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The evolution of human skin coloration

Skin color is one of the most conspicuous ways in which humans vary and has been widely used to define human races. Here we present new evidence indicating that variations in skin color are adaptive, and are related to the regulation of ultraviolet (UV) radiation penetration in the integument and its direct and indirect effects on fitness. Using remotely sensed data on UV radiation levels, hypotheses concerning the distribution of the skin colors of indigenous peoples relative to UV levels were tested quantitatively in this study for the first time.

The major results of this study are: (1) skin reflectance is strongly correlated with absolute latitude and UV radiation levels. The highest correlation between skin reflectance and UV levels was observed at 545 nm, near the absorption maximum for oxyhemoglobin, suggesting that the main role of melanin pigmentation in humans is regulation of the effects of UV radiation on the contents of cutaneous blood vessels located in the dermis. (2) Predicted skin reflectances deviated little from observed values. (3) In all populations for which skin reflectance data were available for males and females, females were found to be lighter skinned than males. (4) The clinal gradation of skin coloration observed among indigenous peoples is correlated with UV radiation levels and represents a compromise solution to the conflicting physiological requirements of photoprotection and vitamin D synthesis.

The earliest members of the hominid lineage probably had a mostly unpigmented or lightly pigmented integument covered with dark black hair, similar to that of the modern chimpanzee. The evolution of a naked, darkly pigmented integument occurred early in the evolution of the genus *Homo*. A dark epidermis protected sweat glands from UV-induced injury, thus insuring the integrity of somatic thermoregulation. Of greater significance to individual reproductive success was that highly melanized skin protected against UV-induced photolysis of folate (Branda & Eaton, 1978, *Science* **201,** 625–626; Jablonski, 1992, *Proc. Australas. Soc. Hum. Biol.* **5,** 455–462, 1999, *Med. Hypotheses* **52,** 581–582), a metabolite essential for normal development of the embryonic neural tube (Bower & Stanley, 1989, *The Medical Journal of Australia* **150,** 613–619; Medical Research Council Vitamin Research Group, 1991, *The Lancet* **338,** 31–37) and spermatogenesis (Cosentino *et al.*, 1990, *Proc. Natn. Acad. Sci. U.S.A.* **87,** 1431–1435; Mathur *et al.*, 1977, *Fertility Sterility* **28,** 1356–1360).

As hominids migrated outside of the tropics, varying degrees of depigmentation evolved in order to permit UVB-induced synthesis of previtamin D_3. The lighter color of female skin may be required to permit synthesis of the relatively higher amounts of vitamin D_3 necessary during pregnancy and lactation.

Skin coloration in humans is adaptive and labile. Skin pigmentation levels have changed more than once in human evolution. Because of this, skin coloration is of no value in determining phylogenetic relationships among modern human groups.

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Introduction

Melanin accounts for most of the variation in the visual appearance of human skin. Variation in cutaneous melanin pigmentation in humans has been attributed to many factors, with most authorities agreeing that the observed variations reflect biological adaptations to some aspect of the environment. Many hypotheses have centered on the role of melanin pigmentation in the regulation of the penetration of sunlight and, more specifically, ultraviolet (UV) radiation, into the skin. The more highly melanized skins of indigenous tropical peoples have been said to afford greater protection against the deleterious effects of UV radiation, such as sunburn, skin cancer (Fitzpatrick, 1965) and nutrient photolysis (Branda & Eaton, 1978). The more lightly pigmented skins of peoples inhabiting latitudes nearer the Arctic have been explained as adaptations to the lower UV radiation regimes of those regions and the importance of maintaining UV-induced biosynthesis of vitamin D_3 in the skin (Murray, 1934; Loomis, 1967). Other adaptationist hypotheses have emphasized the role of skin pigmentation in regulating sensitivity to frostbite (Post *et al.*, 1975*a*), in disease prevention (Wassermann, 1965, 1974), thermoregulation (Roberts & Kahlon, 1976; Roberts, 1977), concealment (Cowles, 1959), or combinations of these factors (Roberts & Kahlon, 1976; Roberts, 1977).

