DOES THE MELANIN PIGMENT OF HUMAN SKIN HAVE ADAPTIVE VALUE?

An Essay in Human Ecology and the Evolution of Race

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ABSTRACT

The widely accepted idea that melanin pigment in human skin protects against sunlight, and that this has bearing upon adaptation to life in the tropics and the distribution of races, is examined in terms of its physical and physiological aspects. Regarded in such terms the concept appears to have little merit. It is concluded that whereas the pigment may have a slight adaptive value as regards some aspects of the organism-environment relationship, it may be non-adaptive as regards others; and the respective values may depend upon various complicating factors of the environment. Moreover, the distribution of races according to skin color does not appear to conform well to what would be expected from the spectral distribution of sunlight.

"IT is unnecessary to point out my admiration in general for the great modern synthesis which the science of evolution represents, but I may venture to observe that some examples of adaptive mechanisms are being paraded where the physiological interpretations are taken much too lightly."—P. F. Scholander (1956).

Melanin pigment plays a predominant role in giving the brown and black color to the skin, which provides some of the most striking differences in outward appearance of human races. This would seem a very superficial difference, yet there has been attempt to find adaptive significance in the presence of the pigment itself. It is quite generally accepted, without qualification, that the pigment constitutes a protective barrier against injurious effects of sunlight. Reasoning on this basis, Negroes have been thought to be better adapted than white-skinned peoples to life in the tropics, and this has been attributed to natural selection. Charles Darwin himself made this suggestion, although he hedged it with characteristic caution. The argument has been expanded since, and the idea has come to be widely accepted. This is sometimes cited today as a definite example of natural selection in Man.

In Darwin's day very little was known about the effects of sunlight on the human body or their relation to the spectrum of sunlight, nor about the geographical distribution of sunlight; and although a good deal has been learned since, the knowledge does not seem to have been widely disseminated. There are still many things to be explained, but enough is known for a reasonably critical examination of various aspects of the above thesis. When one attempts such an examination he cannot but be surprised that such far-reaching conclusions, based on such tenuous evidence, should have received so much credence.

MELANIN AND ITS POSITION IN HUMAN SKIN

The term melanin is applied to a type of finely granular, dark-colored substances in skin, hair, and some other organs of animals. While there is basic similarity in chemical composition there is a good deal of variety among the types of melanins. The color, which ranges through various shades of brown to black, is strongly affected by scattering of light by the pigment particles. The latter factor makes it difficult to relate the color to chemical composition, because of the difficulty it introduces into the measurement of absorption spectra.

In human skin the melanin is normally contained in the *epidermis*—a thin outer layer ranging from about 0.07 to 1.2 millimeters in thickness.

The relationship of the epidermis to other structures, and some approximate dimensions, are indicated in Fig. 1, B. In discussing the optical properties of skin, which concerns us here, it may be necessary to oversimplify the details of structure, which are quite complex. To this end I shall treat the epidermis as composed of two layers; the *malpighian*, made of living cells; and exterior to this the *corneum*, a dead layer which is produced from the living malpighian. The optical properties of these two layers differ greatly, although it would be difficult to demonstrate a sharp boundary between them, either optically or biologically. The distinction is useful, however, because the corneum obviously serves as an efficient barrier to ultraviolet light, greatly diminishing the amount that reaches the viable cells of the malpighian. Beneath the epidermis is the dermis, where are found a variety of structures, including the hair follicles, sebaceous glands, and sweat glands. The most superficial blood vessels are located in the dermis just underneath the epidermis. The melanin is produced in specialized cells, the *melanocytes*; but passes into neighboring cells of the malphigian, and may be carried up into the corneum. For a discussion of the melanocytes and the general histology of the epidermis the reader is referred to the excellent review of Billingham and Silvers (1960). In the white races the corneum and upper part of the malpighian may be relatively free of melanin except after injury—including the action of ultraviolet light which results in the familiar suntan. Negro skin, on the other hand, not only contains more melanin, but this is more evenly distributed throughout the epidermis, including the corneum.

The distinction made here between "negro skin" and "white skin" is perforce somewhat arbitrary. With few exceptions neither optical nor histological studies specify exactly the race or origin of the subject; and one can only assume that these terms apply to some reasonably well distinguished extremes of pigmentation. There seems to have been little or no optical study of skins of intermediate color, beyond reflectance measurements, which are not very instructive in the present regard.

While the study of evolution of races is one of separation of genotypes, the role of natural selection in such a process must depend upon interrelationships between phenotype and environment, and it is at this level that we find ourselves in the present discussion. Thus the mechanism of inheritance of the melanin of human skin need not enter directly here. This is fortunate because of the complicated nature of the problem, into which many facets of the phenotype may enter. For example, a matter of first importance is the penetration of light into the skin, and while one may measure this directly with some success the contributing factors might be very difficult to analyze. They include the absorption and light scattering properties of the various layers; and to what extent melanin is concerned in this must depend upon such factors as dispersion and distribution of the pigment, its chemical composition and spectral absorption, and the character of the other components. To disentangle the genetics pertinent to all these factors, some of which we do not understand at all clearly, would be a difficult matter indeed. For the recent status of genetic studies on melanin of mammal skin, the reader is again referred to Billingham and Silver (1960).

