were taken using all or most of the filters. In every case measurements were made on the medial aspect of the right upper arm, and except in the case of young children, the position was standardized as precisely as possible by placing the rim of the applicator head against the medial epicondyle of the humerus.

Most of the subjects were residents of Liverpool and were contacted by house to house surveys in areas where there is a large West African population. The European, 105, with a large Irish component, came from the same areas as the hybrids and were of comparable social class; in many cases they were the mothers of hybrid families, or relatives of these mothers. The sample of West Africans (106) is made up of three groups: (1) a group of settled Liverpool residents, (2) a group of seamen who are usually on the West African 'run' but often have homes in Liverpool, and (3) a small group of university students. Analysis of the results has shown that these groups do not differ in skin colour, but there are three important points about this sample of West Africans. First, it covers a wide range of West African populations (mostly from coastal regions of Ghana and Nigeria) and is of diverse tribal origin; Barnicot (1958) has shown

* Evans Electro-Selenium Co. Ltd., Halstead.

that there are considerable differences in colour between such neighbouring tribes as the Yoruba and Ibo. Secondly, it is possible that a few individuals in the group have had some distant white ancestry, since some miscegenation has occurred in West Africa—particularly along the coast. Finally, it is a sample composed almost exclusively of males, and it has been shown in a number of studies (Lasker, 1954; Barnicot, 1958) that males tend to have slightly darker skins than females, partly because of a richer blood supply to their skin (Edwards & Duntley, 1939) and partly because they tend to expose themselves to more sunlight. In the present data on Europeans and F_1 hybrids the same tendency is evident but in neither case is the sex difference significant and it has been ignored in the subsequent analysis. Since measurements were made on the medial aspect of the upper arm, rather than on the forearm or forehead as in other investigations there are no *a priori* grounds for expecting a sex difference.

Four types of hybrid have been found: first generation (94) F_1, hybrids between African males and European females; and backcross European (30), backcross African (26) and (14), F_2, hybrids, but the second generation hybrids, particularly F_2s, are still rare. Further, the likelihood of the numbers increasing is remote, since the recent large-scale immigration of West Indians of unknown ancestry has markedly widened the variety of possible mates. All the hybrid samples, and especially the second generation hybrids, are of lower mean age than the parental samples, but there is evidence that after the first few years of life there is no change in pigmentation (Lasker, 1954). No children under 2 years of age were included. The pedigrees of the hybrids were ascertained as carefully as possible and in many cases the legitimacy of children was checked by blood-grouping. No cases of undisclosed illegitimacy were found

RESULTS

Reflectance curves

The mean reflectance values of the parental and various hybrid groups, together with their standard errors and the number of individuals on which they are based are presented in Table 1 The means are also represented graphically in Fig. 1. Although the various reflectance curves are based only on a series of sample wavelengths, their general form is very similar to that obtained with a continuous recording instrument, e.g. the Hardy reflectance spectrophotometer (Weiner, 1951). In particular, they show the characteristic absorption of melanin at the shorter wavelengths, and the absorption band of haemoglobin at 545 mμ which is increasingly obvious with decreasing amounts of melanin. The F_1 hybrid curve is approximately intermediate between the two parental groups, but it is evident that the precise relationship changes with wavelength. In particular the curve is nearer that of the African parent than the European parent at 425 mμ, whilst at 685 mμ the relationship is reversed. In both instances, the curves for the backcrosses fall roughly intermediate between the curves for the F_1 hybrid and the respective parent, but obviously in the case of the backcross African the curve lies nearer the F_1 hybrid than the African parent.

Melanin concentration

It has been shown (Harrison & Owen, 1956) that *in vitro*, melanin concentration is linearly proportional to the reciprocal of the reflectance values. At short wavelengths and high concentrations of melanin the relationship tends to be disturbed but at long wavelengths linearity is evident over a considerable range of concentrations. It has further been found that the effects of scattering of light by the skin do not profoundly affect this relationship.