The concept of integumentary pigmentation as an environmental adaptation has not been universally accepted, however. Some authorities have argued that because UV-radiation-induced sunburn or skin cancers rarely affect reproductive success, melanin pigmentation must be considered only slightly adaptive or nonadaptive (Blum, 1961; Diamond, 1991). It has also been argued that because the relationship between skin color and sunlight appears imperfect, skin color should not be viewed only as an adaptation to the environment (Diamond, 1991). Integumentary pigmentation has also been regarded as a pleiotropic byproduct of selection acting on first functions of pigmentation genes, such as the regulation of metabolic pathways (Deol, 1975), or as a characteristic controlled by sexual selection for the enhancement of attractiveness to the opposite sex (Diamond, 1988, 1991).

In this paper we demonstrate that the previously observed relationship between skin pigmentation in indigenous human populations and latitude is traceable to the strong correlation between skin color and UV radiation. We also present evidence supporting the theory that variations in melanin pigmentation of human skin are adaptive and that they represent adaptations for the regulation of the effects of UV radiation on deep strata of the integument. Our presentation combines analysis and visualization of data on the skin coloration of indigenous peoples coupled with remote sensing data on UV radiation levels at the Earth's surface and physiological evidence concerning the effects of UV radiation on levels of essential vitamins and metabolites.

What skin color was primitive for the hominid lineage?

Before questions about changes in integumentary pigmentation in modern human evolution can be addressed, consideration must be given to the probable primitive condition of the integument in the earliest members of the human lineage. It is likely that the integument of the earliest protohominids was similar to that of our closest living relative, the chimpanzee, being white or lightly pigmented and covered with dark hair (Post *et al.*, 1975*b*). In the chimpanzee, exposed areas of skin vary considerably in their coloration depending on the species and subspecies under consideration, but in all groups facial pigmentation increases with

age and exposure to UV radiation (Post *et al.*, 1975*b*). Except for the face, eyelids, lips, pinnae, friction surfaces, and anogenital areas, the epidermis of most nonhuman primates is unpigmented due to an absence of active melanocytes (Montagna & Machida, 1966; Montagna *et al.*, 1966*a*,*b*), suggesting that this is the primitive condition for primates in general. The hairless areas listed above are pigmented to greater or lesser extents in all primate species (Montagna & Machida, 1966; Montagna *et al.*, 1966*a*,*b*), suggesting that the potential for induction of melanogenesis (Erickson & Montagna, 1975) in exposed skin is also primitive for the group.

Physiological models have demonstrated that the evolution of hairlessness and an essentially modern sweating mechanism were coordinated with the higher activity levels associated with the modern limb proportions and striding bipedalism (Montagna, 1981; Schwartz & Rosenblum, 1981; Wheeler, 1984, 1996; Chaplin *et al.*, 1994). Throughout this transitional period, the critical function of the integument in thermoregulation was maintained through evolution of an increased number of sweat glands, particularly on the face (Cabanac & Caputa, 1979; Falk, 1990), that increased the maximum rate of evaporative cooling available at any one time (Wheeler, 1996; see also Mahoney, 1980). The brain is extremely heat sensitive, and its temperature closely follows arterial temperature (Nelson & Nunneley, 1998). Evolution of a whole-body cooling mechanism capable of finely regulating arterial temperature was, therefore, a prerequisite for brain expansion and increased activity levels. Naked skin itself affords a thermoregulatory advantage because it makes for a reduced total thermal load requiring evaporative dissipation (Wheeler, 1996). As the density of body hair decreased and the density of sweat glands increased, the need for protection of subepidermal tissues against the destructive effects of UV radiation, particularly UVB, also increased. This protection was accomplished by an increase in melanization of the skin.

UV radiation at the surface of the Earth

The sun emits electromagnetic radiation from short-wavelength X-rays to long-wavelength radio waves. Because X-rays and the shortest UV waves (UVC, <280 nm) do not penetrate the atmosphere, middle (UVB, 280–320 nm) and long (UVA 320–400 nm) wavelength UV radiation, along with the visible wavelengths and infrared, are of greatest biological significance.