SUNLIGHT AND ITS PENETRATION INTO SKIN

Fig. 1, A shows the spectral distribution of sunlight at the surface of the earth, when the sun is at two different angles; curve 1 for the sun at zenith, and curve 2, for the sun at 60° (four hours) from zenith. The lower wavelength limit (i.e., in the ultraviolet) is set at about 0.29 μ by absorption of the shorter wavelengths by ozone in the upper atmosphere. The serrated appearance in the infrared part of the spectrum is due principally to spectral absorption bands of water vapor. The human eye detects only a small part of this spectrum, as the line labelled V indicates—normally a range from about 0.4 μ to 0.65 μ. Thus the eye is a poor judge of total sunlight, and no judge at all of the ultraviolet or infrared parts. The very short wavelengths of sunlight are those which cause sunburn, that is, a range from the lower limit at 0.29 μ to about 0.32 μ, as indicated at E in the figure. This is a very tiny fraction of the total (less than 0.1%) under the maximal conditions represented by curve 1; and is reduced to a negligible amount when the sun moves a few hours from zenith, as indicated by curve 2. On the other hand, total sunlight varies much less with zenith angle, that is, with season, latitude, and time of day, as is easily seen by comparing curves 1 and 2 for the whole range of wavelengths.

In order to interpret the various physiological effects of sunlight on Man, it is necessary to have some idea of the extent of penetration of the different wavelengths into the skin. But this is not an easy matter to determine, and although a number of dependable measurements have been made for

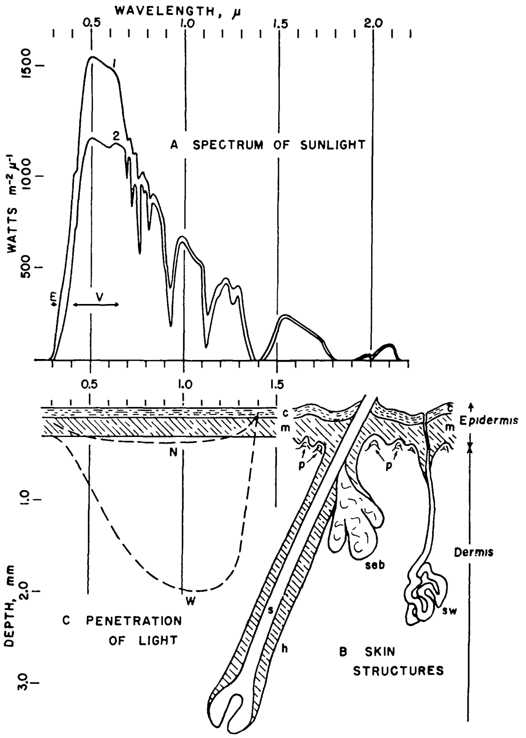

FIG. 1

A. SPECTRAL DISTRIBUTION OF SUNLIGHT AT THE SURFACE OF THE EARTH (after Moon, 1941). Curve 1, with sun at zenith. Curve 2, with sun at 60° (four hours) from zenith. V, spectral limits of human vision. E, spectral limits (within sunlight) for sunburn, antirachitic action and cancer induction.

B. DIAGRAMMATIC REPRESENTATION OF SKIN STRUCTURES. A schematized conception in which the dimensions should not be taken as generally representative, since the skin may vary widely in its thickness. c, corneum, i.e. horny layer of epidermis. m, malpighian layer of epidermis. sw., sweat gland. seb., sebaceous gland. p, the most superficial blood vessels, arterioles, capillaries, and venules. h, hair follicle. s, hair shaft.

C. PENETRATION OF LIGHT INTO HUMAN SKIN AS A FUNCTION OF WAVELENGTH. The curves N and W indicate for Negro and White skin, respectively, *rough estimates* of depths at which radiation of the corresponding wavelengths is reduced to 5 per cent of its incident value. There are insufficient data to make more than rough estimates, and these curves should be regarded as suggestive rather than in any way exact (see text). Curve W is based on Hardy and Muschenheim (1934, 1936), and on Kirby-Smith, Blum, and Grady (1942). Curve N is based on Hardy and Muschenheim (1934, 1936) and on Thompson (1955).

limited spectral regions these cannot be put together into more than a rough composite picture. Skin is made up of optically inhomogeneous layers, having different properties and varying in thickness and structure from one part of the body to another, and since different investigators have measured different samples of skin the results cannot be fitted together accurately. Even with more complete measurements no universal values for skin transmission could be assigned which would apply to skin from all parts of the body. The curves drawn in Fig. 1,C, which purport to show the depth of penetration of 5 per cent of the incident radiation, for negro skin (N) and for white skin (W), cannot therefore be accepted as more than rough estimates; but I think they will be useful and not misleading if they are employed only as approximate guides.

Referring to these curves, it is seen that the sunburning radiation (wavelengths shorter than 0.32 μ) is nearly all absorbed in the epidermis—it is here, then, that this radiation must have its effect. Penetration increases toward longer wavelengths—reaching the superficial blood vessels and other structures of the epidermis—until a maximum depth is reached around 1.0 μ in the infrared. The penetration then decreases rapidly as wavelength increases, there being little of importance beyond 1.4 μ, within the spectral range of sunlight. While some investigators have claimed greater transmission of some wavelengths in the visible and infrared, it seems clear that no portion of the radiation of sunlight penetrates in important amount below a few millimeters. General discussions often fail to recognize the great importance of differences in penetration of different spectral regions of sunlight, and that different regions have different physiological effects (e.g., Coon, Garn, and Birdsell, 1950).

Faulty measurements have led from time to time to misconceptions regarding the depth of penetration of sunlight into skin. Important errors may enter in two ways: (1) low measurements are obtained when scattering is neglected, this error being increased by drying out of the skin sample; (2) if care is not taken to minimize heating of the skin by absorbed radiation, or proper shielding is not provided, the measurements may indicate too great penetration. In preparing the curves in Fig. 1, C, the measurements of Hardy and Muschenheim (1934, 1936), of Kirby-Smith, Blum, and Grady (1942), and of Thomson (1955) have been relied upon. For a discussion and other references, see Blum (1945a).