Table 1. *Means and standard errors of reflectance values at nine wavelengths of Europeans, West Africans and various hybrid groups*

B_E, backcross European. B_A, backcross African

Wavelength (mμ)	European		West African		F_1 hybrid		B_E hybrid		B_A hybrid		F_2 hybrid	
	No.	Mean ± S.E.	No.	Mean ± S.E.	No.	Mean ± S.E.	No.	Mean ± S.E.	No.	Mean ± S.E.	No.	Mean ± S.E.
425	104	36·1 ± 0·453	40	12·3 ± 0·484	94	20·8 ± 0·508	30	27·2 ± 1·320	21	18·0 ± 0·915	13	22·2 ± 1·566
465	51	41·6 ± 0·710	40	13·2 ± 0·522	86	24·5 ± 0·572	29	33·5 ± 1·319	18	21·1 ± 1·275	6	28·5 ± 1·962
485	49	43·0 ± 0·668	39	13·4 ± 0·567	85	26·0 ± 0·620	26	34·1 ± 1·371	18	22·1 ± 1·553	6	27·7 ± 2·304
515	46	43·7 ± 0·640	37	14·6 ± 0·680	77	27·4 ± 0·590	14	36·7 ± 2·056	16	23·3 ± 1·685	3	25·7 ± 1·517
545	103	41·0 ± 0·453	40	14·4 ± 0·611	94	28·4 ± 0·581	30	34·7 ± 1·122	21	24·2 ± 1·334	12	30·3 ± 1·483
575	51	45·2 ± 0·526	40	16·6 ± 0·704	86	31·7 ± 0·585	28	38·2 ± 1·206	18	27·2 ± 1·515	6	33·5 ± 1·944
595	51	54·8 ± 0·529	40	21·7 ± 0·834	86	40·5 ± 0·633	29	48·2 ± 1·145	18	34·6 ± 1·699	6	43·7 ± 1·943
655	51	61·7 ± 0·436	40	29·9 ± 1·062	87	49·7 ± 0·586	29	56·7 ± 0·947	18	44·7 ± 1·615	6	53·0 ± 1·789
685	105	62·3 ± 0·342	106	34·7 ± 0·591	94	52·0 ± 0·546	30	57·9 ± 0·926	26	47·8 ± 1·205	14	53·4 ± 1·455

The reflectance values of the two parental groups and the F_1 hybrids have therefore been transformed to reciprocals and the means of these are plotted in Fig. 2. This clearly shows that the F_1 hybrid is more similar to the European than the African parent in terms of melanin concentration. It is also evident that on the reciprocal of reflectance scale, the relationship of the F_1 hybrid to the two parents is more comparable at the different wavelengths than it is on the reflectance scale. Indeed at wavelengths longer than 545 mμ the relationship is exactly

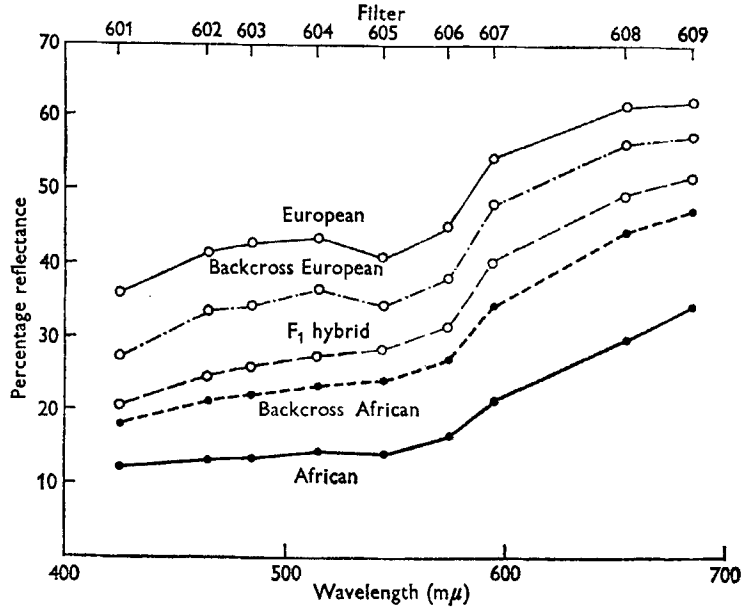

Fig. 1. Mean reflectance curves of European, African and various hybrid groups.