In order for solar radiation to produce a photochemical effect, it must be absorbed. For an effective photon of radiation to be absorbed, it must first travel from the sun to the body's surface through the atmosphere. Atmospheric absorption and scattering of light are functions of the air mass through which light must travel (Daniels, 1959). The air mass, in turn, is a function of the angle of the sun to the observer, which is determined by the time of day, season, latitude and altitude. The air mass has a great influence on the transmission of UV radiation because, in general, scattering is greatest in the UV and shorter visible wavelengths (Daniels, 1959). The transmission of UV and visible radiation to the Earth's surface are also determined by absorption in the ozone layer, clouds, dust, haze and various organic compounds (Daniels, 1959, 1964).

Prior to the utilization of remote sensing technology, the intensity of UV radiation at the Earth's surface and the erythemal response of human skin to UV radiation were estimated using mathematical models (Paltridge & Barton, 1978). Although these models were parameterized to account for the effects of solar elevation, the amounts of ozone and aerosols in the atmosphere, and the surface albedo on estimated UV

radiation, they were merely models, not direct measurements. With the application of remote sensing to this problem, however, it has been possible to directly measure the UV radiation reaching the Earth's surface, taking ozone concentration and scene reflectivities (cloud conditions, and snow and ice cover) into account (Herman & Celarier, 1996). The existence of directly measured data means that it is possible to know exactly how much UV radiation made it to the Earth's surface at a specific day and time; it is no longer necessary to rely on calculated estimates. The present study is the first in which direct measurements of UV radiation at the Earth's surface have been used to test hypotheses concerning the evolution of human skin pigmentation.

Relethford (1997) recently suggested that hemispheric differences in human skin color were due to hemispheric differences in UV radiation. In response to this claim, we have demonstrated, using direct measurements of UV radiation, that the annual erythemal means for UV radiation in the northern and southern hemispheres were not significantly different, but that significant differences between the hemispheres are found at the summer and winter solstices (Chaplin & Jablonski, 1998). The magnitude of these differences can be predicted from today's perihelion effect (i.e., that the Earth is closest to the sun on 3 January, during the Austral Summer). We have also shown (Chaplin & Jablonski, 1998) that the hemispheric differences in skin color that Relethford demonstrated are due in large part to the fact that, in the southern hemisphere, the areas receiving high annual UV radiation constitute a much larger percentage of the total habitable land area than in the northern hemisphere. In other words, a larger proportion of the habitable land of the southern hemisphere lies closer to the equator than it does in the northern hemisphere. This area receives high annual doses of UV radiation. In contrast, the vast majority of habitable land in the northern hemisphere lies north of the Tropic of Cancer and receives low annual doses of UV radiation. The hemispheric bias in the latitudinal distribution of land masses has had profound consequences for the evolution of skin pigmentation for the humans inhabiting the two hemispheres (Chaplin & Jablonski, 1998).

Melanin and the effects of UV radiation on human skin

In the skin, melanin acts as an optical and chemical photoprotective filter, which reduces the penetration of all wavelengths of light into subepidermal tissues (Daniels, 1959; Kaidbey *et al.*, 1979). Electromagnetic radiation impinging on the human skin can undergo a number of interactions: it can be reflected by the surface of the stratum corneum; it can enter the stratum corneum after a slight change in its direction of travel; it can interact with melanin dust in the stratum corneum, resulting in partial or total absorption; it can traverse deeper layers and experience a possible additional scattering; or it can enter the viable epidermis where it encounters melanin packaged within melanosomes (Kollias *et al.*, 1991). Epidermal melanin has different forms at different sites within the skin and these interact differently with radiation (Kollias *et al.*, 1991). At all of these sites, melanin works an optical filter to attenuate radiation by scattering (Kollias *et al.*, 1991). It also acts as a chemical filter through its function as a stable free radical that can absorb compounds produced by photochemical action which would be toxic or carcinogenic (Daniels, 1959; Kollias *et al.*, 1991). The melanin dust of the stratum corneum appears to be a degradation product of the melanosomes, the organelles in which the melanin pigment resides. This serves the highly desirable function of attenuating radiation close to the skin's surface, thus