The curves in Fig. 1, C neglect the specific absorption bands of hemoglobin, carotenoids, and other substances. Hemoglobin in the superficial vessels absorbs the shorter wavelengths of the visible spectrum quite strongly, so that light reflected back in predominantly red, this giving the ruddy tint to many complexions. The curves indicate that negro skin is less transparent in the visible spectrum than white skin, and this is no doubt due chiefly to the difference in melanin content. But negro skin also has a thicker corneum than white skin, an important factor with regard to sunburning radiation (see below).

PHYSIOLOGICAL EFFECTS OF SUNLIGHT ON MAN, AND FACTORS AFFECTING THEM

Sunlight has several physiological effects on Man, which may be separated into two general categories on the basis of the spectra involved: (1) the effect of adding the energy of sunlight to the heat load of the body; and (2) specific effects of those wavelengths that cause sunburn, which also have carcinogenic and antirachitic action. The latter are classed together, not because of physiological similarity, but because they are produced by the same spectral region of sunlight, since this factor is of basic importance if we are to relate them to geographical distribution.

At least one other, minor, effect will be mentioned below, and there are certain pathological conditions brought about by parts of the solar spectrum (e.g. see Blum 1941, 1950) which are so rare that they are of no interest in the present discussion. There are also diseases of domestic animals in which sunlight is the precipitating factor; but which, for physiological or dietetic reasons do not have their counterpart in Man (e.g., Blum, 1941; Clare, 1955).

THE SOLAR HEAT LOAD

In the standard resting state the human body produces a certain amount of heat by its own metabolism, which must be dissipated in some way. If the body becomes active this heat production increases, and in case of severe exercise may rise several fold above the resting condition. The human body has several means of getting rid of this heat load. The blood, heated internally, comes to the surface to pass through the vessels of the skin, and a certain amount of heat may be *conducted* to the surrounding air. The rate of dissipation is increased by movement of air over the skin, that is, *convection* is a factor. Another important means of dissipating heat is by *evaporation* of water from sweat at the surface of the skin. A factor less commonly recognized and more difficult to assess is the loss to cooler surroundings by *radiation*.

All bodies emit radiation according to their temperature and size. In the ordinary range of temperatures, all this radiation is in the infrared spectrum and hence invisible, although it may be detected through the sense organs of the skin as a sensation of coolness, warmth or, if intense, of pain (Oppel and Hardy, 1937 a, b; Hardy and Oppel, 1937). The human body radiates to its surroundings and receives radiation from them; it may gain or lose in the exchange, for example, it gains heat from a hot radiator or loses heat to a block of ice, even though these objects are at some distance. But there is also a constant imperceptible or barely perceptible exchange with objects nearer the temperature of the body—indoors with the walls of the room, outdoors with hot soil or rocks or the cool foliage of plants. It is clear that the effective temperature of the environment, with respect to the human body, is a complex matter, and is not to be measured adequately in terms of the temperature and humidity of the ambient air alone.

Out-of-doors one may receive an important amount of heat from direct exposure to the sun; that is, the total spectrum of sunlight impinging upon the body adds a certain amount of heat load. On the other hand, the body may lose a considerable amount of heat by radiation to the clear sky, which is, effectively, at a lower temperature than the body, the amount of loss through this channel being largely determined by the quantity of water vapor in the atmosphere. This radiation to "space" may be an important factor in desert areas, where the atmospheric water vapor is low (see Blum, 1945b, for a consideration of various factors involved under desert conditions).

It is clear that the human body is constantly exchanging heat with its environment in a number of ways. Hence the amount of heat lost, and the means of losing it, must vary according to the particular environmental conditions, and some of these may be difficult to evaluate. The radiation factor is among the most difficult to assess because it involves both the geometry of the human body and that of the surroundings, since the amount of heat exchange by radiation must depend upon the profiles which the radiating masses present to each other (see Blum, 1945b). The heat dissipation is modified by clothing, which may prevent the conduction of heat away, and may absorb or reflect the incident radiation according to the wavelengths concerned. Thus, dissipation of the heat load—which is essential if the man is going to live—becomes quite a complicated matter, and one that can be treated only with reference to the particular complex of environmental conditions that may obtain.

If the conditions are such that the man cannot adequately dispose of his heat load the temperature of the body must rise, but there are no climatic conditions in the world inhabited by Man where death is likely to result directly from raising the body temperature—the body is not likely to be "cooked" by coagulation of its proteins. Even under maximum conditions, the energy of sunlight is not nearly sufficient to burn the skin by heating unless concentrated by means of a lens, sunburn being caused by ultraviolet light acting in a very different way. Contrary to common impression, there is no evidence that the brain may be unduly heated by exposure of the head to direct sunlight (see Aron, 1911).

A man may, however, suffer collapse due to circulatory failure under environmental conditions that lead to excessive water loss, as, for example, in desert climate, and sunlight may be a factor in this. If the intake of water is not sufficient to compensate for the loss by evaporation and through other channels, the blood volume may fall so low that the heart can no longer maintain sufficient blood flow. The resulting collapse may be sudden, although the condition of low blood volume has accumulated for hours. Being usually associated with high environmental temperature, such collapse has been called "heat stroke," or—since it often occurs when the person is exposed to the sun—"sunstroke." The factors contributing to the depletion of water may be complex. They are most easily analyzed, perhaps, in the case of desert conditions where the temperature of the air is above that of the body, so that loss of heat by conduction and convection is virtually nil, and cooling must be accomplished almost entirely by evaporation of water from sweat. Such conditions may be exaggerated by the solar heat load, coming both directly from sunlight impinging on the body and also from reflection and reradiation from heated surroundings. Walking under these conditions, a man may lose as much as one liter of water per hour, and if this is not adequately replaced the blood volume must be eventually reduced, with ultimate collapse (Adolph et al., 1947).