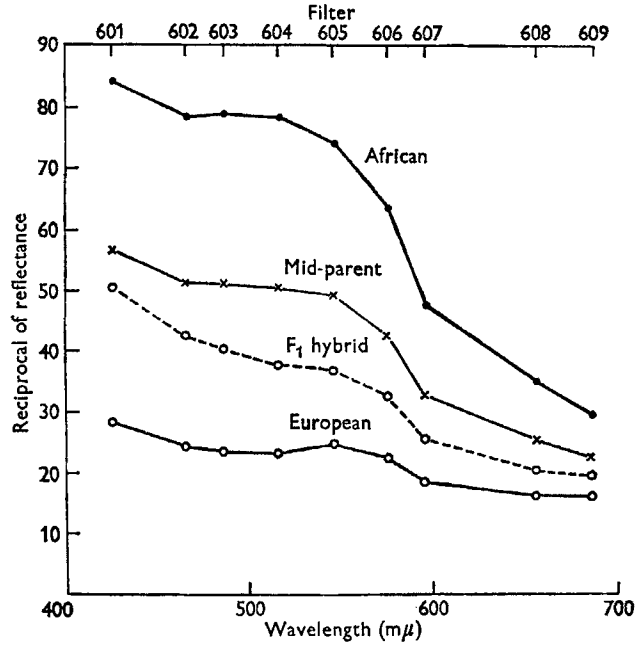

Fig. 2. Mean reciprocal of reflectance curves of Europeans, Africans and F_1 hybrids. The midparent values are also shown.

Table 2. *Means and variances of reflectances at different wavelengths and with various transformations*

B_E, European backcross, B_A, African backcross

	European		African		F_1 hybrid		B_E hybrid		B_A hybrid		F_2 hybrid	
Scale (mμ) R	Mean $\bar{E}$	Variance $V_{\bar{E}}$	Mean $\bar{A}$	Variance $V_{\bar{A}}$	Mean $\bar{F}_1$	Variance $V_{\bar{F}_1}$	Mean $\bar{B}_E$	Variance $V_{\bar{B}_E}$	Mean $\bar{B}_A$	Variance $V_{\bar{B}}$	Mean $\bar{F}_2$	Variance $V_{\bar{F}_2}$
425	36·1	21·283	12·3	9·354	20·8	20·428	27·2	52·305	18·0	17·600	22·2	31·858
545	41·0	21·098	14·4	14·918	28·4	31·748	34·7	37·766	24·2	37·366	30·3	26·382
685	62·3	12·248	34·7	37·039	52·0	28·011	57·9	25·697	47·8	37·760	53·4	29·646
$1/R \times 1000$												
425	28·2	16·194	85·4	632·423	50·6	125·760	39·4	109·822	58·5	189·440	47·4	112·818
545	24·7	8·829	74·0	356·608	36·5	50·260	29·9	30·099	44·1	150·098	34·0	35·282
685	16·1	0·956	29·5	38·064	19·5	4·494	17·5	2·499	21·3	10·288	18·9	3·928
$\text{Log}_{10} R$												
425	1·556	0·00317	1·082	0·01236	1·308	0·00885	1·420	0·01310	1·245	0·01024	1·336	0·01047
Antilog R												
685	0·421	0·00109	0·225	0·00105	0·334	0·00159	0·382	0·00200	0·304	0·00171	0·346	0·00199

comparable for the different filters. At shorter wavelengths the comparability is less exact but, as already mentioned, at these wavelengths the linear relationship between concentration and the reciprocal of reflectance exists over a much smaller range of melanin concentration.