sparing the deeper, viable layers. Most epidermal melanin is packaged in intact melanosomes that are located deeper in the skin, however. These organelles are distributed to keratinocytes throughout the Malpighian layer of the epidermis by the dendritic processes of melanocytes. Thus, the superior photoprotection of highly melanized skin is accomplished by absorption and scattering, which are influenced by the density and distribution of melanosomes within keratinocytes in the basal and parabasal layers of the epidermis (Kaidbey *et al.*, 1979) and by the presence of specks of melanin dust in the stratum corneum (Daniels, 1964). The heavily pigmented melanocytes of darker skins also have the ability to resume proliferation after irradiation with UVB radiation, indicating that they can recover more quickly from the growth-inhibitory effects of UVB exposure (Barker *et al.*, 1995).

Most studies of the effects of UV radiation on human skin have utilized as a standard the minimum-erythemal dose (UVMED), which is the quantity of UV radiation required to produce a barely perceptible reddening of lightly-pigmented skin.

Apart from its beneficial role in vitamin D synthesis, the effects of UVB radiation on the skin are universally harmful. Suppression of sweating and subsequent disruption of thermoregulation due to sunburn-induced damage to sweat glands are the most serious immediate effects of excessive UVB exposure (Daniels, 1964; Pandolf *et al.*, 1992). Other short-term harmful effects include discomfort, lowering of the pain threshold, vesiculation and possible secondary infection following severe sunburn, desquamation and nutrient photolysis (Branda & Eaton, 1978; Daniels, 1964). Degenerative changes in the dermis and epidermis due to UVB exposure are realized over longer time courses, some eventually resulting in skin cancers. The question from an evolutionary point of view is do any of these effects, singly or in combination, have direct effects on reproductive success? Basal cell and squamous cell carcinomas, for instance, while a significant cause of morbidity in lightly pigmented peoples, rarely influence fitness because they generally affect individuals after reproductive age and are rarely fatal (Blum, 1961; Roberts, 1977; Robins, 1991). Malignant melanomas, though rare (representing 4% of skin cancer diagnoses) are more often fatal than other skin cancers, but their effect on reproductive success is still limited because of their late onset, well beyond the age of first reproduction (Johnson *et al.*, 1998).

We argue here that protection against nutrient photolysis, and specifically photolysis of folate, was a prime selective agent which brought about the evolution of deeply pigmented skins among people living under regimes of high UVB radiation throughout most of the year because of the direct connection between folate and individual reproductive success. The importance to individual fitness of protection of sweat glands and maintenance of thermoregulatory capability is also seen as contributing to increased melanization.

Folate and human reproductive success

Folic acid is an essential nutrient, which is required for nucleotide and, therefore, DNA biosynthesis. Folic acid is converted in the body to its conjugated form, folate. The lack of folate has long been known to bring about a macrocystic megaloblastic anemia because folate is required for the maturation of bone marrow and the development of red blood cells. Folate deficiency in nonhuman mammals has also been shown to produce multiple fetal anomalies including malformations of the eye, central nervous system, palate, lip, gastrointestinal system, aorta, kidney and skeleton (Omaye, 1993, and references cited therein). All of these

problems can ultimately be traced to folate's roles in purine and pyrimidine biosynthesis (Omaye, 1993; Fleming & Copp, 1998).

It has recently been confirmed that there is a connection between defective folate metabolism and neural tube defects (NTDs) in humans (Fleming & Copp, 1998; Bower & Stanley, 1989; Medical Research Council Vitamin Research Group, 1991). Neural tube defects comprise a family of congenital malformations that result from incomplete neurulation and that are expressed as deformities of varying severity. In *craniorachischisis totalis*, the entire neural tube fails to close; embryos fail early in their development and are spontaneously aborted. Failure of the cranial neuropore to fuse results in *anencephalus* or *craniorachischisis*, in which the brain is represented by an exposed dorsal mass of undifferentiated tissue. Anencephalic embryos often survive into late fetal life or term, but invariably die soon after birth. When failure of neural tube closure disrupts the induction of the overlying vertebral arches, the resulting condition of an open neural canal is called *spina bifida*. Cases of *spina bifida* vary in their seriousness. The most disabling involve the protrusion of neural tissue and meninges through an open neural canal (meningomyelocele). The least serious involve failure of a single vertebral arch to fuse with no herniation of underlying neural tissue (*spina bifida occulta*).