TABLE 1

Estimated relative absorption of sunlight by White and Negro skin, based on Heer (1952); values for color temperature 6000°C, which is approximately that of the photosphere of the sun.

WHITE		NEGRO	
untanned (inner forearm)	tanned (forehead)	untanned (inner forearm)	tanned (forehead)
1.00	1.16	1.36	1.46

Under such conditions the radiant energy absorbed from sunlight may constitute a critical increment of heat load, and the man who can most readily reduce this increment would have an advantage, and might survive longest. In this case the man whose skin reflected more of this load should be better off. Table 1 indicates that negro skin absorbs roughly 30 per cent more sunlight than white skin; but it is to be remembered that this figure applies to only a part of the total heat load. Thus, if a Negro and a white-skinned man walked side by side, naked, in direct sunlight, across a desert where the temperature of the air was above that of the body, the Negro might be expected—other things being equal—to collapse before the white man. But these particular competitive conditions are not likely to be often met. If the bodies of both men were similarly clothed or otherwise covered any advantage would, of course, be largely lost.

It has been suggested that the melanin of the Negro, because it brings about greater local heating of the skin, leads to more profuse sweating, and that this is of advantage to him in the tropics Thomson (1951) has recently shown that sunburn tends to reduce sweating in white skins to a greater degree than in negro skins, and this might conceivably give the Negro a certain advantage in this regard. But while profuse sweating may confer a somewhat greater degree of comfort under conditions where water is rapidly evaporated, it could only increase the water loss, and this would seem to be the factor of real importance—a disadvantageous one—with regard to survival.

Taking all things into consideration, it seems necessary to assume that the possession of a dark skin should be a disadvantage to the Negro, as regards heat load and life in hot desert areas, but that the disadvantage is not a very great one, and probably of little importance under his usual conditions of life. It would seem that, if anything, his melanin pigment might be of some, although limited, advantage to the Negro in a cooler climate where it was important to conserve rather than to lose heat.

EFFECTS OF ULTRAVIOLET LIGHT

We now come to consider some other effects of sunlight in which melanin may also play a role. These are: (1) *sunburn*, a phenomenon with which everyone is acquainted; (2) *carcinogenesis*, i.e., the induction of cancer of the skin; and (3) *antirachitic action*, the prevention of rickets, a disease of bone. All three effects are caused only by wavelengths shorter than about 0.32 μ, which, as we have seen, constitutes a very tiny fraction of sunlight. The fact that all three effects have the same long wavelength limit does not mean, however, that all are closely related. The first and last are very separate entities; the second is probably related to the first but this cannot be said with complete assurance (see Blum, 1959).

Sunburn

To most readers sunburn means an unpleasant blistering of the skin following exposure to sunlight. I use the term, however, to include a complex of related effects, ranging from a mild reddening of the skin, or *erythema*, to the severe blistering just mentioned. As a result of any degree of sunburn, melanin may increase in the epidermis—this we recognize as *suntan.* (For a more complete discussion, of sunburn, with extensive references see Blum, 1955a).

The erythema is the manifestation of dilation and consequent increased blood content of the minute vessels lying just beneath the epidermis. The photochemical reaction bringing about the dilation of the vessels has its locus in the epidermis, however, principally in the viable malpighian, where histological examination shows that cells may be injured or killed. The dilation of the vessels in the dermis is presumably due to substances which diffuse down from the injured epidermis. The corneum or outer horny layer of the epidermis protects against sunburn by absorbing a large proportion of the incident sunburning radiation before it reaches the malpighian—it is a very effective absorber.

While it seems safe for our purposes to consider the malpighian to be the locus of the principle changes underlying sunburn, the overlying corneum serving only a protective function, certain factors should be mentioned in this regard. Studies by Rottier and Mullink (1952) and Rottier (1953) indicate that photochemical changes brought about in the corneum may contribute to the erythema. But the eliciting wavelengths are, at least for the greater part, shorter than those found in sunlight, so this finding can have little or no concern in the present context. The sunburning radiation is absorbed in greatest part in the epidermis; but, at least in some white skins that have not been exposed for some time the longer wavelengths may penetrate to a small extent below, particularly in unexposed areas. The small fraction which reaches the minute vessels of the dermis may cause damage there, as shown by the inhibition of erythema (Blum and Terus, 1946); and it is possible that this may contribute to the blistering that occurs in some cases after severe exposure to sunlight.

The brownish color, or *suntan*, which develops some days after exposure of white skins to sunlight, involves the production of new melanin in the epidermis, although the earliest stage may represent migration of melanin that is already present, to a more superficial position. The formation of new melanin seems to be a response to injury—it also follows other kinds of insult to the epidermis. The color begins to fade after a time, but traces may persist for years. The fading is not all the result of removal or destruction of the melanin, but represents in part bleaching of the pigment by reduction, and the pigment may be subsequently darkened again by oxidation. It was shown just before the second World War by Henschke and Schultze (1939 a, b), that the bleached pigment may be caused to darken by exposure to longer wavelengths than those that elicit its formation. These wavelengths—0.3 μ to 0.44μ —are much more plentiful in sunlight, and much less affected by the angle of the sun, than are those that produce the suntan. Darkening of preformed pigment may also be brought about by endocrine secretions, and probably by other influences mediated by the circulation. The pigment-darkening reaction seems to have no physiological significance in itself; but it is interesting to us, because it shows that the color of the skin cannot be taken as a reliable quantitative index of the amount of melanin present in the human epidermis. The degree of bleaching and darkening seems to vary widely in white skins.