The criteria of scaling

For purposes of a genetical analysis it is necessary that the measurements should be made on a scale in which (1) non-heritable variation is independent of that due to gene segregation, and (2) the responsible genes are additive on average in their effects. In analysing the genetical differences between true breeding lines the first criterion can be tested by comparing the variances of the true breeding parents and their F_1 hybrid. Under most circumstances, one would expect to find equality of variances on that scale which removes environmental interaction. In the present situation, of course, the two parental populations cannot strictly be regarded as true breeding. Not only must there be some genetical component to the intra-parental variation, but one would also expect the African variance to be larger than the European variance because of the more heterogeneous origin of the African sample. However, the genetical variability within either parental group must be small in comparison with that between the parental groups. A scale has, therefore, been sought in which the parental and F_1 hybrid variances are of essentially the same magnitude and are each small by comparison with the inter-parental variation. Because of the very small number of F_2s available, no attention has been given to this type of hybrid, but it has been assumed that the estimated backcross variances are not too awry.

In Table 2, the variances of the different groups, together with the corresponding means at three wavelengths and on various scales are presented. The comparative magnitudes of these variances on the reflectance scale are obviously related to mean measurement. For instance, the European variance tends to decrease with the rise in mean measurement which occurs with increasing wavelength. Conversely the African variance tends to rise from its value at 425 mμ to that at 685 mμ. It would in fact appear that there is a falling off of variance with high and low reflectance values, as sampled respectively by the European and African groups. This trend is fully confirmed by the results obtained at intermediate wavelengths. It is of interest to note that the estimated F_1 and F_2 variances are fairly constant at the different wavelengths, no doubt because their mean measurements fall intermediate in the reflectance scale, but both backcross hybrids show the same trend as the parental groups. This effect has been noted in other work on the reflectometry of hair and skin colour (Sunderland, 1956; Barnicot, 1958) and seems to be intrinsic in the method of measuring pigmentation by reflectance spectrophotometry.

This factor would seem to account for the anomalous comparative variances that one finds at short and long wavelengths on the reflectance scale. At 425 mμ, not only does one find that the estimated African variance is lower than that of the European—an unlikely situation—but also that the backcross African variance is less than both the European and F_1 variances! Similarly, on reflectance at 685 mμ the backcross European variance is less than the African and F_1 variances. On these grounds alone, these two scales are clearly unsuitable for a genetical analysis, since there is obvious interaction between genotype and the 'environment'. In this case, of course, the environment relates to the method of measurement. On the other hand, at 545 mμ, although the estimated African variance is lower than one would expect in comparison

with the European, and is also significantly smaller than the F_1 variance, both backcross variances exceed those of the non-segregating populations. It would seem, therefore, that of the three different wavelengths environmental interaction is least at 545 mμ and it is possible that it is sufficiently small to permit a genetical analysis.

Table 3. *Scaling tests using the mean values and the corresponding variances as given in Table 2*

Scale (mμ) R	A	S.E.	B	S.E.	C	S.E.
425	−2·46	2·7196	+2·88	1·9504	− 1·08	6·3560
545	−0·08	2·3618	+5·55*	2·7978	+ 8·75	6·0910
685	+1·53	1·9599	+8·97***	2·5409	+12·80*	5·9616
$\log_{10} R$ 425	−0·023	0·04326	+0·100*	0·04817	+ 0·090	0·11602
Antilog R 685	+0·008	0·01711	+0·049*	0·01703	+ 0·070	0·04861

$$A = 2\bar{B}_E - \bar{F}_1 - \bar{E}, \qquad V_A = 4V_{\bar{B}_E} + V_{\bar{F}_1} + V_{\bar{E}},$$

$$B = 2\bar{B}_A - \bar{F}_1 - \bar{A}, \qquad V_B = 4V_{\bar{B}_A} + V_{\bar{F}_1} + V_{\bar{A}},$$

$$C = 4\bar{F}_2 - 2\bar{F}_1 - \bar{E} - \bar{A} \qquad V_C = 16V_{\bar{F}_2} + 4V_{\bar{F}_1} + V_{\bar{E}} + V_{\bar{A}}$$

* Represents significance at the 5 % probability level. *** Represents significance at the 0·1 % probability level.