Since records have been kept in developed countries, *anencephalus* and *spina bifida* have been found to be particularly common in light-skinned populations. These defects accounted for as much as 15% of all perinatal and 10% of all postperinatal mortality in the worst-affected populations prior to the introduction of preventative nutritional supplementation (Elwood & Elwood, 1980). Since the advent of prenatal diagnosis, the prevalence of NTDs in relation to all conceptions has been shown to be significantly higher than birth prevalence (Velie & Shaw, 1996; Forrester *et al.*, 1998), partly because of the high rate of early miscarriage in the case of the most serious defects (C. Bower, personal communication).

Folic acid prevents 70% of NTDs in humans and is thought to act by direct normalization of neurulation through regulation of pyrimidine biosynthesis necessary for DNA production (Minns, 1996; Fleming & Copp, 1998). In the body, folate is most sensitive to two major environmental agents, ethanol and UV radiation. In the case of ethanol, folate deficiency is a well-documented problem of chronic alcoholics (Tamura & Halsted, 1983). The photosensitivity of folate is significant, and the nutrient can be readily degraded by natural sunlight or UV light (Kaunitz & Lindenbaum, 1977). Photolysis of folate in humans has been demonstrated by a significant decline in folate levels when serum (*in vitro*) or light-skinned subjects (*in vivo*) were exposed to simulated natural sunlight (Branda & Eaton, 1978). A causal relationship between *in vivo* folate photolysis in humans and NTDs, first suggested by Jablonski (1992, 1999), has recently been supported by the report of NTDs in three unrelated subjects whose mothers had been exposed to UV light on the sun beds of tanning salons during the first weeks of their pregnancies (Lapunzina, 1996). Folate deficiencies brought about by UV photolysis have also been implicated in the etiology of NTDs in some amphibian populations (Jablonski, 1998) because such defects have been seen in amphibian embryos exposed to UV radiation (Higgins & Sheard, 1926; Licht & Grant, 1997).

In addition to its important role in ensuring embryonic survival through proper neurulation, folate has been shown to be critical to another important process central to reproduction, spermatogenesis. In both mice (Cosentino *et al.*, 1990) and rats (Mathur *et al.*, 1977), chemically induced folate deficiency resulted in spermatogenic

arrest and male infertility, findings which prompted investigations of antifolate agents as male contraceptives in humans.

Thus, through folate's roles in the survival of embryos through normalization of neurulation and maintenance of male fertility, and its involvement in a range of other physiological processes dependent on nucleotide biosynthesis, regulation of folate levels appears to be critical to individual reproductive success. Folate levels in humans are influenced by dietary intake of folic acid and by destructive, exogenous factors such as UV radiation. Therefore, the solution to the evolutionary problem of maintaining adequate folate levels in areas of high UV radiation involved the ingestion of adequate amounts of folic acid in the diet and protection against UV radiation-induced folate photolysis. The latter was accomplished by increasing the concentration of the natural sunscreen, melanin, in the skin. The low prevalences of severe folate deficiency (Lawrence, 1983; Lamparelli *et al.*, 1988) and NTDs (Carter, 1970; Elwood & Elwood, 1980; Buccimazza *et al.*, 1994; Wiswell *et al.*, 1990; Shaw *et al.*, 1994) observed among native Africans and African Americans, even among individuals of marginal nutritional status, are probably due to a highly melanized integument, which protects against folate photolysis.