It is common knowledge that the development of suntan is generally accompanied by a decreased sensitivity to sunburn, and it is perhaps natural to relate the two events—the eye tells us that the skin has darkened, and we may jump to the conclusion that it transmits less light of all wavelengths, including those we do not detect. About 1899, Niels Finsen performed a simple experiment which he supposed to prove this point. He painted areas of his arm with India ink before exposing it to sunlight. When he scaled the ink off later he found that the areas it had covered had not been sunburned. He reasoned that the melanin in the skin has the same protective effect as the India ink. Very little being known about sunburn at the time, he did not recognize that while India ink is opaque to ultraviolet light, he had no evidence that the same was true for melanin. Nevertheless Finsen's interpretation was accepted for 20 years without question, and still is by the majority of people.

About 1920, however, doubts began to arise as the result of observations by several investigators. It was noted that the immunity to sunburn disappears much more rapidly than the suntan—the immunity is usually gone in two months, whereas the tan may persist for years. And it was found that vitiliginous and albino skins, which do not form melanin, may develop a degree of immunity to ultraviolet light. An explanation was given in 1926 by Guillaume, who found that after exposure to ultraviolet light the epidermis, particularly the corneum, becomes thickened, and attributed the accompanying immunity to the enhanced absorption of the sunburning radiation in the latter layer. His findings were soon confirmed, and somewhat later it was shown by direct measurement that albino mouse epidermis increases its absorption of ultraviolet light after repeated exposures (Kirby-Smith et al., 1942). As a result, it was generally accepted by those actively working in this field that the relative immunity to sunburn which follows exposure is due to a resultant thickening of the outer horny layer, although the acceptance of the role of melanin pigment in this regard persisted, generally, outside this small group. After all, there seemed no good reason to think that melanin should be a better absorber of ultraviolet light than the protein which makes up the greater part of the corneum.

But Negro skin is very refractory to sunburn, and if this could not be accounted for by high melanin content, some other explanation was needed. The epidermis of Negro skin had been reported to be thicker than that of white skins, and it seems to have been generally assumed by those working in this field that it was the thicker corneum which made the Negro skin less susceptible to sunburn—at least I accepted this explanation myself. A few years ago, however, Thomson (1955) made a comparative study and found that Negro corneum was indeed thicker than that of white skins, but also that the former was more opaque to the sunburning radiation per unit thickness. It seems reasonable to attribute the greater opacity to the higher melanin content, although this may not be fully established. The corneum is composed principally of protein which absorbs the sunburning radiation strongly; but its effectiveness as a protective light-filter is greatly enhanced by its flake-like structure, which scatters the light and thus increases the path-length through which the light rays must travel in the absorbing medium. The amount of melanin is much less than that of the protein, and it is unlikely that it is a much better absorber of the sunburning radiation; but because it is made up of small particles it is an effective scattering agent, and this may make it an important additional factor in the absorption of the sunburning radiation by the corneum. Thus, after all, the melanin may play a considerable protective role, as regards sunburn—but all we know definitely is that the horny layer of the epidermis of Negro skin is a more effective shield against the sunburning radiation than is the epidermis of white skins. Thus, while it is reasonable to assume that melanin plays a role in protection against sunburn—and this assumption will be made in the following discussion in this paper—it should be kept in mind that the point is not definitely proven.

But can immunity to sunburn be regarded as having survival value? Sunburn is essentially an acute effect, which while it may be briefly debilitating in severe cases involving a considerable area of the body, does not cause prolonged, systemic damage. It is seldom disfiguring, although it may cause deterioration of complexion after many years of exposure—this coming late in the lifespan is not likely to play a role in sexual selection. In many white societies suntan is looked upon today as a sign of health and beauty. As regards the female sex, fashion reversed itself in this regard about half a century ago, but the survival of the societies concerned does not seem to have been seriously affected thereby.

Cancer of the Skin

Although it does not seem to be a matter of common knowledge, clinical, experimental, and geographical evidence converge to indict the sunburning portion of sunlight as a principal cause of cancer of human skin (see Blum, 1959). The cancers involved grow from the malpighian layer of the epidermis—many of them are not very malignant and mortality from this cause is relatively low. In white skinned people these cancers are limited almost exclusively to the exposed parts, particularly the face. They are very rare in Negro skin, and when they occur show no preference for the exposed parts. There seems every reason to draw a parallel with the Negro's immunity to sunburn, attributing his low incidence to skin cancer likewise to the opacity of his corneum. Negroes do not show comparable immunity to other types of cancer, and indeed it is reported from the Kenya region of Africa that cancers of the skin occur not infrequently among natives in association with parasitic infection (Vindt, 1935).

Skin cancer does not, so far as we know, result from a single bout of sunburn, no matter how severe, but is a cumulative, "chronic" effect of exposures to sunlight repeated over a long period (Blum, 1959). Since these cancers are usually not lethal, and not very disfiguring except in late stages—as a rule they do not appear until late in life, well after mating—it would seem unlikely that cancer due to sunlight could have any great effect on racial survival in the sense of biological evolution.

Clear distinction should be made between these cancers and the very dangerous, though fortunately very rare, malignant melanomas which are cancers of a different type. The latter occur largely on parts of the body not exposed to sunlight,

Antirachitic Action

The same wavelengths that cause sunburn bring about an entirely different photochemical reaction—transformation of precursor substance into vitamin D. The site of the reaction can hardly be deeper than the epidermis, where these wavelengths are principally absorbed. It is difficult to estimate the effect of melanin on the efficiency of sunlight in producing Vitamin D—it might decrease formation by absorbing some of the effective radiation, or it is conceivable that by scattering in the corneum and consequent increase in path length, it might even enhance vitamin production in that layer.