It is evident from Table 2 that although the reciprocal of reflectance is proportional to melanin concentration, and would afford a scale which is more or less independent of wavelength, it is completely unsuitable for a genetical analysis. The transformation is so strong that the African variance becomes not only about 40 times that of the European variance but is also greater than the variances of all the other genotypes. It would be possible to weaken this type of transformation by employing a scale such as $1/(1-R)$ but in terms of simple transformations, which are likely to more or less equalize the parental variances at 425 and 685 mμ, logarithmic and antilogarithmic scales respectively would seem to be the most obvious choices. Table 2 shows that these transformations meet the criteria of scaling better than the corresponding reflectance scales. Admittedly at 425 mμ the backcross African variance has become smaller than the African variance, indicating that the transformation is too strong and that there is still considerable environmental interaction. However, compared with the European the magnitude of the African variance is in the expected direction, and the backcross African variance, instead of being less than the variances of two of the non-segregating groups, is now only less than one. The antilog of reflectance at 685 mμ is even better. Not only is there approximate equality of the parental and F_1 variances, but both backcross variances are in excess of these. From the point of view of removing environmental interaction this scale would seem to be the best of those tested.

The second criterion for scaling is that the effect of a particular gene substitution should be independent of the rest of the genotype. This can be tested by comparing the means of the second generation hybrids with those of the parents and F_1 hybrid. Additiveness of genic effect is evidenced, on the one hand, by strict intermediacy of the backcross mean between the F_1 mean and the corresponding parental mean, and on the other, by the relationship of the F_2 mean to the means of the three non-segregating groups. The results of such tests on various scales are shown in Table 3.

It is apparent that the backcross European mean does not deviate significantly from strict intermediacy on any of the scales tested. However, some significant departure of the backcross African mean does occur on all the scales, with the exception of reflectance at 425 mμ, though in all but one case the significance of this departure is only just over the 5 % level. Tests using the F_2 mean do not discriminate between the various scales apart from confirming that reflectance measured at 685 mμ gives the poorest fit. Whilst reflectance at 425 mμ would seem on this test of means to afford the best scale, it has already been shown that it is totally inadequate on the variance criteria, and although the logarithmic transformation of reflectance at this wavelength gives a poorer fit for additiveness, on an overall judgement of both criteria it is to be preferred. Although there is some small departure of the backcross African mean from strict intermediacy on reflectance at 545 mμ, this scale seems to fit fairly well the criterion of additiveness, as well as being the reflectance scale on which there is least environmental interaction. The antilog transformation at 685 mμ, not only provides more acceptable variances than reflectance at this wavelength, but also considerably improves the scaling on means.

On the basis of the scaling criteria it seemed justifiable to proceed to a partition of variation on the following three scales: log R 425 mμ, R 545 mμ and antilog R 685 mμ.

Partition of variation

Quantitative variation is typically made up of three components. Following the nomenclature of Mather (1949) these may be represented as (1) E, a component which arises from non-heritable causes, (2) D, a heritable component arising from the differences in phenotypic expression associated with the two homozygotes for each gene pair, i.e. fixable variation due to the parental difference, and (3) H, a heritable component due to the differences in expression between heterozygotes for each gene pair and the average of the two corresponding homozygotes, i.e. unfixable variation due to the average dominance of the gene sets involved.

In the present data an estimate of E is provided by the mean of the European, African and F_1 hybrid variances. Genetical differences within the parental groups, but not contributing to the differences between these groups, will necessarily be included within this component and thus will lead to an overestimation of the true effect of the external environment. However, this should not seriously affect the estimations of the heritable inter-population difference. On the assumption that the parental populations are essentially homozygous for the genes responsible for this difference the principles of the method developed by Fisher, Immer & Tedin (1932) and Mather (1949) for partitioning D and H can be applied. These authors have shown that the sum of the two backcross variances equals $\frac{1}{2}D+\frac{1}{2}H+2E$ and that the F_2 variance equals $\frac{1}{2}D+\frac{1}{4}H+E$. Since in the present data the estimate of F_2 variance is too unreliable to be of use, some other equation relating H and D is required. The deviation of the F_1 mean from the mid-parent expressed as a ratio of half the parental difference provides a measure of the relative potence of the gene sets. Although this potence ratio is not representative of average dominance, unless the dominance is isodirectional, it does provide a minimal estimate of t. magnitude of H in relation to D, since with isodirectional dominance $\sqrt{(H/D)}$ equals the potence ratio. It would seem that the estimate of H which can be obtained from the equations relating backcross variance with the potence ratio, however inaccurate, is better than none at all. It must be noted that there are no *a priori* grounds for assuming that dominance is likely to be iso-

directional, though one might have expected from the results of other interracial crosses that dominance would be slight.