Vitamin D is required for bone development and if it is lacking, the bone disease, rickets, results. Exposure to sunlight may prevent or cure this disease; but Man is not strictly dependent on sunlight in this regard, since vitamin D may also be introduced in the diet, and under most conditions of life the role of sunlight is probably not very great. Rickets is most frequent under crowded urban conditions where both diet and sunlight are limited. The disease most often affects children, and, since it is of crippling nature, its prevention could have survival value. But because of the complicating factor of diet, it would be difficult to estimate just how important sunlight might be as regards a given population living under natural conditions.

A TENTATIVE BALANCE SHEET

It is clear that the part played by melanin in the physiological responses of the human body to sunlight has aspects which require analysis in different ways, with regard not only to sunlight but to other environmental factors as well. Any classification of these aspects with regard to their advantages or disadvantages must be a very rough one. Still, it may be worth while to draw up a tentative balance sheet at this point in our discussion. In the one that follows, plus or minus ratings indicate estimated relative advantage of the high melanin content of negro skin as compared to the low melanin content of white skin.

PHYSIOLOGICAL EFFECT	NEGRO SKIN	WHITE SKIN
Solar heat load at high environmental temperature	−	+
Sunburn	+	−
Cancer of the skin	+	−
Prevention of rickets	±	±

Presented in this way the result seems equivocal, Negro skin having an advantage as regards sunburn and skin cancer, but a disadvantage as regards heat load at high ambient temperature. The advantage or disadvantage as regards antirachitic action is uncertain, but the latter seems the more probable. The balance sheet avoids the question of whether the advantages listed have significant survival value or not, and also how they might be related to the distribution of sunlight with latitude, that is, between the tropic zone and other zones. The latter question must now be taken up.

DISTRIBUTION OF SUNLIGHT WITH LATITUDE AS REGARDS PHYSIOLOGICAL RESPONSES OF MAN

On the whole, those who have assumed that Negroes inhabit the tropics because their skin pigment adapts them to the conditions of insolation in that zone, seem to have given little attention to the spectral character of sunlight and its distribution with latitude. It seems to have been generally assumed that since the tropics are hot there is more sunlight there, but the problem is

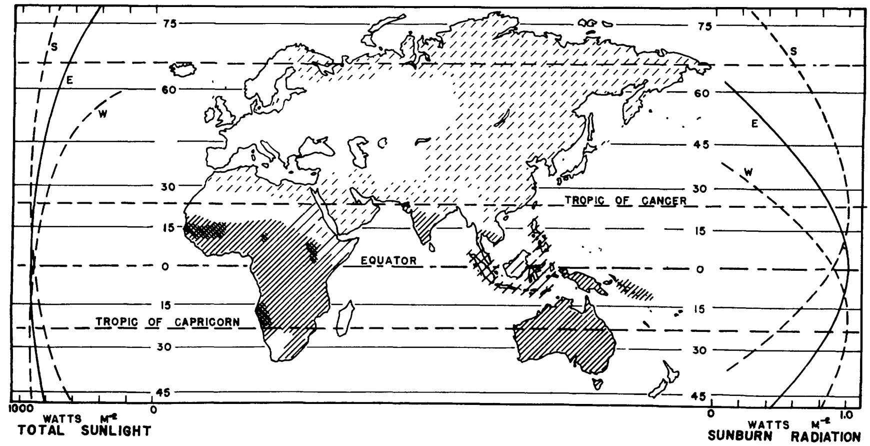

FIG. 2. Map of the distribution of brown skin color (After Fleure, 1945)

On the left, distribution of total sunlight with latitude. E, at equinox; S, at summer solstice; W, at winter solstice. On the right, distribution of sunburning radiation (wavelength shorter than 0.32μ) with latitude. E, at equinox; S, at summer solstice; W, at winter solstice. The curves on the right and left are based on values from Moon (1941). Note that the curves for summer and winter solstices are distorted by the Mercator projection. These curves, based on light incident upon a surface normal to the sun's rays, neglect scattering from the sky, which may be very important in the case of the sunburning radiation, and also neglect geometrical relationships of the human body profile with respect to the radiant environment. They are thus to be considered only as rough guides.

not so simple as this. Reference to Fig. 1, A will show that total sunlight decreases less rapidly as the sun moves away from the zenith than does the sunburning portion. Obviously the solar heat load, being related to total sunlight, must vary differently with latitude than does the sunburning radiation.

Fig. 2 gives a rough, general idea of the distribution of sunlight with latitude. Represented on the left of the map are distributions, with latitude, of the total energy of sunlight at noon under three conditions: (W) with the sun at its northernmost excursion (summer solstice), when it is over the tropic of cancer (23° 44′ N); (S) with the sun at its southernmost excursion (winter solstice) when the sun is over the tropic of capricorn (23° 44′ S); and (E) with the sun over the equator (equinox). On the right of the figure are represented the distributions of the sunburning fraction of sunlight at the same respective positions of the sun. It is noted that the sunburning radiation is much more "concentrated" in terms of latitude than total sunlight; the amounts of energy are, of course, very different in the two cases.

It is clear from the diagram on the left, that at some times of the year a part of one temperate zone may receive more total sunlight than does a part of the tropic zone; indeed, the difference in this regard between the temperate and tropic zones is not so great as is commonly conceived. Even the Arctic and Antarctic zones receive a considerable amount of solar energy during parts of the year. So it is seen that the effect of the solar heat load in exacerbating collapse due to water loss should not be restricted to the tropics—at the time of the summer solstice, for example, other things being equal, it should be just as likely to occur at 47° N (about the latitude of Zürich or Quebec) as at the equator. The fact that the sun crosses the equator twice during the year, but reaches the tropic of cancer only once, should not be of importance in this regard, since "heat stroke" is an acute effect, that is, one that involves, at most, a few days' exposure to the sun. Much more important would be other aspects of the environment such as desert conditions, which are to be found in the temperate zones as well as in the tropics. As has been said, high melanin content of the skin should be a slight disadvantage under those conditions. But it could be of limited advantage in a cooler climate where heat gain might be desirable.

In a recent paper, Cowles (1959) stresses the advantage of black or brown pigment in reducing visibility, and suggests that this might have had survival value for Man, in the role either of predator or pursued, at some time in his evolution.

Whatever the importance of this factor in natural selection, it would seem to be one which should be related more to local environmental situations than to a global distribution such as has been supposed as regards adaptation of Negro skin to life in the tropics. From the curves in Fig. 2 it may be seen that the visible portion of sunlight, which is that part pertaining to Cowles' thesis, varies relatively little in its maximum intensity, from Tropic to Temperate zones, or even the Arctic, where summer sunlight is bright. On the whole it would seem that Cowles' argument should apply more to noctural vs. diurnal life, than to geographical distribution.

It is to be noted from the curves on the right of Fig. 2 that the sunburning radiation varies more with latitude than does the total solar heat load. But nevertheless part of the temperate zones receive relatively high amounts at certain times of the year. At summer or winter solstice the chances of being sunburned should be about as great at 47° N or S, respectively, as at the equator, and with sufficient exposure sunburn may occur above the Artic Circle. Of course, sunburn is an acute effect, and the situation should be somewhat different as regards the "chronic" effects, carcinogenesis and antirachitic action—because these depend on the total exposure to the sunburning radiation throughout the year, and the sun is near zenith in the tropics for a greater part of the year than it is in the temperate zones. But, nevertheless, parts of the temperate zones receive a relatively high annual incidence of the sunburning radiation.

In the United States the occurrence of skin cancer within the white population shows a north-south distribution which fits reasonably well with estimates of the distribution of the sunburning radiation, within the latitude range (32° to 41° N) (see Blum, 1959). But at most the incidence of these cancers is small, and, as has been said, probably could have little effect on racial survival. The Negro population has a very low incidence of skin cancer, but I think no one would venture to say that this in itself has played a significant role in the relative distribution of the Negro and White populations in our country. Fairly recent historical events have been obviously much more important in determining this distribution than has natural selection. Would it not seem reasonable to think that, correspondingly, at a much earlier time events not directly related to the environment played a dominant role in determining the distribution of the Negro and White races in the eastern hemisphere rather than biological adaptation to the climate of the particular areas they now inhabit?

As regards historical factors in the distribution of races, the Bushmen of Southern Africa offer a most interesting example. These people, at present restricted to the region of the Kalahari Desert, occupied a much greater area, including quite different terrain and climatic conditions, at the time of the entrance of Europeans into this region. Subsequently the Bushmen have been pushed gradually out of other areas and have taken refuge in the Kalahari. Here the remnants of the race live under very difficult conditions in an arid land with relatively sparse vegetation. They appear to have adapted themselves to a precarious existence under these conditions by learning to take advantage of what corners of the environment they may grasp, rather, so far as we know, than by any particular physiological adaptation. If we read the record right, they have lost at least one remarkable facet of their previous culture in doing this, the making of the rock paintings that have been attributed to them—not a surprising loss considering the complete preoccupation with survival which seems to be their present lot. (See Willcox, 1956; Van der Post, 1958; Thomas, 1959). A cultural change resulting from recent historical events imposing a new habitation area would thus seem to account for the Bushmen's present adjustment to a rigorous environment, rather than selection on a biological basis. May a similar situation not affect other distributions and cultures where the history is unknown, being farther in the past?

My information regarding the Bushmen has been greatly increased since this paper was first written, by conversations with Dr. B. Kaminer, who has studied these people at first hand in the Kalahari, and has taken color photographs of them. Dr. Kaminer pointed out to me by means of his photographs, the great amount of dirt and desert soil which these people, who have no opportunity to bathe, carry about on their skins. Even without physical measurements one can be quite sure, I think, that the amount of sunburning radiation that reaches the skin is greatly reduced, and consequently the importance of melanin as protection in this regard. Seeing these photographs one might conclude that the solar heat load should be determined more in terms of the reflectance of the soil from the local terrain, than in terms of that of the uncoated skin. The fact that the Bushmen tend to be brown rather than black would not seem of great importance. This observation seems still further to confuse the question of the adaptive value of melanin in "feral" Man or his ancestors, making its importance even more questionable.

Finally, we may ask whether the distribution of the dark-skinned races really fits very well with the distribution of sunlight. The comparison in Fig. 2 does not seem to give very strong support. The map shown there is drawn after Fleure (1945), who has attempted to explain the distribution of skin color in part in terms of local climatic conditions, but his argument does not take into account the nature of the physiological factors concerned. Actually, the comparisons made in the present paper, regarding melanin pigment and physiological effects of sunlight, are based on what is known about White and Negro skins, since applicable data are only available regarding these; to what extent the brown-skinned peoples may fall into an intermediate position with regard to the physical and physiological factors that have been discussed we do not know.

A HISTORICAL NOTE

In 1871, Darwin wrote in his *Descent of Man* (p. 200 in the Appleton edition of 1913), as follows: "Dr. Sharpe remarks, that a tropical sun, which burns and blisters a white skin, does not injure a black one at all. . . . I have been assured by a medical man that some years ago during each summer, but not during the winter, his hands became marked with light brown patches, like, although larger than, freckles, and that these patches were never affected by sun-burning, while the white parts of his skin have on several occasions been much inflamed and blistered. . . . Whether the saving of the skin from being thus burned is of sufficient importance to account for a dark tint having been gradually acquired through natural selection, I am unable to judge."