The various components of variation as measured on the most suitable scales are presented in Table 4. It can be seen that in each instance the potence ratio is negligible in amount, but it is always directed towards the European. It follows from the method of analysis used that the estimate of H is also small in all cases. There is further agreement on the different scales in the relative proportions of the D and E components, with the D component contributing between 63 and 72 % of the total variation and conversely E contributing between 36 and 27 %. An estimate of the number of effective factors responsible for the interparental difference (k_1) can be shown to be equal to the ratio of the square of half the parental difference to D (Mather, 1949). Using the various scales at different wavelengths, the number of effective factors has been found to be between 3 and 4.

Table 4. *Components of variation, where D, H, E are described in the text* (*p.* 34)

Scale	D	H	E	Potence ratio = Deviation of F_1 from midparent / ½ Parental difference	K = (difference between parents)² / $4D$		
R						E / D	H
545 mμ	59·746	0·165	22·588	0·053	2·96		
$\text{Log}_{10} R$						E / D	H
425 mμ	0·01414	0·00003	0·00813	0·046	3·97		
Antilog R						E / D	H
685 mμ	0·002417	0·000030	0·001243	0·112	3·97		

DISCUSSION

The deficiencies in the data in this study are keenly appreciated by the writers, but since there appear at present to be no opportunities for improving the data, it seems justifiable to take the analysis as far as possible. In considering where the deficiencies mainly lie the principal factor is the small number of segregating hybrids available. This is of particular importance in view of the reliance which must be placed on the estimated variance of at least the backcross generations. As is well known variances are less robust statistics than means, and as Gilbert (1961) has suggested it would be preferable for an analysis to be based on means alone. However, it may be noted that on the scales used the backcross variances are approximately equal and this is consistent with the small potence ratio found in Table 4. The latter is based upon well substantiated mean measurements.

A second source of error may be a failure to find the best scale. Scales, however, can, in most cases, only be sought on an empirical basis, and on the basis of the present data there seemed little justification for testing complex transformations. Even the functional representation of

reflectance curves is proving an extremely complex problem. The fact that there is general agreement on three scales which more or less meet the required criteria suggests that any error due to scale effect is small.

In the genetical analysis the use of the potence ratio as a measure of average dominance has probably led to an underestimation of H, but it can be said that if, in fact, dominance does exist it must be evenly balanced. Although there are no theoretical limits to the possible error in the estimated magnitude of H, even if the D component were half that calculated, the number of effective factors would remain relatively small, i.e. 6–8.

Effective factors, of course, do not necessarily represent individual genes; they could equally well be segments of chromosomes, or indeed whole chromosomes, but in the absence of third-generation hybrid data, it is impossible to detect any linkage that may exist. The analysis does indicate, however, that probably three or four chromosomes are involved in determining the pigmentary differences between Africans and Europeans. Further, the estimate of effective factors agrees closely with determinations made in other studies of quantitative variation (Mather, 1949).

It is impossible at the moment to say whether these conclusions relate solely to the site of measurement—the medial aspect of the upper arm—or whether they are of general applicability to the body as a whole. Certainly one would expect the environmental component to vary with position, since not only are different parts of the body differentially exposed to ultraviolet radiation, but also it has been shown that different areas have varying capacities to tan (Edwards & Duntley, 1939). The reasons for choosing the medial aspect of the upper arm in this study were that, while reasonably accessible, the region is normally not exposed to much sunlight and anyway has a poor tanning capacity. The differences between the present data and the measurements made by Barnicot (1958) on essentially similar populations may well be largely attributable to the differences in the site of measurement, since Barnicot measured reflectance on the forearm. It is interesting to note, however, that in Barnicot's data the comparative relationships of the mean reflectance values of the F_1 hybrids to the two parental types are different from those found in this investigation: the F_1 hybrid being relatively nearer the African. Since Barnicot measured his Europeans in Britain and his Africans and hybrids in West Africa, comparative tanning might account for this difference.

The nature of this analysis raises very clearly the problems involved in using reflectance spectrophotometry (or for that matter any other measure) in comparing the genetical basis for population differences in skin colour. It is apparent that on the reflectance scale comparative similarity is a function of the wavelength at which measurements are made. For instance, the F_1 mean reflectance is relatively nearer the African than the European at 425 mμ and contrariwise at 625 mμ (see Fig. 1). If the F_1 population had been of unknown origin, its genetical affinities would have appeared different at the two wavelengths and, as the present analysis has shown, neither of these would have been correct. The question of scale in the use of anthropometric characters is of crucial importance, yet rarely does one have the opportunity of directly measuring the same character on different scales. It is very easy to forget that the scale of measurement may bear no relation to the underlying genetical differences. The scales of additiveness which this analysis has revealed may be far from perfect, but it seems reasonable to suppose that they will be generally applicable to comparative surveys of skin colour with at least the E.E.L. spectrophotometer.

SUMMARY

Measures of skin colour have been made using an E.E.L. spectrophotometer of 105 Europeans, 106 West Africans, 94 F_1 hybrids, 30 backcross European and 26 backcross African hybrids and 14 F_2 hybrids in Liverpool. Of the scaling tests applied, additiveness of genic effect and independence of non-heritable variations was greatest with a log transformation of reflectance of incident light of 425 mμ, without transformation at 545 mμ and with an antilog transformation at 685 mμ. Using these scales it has been shown that the relative potence of gene sets is negligible. By making the assumption that such potence as does exist provides a measure of average dominance, the number of effective factors responsible for the difference in skin colour between Europeans and Africans has been estimated from the different scales to be between 3 and 4.

Acknowledgement is made to the Eugenics Society for an initial grant which enabled the work to start, and to an anonymous donor in the U.S.A. who provided funds for the continuance of the work through the G.C.L. Bertram Research Account.

REFERENCES

BARNICOT, N. A. (1958). Reflectometry of the skin in southern Nigerians and in some Mulattoes. *Hum. Biol.* **30**, 150.

DAVENPORT, C. B. & DANIELSON, F. H. (1913). Skin colour in Negro–White crosses. *Publ. 188, Carnegie Institvtion of Washington.*

EDWARDS, E. A. & DUNTLEY, S. Q. (1939). Pigments and colour of living human skin. *Amer. J. Anat.* **65**, 1.

FISHER, R. A., IMMER, F. R. & TEDIN, O. (1932). The genetical interpretation of statistics of the third degree in the study of quantitative inheritance. *Genetics*, **17**, 107.

GATES, R. R. (1949). *Pedigrees of Negro Families.* Philadelphia: Blakiston.

GILBERT, N. (1961). Polygene analysis. *Genet. Res.* **2**, 96.

HARRISON, G. A. & OWEN, J. J. T. (1956). The application of spectrophotometry to the study of skin colour inheritance. *Acta Genet.* **6**, 481.

LASKER, G. W. (1954). Photoelectric measurement of skin colour in a Mexican mestizo population. *Amer. J. Phys. Anthrop.*, n.s. **12**, 115.

MATHER, K. (1949). *Biometrical Genetics.* London: Methuen.

STERN, C. (1953). Model estimates of the frequency of white and near-white segregants in the American Negro. *Acta Genet.* **4**, 281.

SUNDERLAND, E. (1956). Hair-colour variation in the United Kingdom. *Ann. Hum. Genet., Lond.*, **20**, 312.

WALSH, R. J. (1963). Variations of melanin pigmentation of the skin in some Asian and Pacific peoples. *J. Roy. Anthrop. Inst.* **93**, 126.

WEINER, J. S. (1951). A spectrophotometer for measurement of skin colour. *Man*, **51**, 253.