The complete passage is of interest, but to conserve space I have quoted only those parts that seem particularly cogent here. It is to be noted that Darwin was properly cautious about his attribution of dark skin to natural selection. The evidence of association of relative immunity to sunburn with pigmentation we need not question, although, as is not infrequently the case, Darwin is using information at secondhand. But one may question the interpretations, while remembering how little was known at the time about the action of sunlight.

The case of apparent immunity of pigmented patches on white skin to sunburn, is intriguing in the light of present knowledge. Was this, perhaps, a case of *vitiligo*?

Although Ritter had shown the existence of ultraviolet light in the sun's spectrum in 1801, only about the middle of the century was it realized that sunburn is caused by such radiation. This came about with an observation by the physicists Foucault and Despretz who were accidentally sunburned by the radiation from an electric arc with which they were experimenting; the matter was reported in a brief note by Charcot (1858). It had been thought before that time that sunburn resulted from heating the skin, and Darwin may still have been under this impression when he wrote. A more definitive demonstration that sunburn is due to ultraviolet light was reported by Widmark in 1889. Some of the more recent developments have already been noted.

Another early suggestion that skin color favors the residence of Negroes in the tropics is of interest. In 1887, Wedding presented, in a brief note before the Berliner Gesellschaft für Anthropologie und Urgeschichte, what appears to have been the first account of buckwheat poisoning in sheep, giving proof that sunlight is a precipitating factor. He showed that animals fed on the buckwheat plant developed lesions of the skin when subsequently exposed to sunlight, but that areas of the skin which he covered with tar did not display the lesions. We know today that this condition is brought about by a substance present in the buckwheat plant. When the plant is ingested, this substance gets into the blood stream and is carried to the skin, which it photosensitizes to wavelengths in the visible spectrum. Man seems never to eat enough buckwheat to become photosensitized in this way, and the basic photochemical mechanism is not related to sunburn (see Blum 1941, 1950). Clearly, the phenomenon observed by Wedding has nothing to do with the normal responses of human skin to sunlight, but he was unaware of this—very little being known about such responses at that time, particularly with regard to spectral relationships. He suggested that the pigment in the Negro skin offered protection in the same way as did the tar he painted on his sheep, and that this was of advantage to the

Negro in the tropics. He even went so far as to suggest that a ship be sent to the tropics with half the crew painted with walnut stain, for the purpose of studying the effects of tropical sunlight. His paper makes no mention of Darwin or natural selection.

I have often wondered how Wedding's paper came to be presented to an anthropological audience rather than to veterinary scientists. It described a discovery of first importance to the latter, but introduced only a misconception with regard to the study of Man.

GENERAL REMARKS

In examining the interrelations between certain physiological responses of Man and a particular facet of his environment—sunlight—we have found the situation more complex than it is generally thought to be. This particular environmental factor has more than one separate physiological effect on Man, and other environmental factors may play important roles in the overall result. The specific thesis examined—that high melanin content of the skin adapts to life in the tropics because it offers protection against sunlight—seems to have little to recommend it. The melanin might provide a degree of protection in some cases but could be detrimental in others. On the whole, one may doubt that the possession of melanin pigment makes very much difference one way or the other, and that it could serve as an important "handle" for natural selection seems most unlikely. And when we examine the distribution of sunlight, we find that the geographical distribution of skin color really does not correspond at all well with the suppositions of the thesis.

The particular point may not seem worth the laboring I have given it, and the removal of the notion from our thinking might not, in itself, affect very greatly our concepts of races and their origins. But certain doubts may be raised. We may be led to ask whether there are not other instances where survival value has been attributed to anatomical or physiological factors which it would be difficult to substantiate, or where pertinent aspects of the environment are not well understood. The case of adaptation of warm-blooded animals to cold climates, where Scholander (1955) has pointed out that the physiological and environmental factors concerned do not coincide with commonly accepted ecological and evolutionary ideas, seems another cogent example. Surely we may question the evidence in such cases without challenging the basic role of natural selection—I believe no one who has read my writings on evolution would accuse me of making such a challenge (e.g., Blum, 1955b, c).

What we really deal with here is the relationship between phenotype and environment, as I have said earlier, selection depending upon the closeness of fit between the two. Complete fitting is not to be expected in the complicated situations that prevail in nature. Rather, one may think of the over-all agreement as the algebraic sum of many positive and negative values, representing advantageous and disadvantageous facets of the phenotype with respect to corresponding facets of the environment. If the sum of these values is positive, the phenotype, and consequently the genotype, should have selective advantage. The total balance sheet could contain many plus and minus values, large and small; the relationship of melanin to sunlight seems one of minor weight in the survival of human races. It might be extremely difficult to analyze the situation accurately, and one could go badly astray by underestimating the complexity of the factors concerned.

If a somewhat facetious illustration is permitted, I may point out that if we consider only the role of melanin pigment with regard to sunlight, Negro skin would seem to be highly adaptive to life on one of the snow-capped mountains near the equator. Here the sunburning radiation should be high, being enhanced by reflection from the snow field, and the protection afforded against it might be assigned a high positive value. The low reflectance of total sunlight from the skin could be also advantageous in this situation in maintaining body temperature by increasing the solar heat load. The importance of antirachitic action, whatever its sign, would seem to be minor compared to the general problem of maintaining adequate nutrition. The negative factor of concealment might also be slight because there would be so little wild game anyway. I am afraid that in spite of the positive values assigned to melanin, the over-all fitting between phenotype and environment would have a rather high negative value in this case.

It seems so easy to read adaptive value into almost any aspect of an organism, particularly if our understanding of both physiology and environment is incomplete, as must so often be the case. If we yield to the temptation to find adaptive value in every racial or specific characteristic, do we not run the risk of reaching a position not unlike that of Dr. Pangloss—in spite of Candide's observations, and our own?

LIST OF LITERATURE

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