Skin pigmentation and vitamin D synthesis

Vitamin D_3 is essential for normal growth, calcium absorption and skeletal development. Deficiency of the vitamin can cause death, immobilization, or pelvic deformities which prevent normal childbirth (Neer, 1975). Requirements for vitamin D_3 are elevated in females during pregnancy and lactation because of the need for enhanced maternal absorption of calcium in order to build the fetal and neonatal skeletal system (Whitehead *et al.*, 1981; Kohlmeier & Marcus, 1995; Brunvand *et al.*, 1996). In most humans, casual exposure to sunlight leads to conversion of 7-dehydrocholesterol in the skin to previtamin D_3 by UV photons and subsequent isomerization of the latter to vitamin D_3 at body temperature (Loomis, 1967; Webb *et al.*, 1988). Increasing the melanin in human skin increases the length of exposure to UV light that is needed to maximize synthesis of previtamin D_3 (Holick *et al.*, 1981). Deeply melanized skins become nonadaptive under conditions where the concentration of melanin is too high to permit sufficient amounts of vitamin D_3 precursor to be synthesized in the skin under conditions of available UV radiation (Loomis, 1967; Holick *et al.*, 1981; Clemens *et al.*, 1982). If the duration of UV exposure is not sufficient to catalyze previtamin D_3 synthesis, individuals are at much higher risk of vitamin D_3 deficiency and its manifestations (rickets, osteomalacia, and osteoporosis), as has been demonstrated by recent migrants from Ethiopia to Israel (Fogelman *et al.*, 1995) or from the Indian subcontinent to urban centers in the U.K. (Henderson *et al.*, 1987).

Following Murray (1934), Loomis (1967) argued that depigmentation of the skin was a necessary adaptation for humans attempting to inhabit regions outside the tropics, especially those north of 40°N, which receive low average amounts of UV radiation throughout the year. In addition, he advocated the position that deeply pigmented skin was also an adaptation for physiological regulation of vitamin D_3 levels. To Loomis, a highly melanized integument prevented UV-radiation-induced vitamin D_3 toxicity caused by over-synthesis of previtamin D_3. Both of Loomis's claims about integumentary pigmentation in humans and vitamin D_3 levels have been challenged.

The hypothesis that deeply pigmented skin protects against hypervitamosis D under conditions of high UV radiation has

been conclusively disproven. Vitamin D toxicity is prevented by a ceiling effect on previtamin D_3 synthesis combined with *in vivo* photolysis of vitamin D_3 itself (Holick *et al.*, 1981; Holick, 1987). Vitamin D_3 intoxication can occur as the result of individuals overdosing on vitamin supplements, but no cases of naturally occurring vitamin D_3 intoxication have ever been reported (Robins, 1991).

Loomis's central hypothesis concerning depigmentation of the integument of humans living at high latitudes as a requirement for adequate vitamin D synthesis has been most strongly challenged by Robins (1991). Robins' main points are that early *Homo* at high latitudes was exposed to the full impact of the natural environment. Even when clad with animal skins and furs, he claims that enough of the body's surface would be exposed to permit synthesis of adequate amounts of previtamin D_3. While he admits that winters in Europe during glacials would have been particularly cold and dim, he indicates that the late spring and summer would have afforded good opportunities for hominids to expose their skin to UV radiation. According to Robins (1991), the long, dull winters would not have triggered widespread hypovitamosis D and rickets because vitamin D can be stored in fat and muscle (Rosenstreich *et al.*, 1971; Mawer *et al.*, 1972). He suggests that vitamin D deficiencies are a product of "industrialization, urbanization and overpopulation" (Robins, 1991:207) and supports his claim by pointing out that the majority of modern human populations that suffer from such problems are urban dwellers, deprived of natural sunlight and the opportunity to synthesize previtamin D_3. According to Robins, dark-skinned human populations living under conditions of low annual UV radiation do not suffer from vitamin D deficiencies that can be attributed to lack of sunlight. The depigmentation conspicuous in peoples inhabiting the northern hemisphere above 40°N cannot be traced, according to Robins, to the need to synthesize vitamin D in their skin. Rather, people with deeply pigmented skin can survive well under conditions of low annual UV radiation provided that they spend sufficient time outdoors in the spring and summer to build up physiological stores of vitamin D for the winter (Robins, 1991). As is discussed below, the findings of the current study and the weight of current clinical evidence do not support Robins' counterarguments against the vitamin D hypothesis of depigmentation.

Testing the relationship between skin color and levels of UV radiation

Previous studies of the relationship between environmental variables and the skin color of indigenous populations using skin reflectance spectrophotometry demonstrated highest associations with latitude (Roberts & Kahlon, 1976; Roberts, 1977; Tasa *et al.*, 1985). These were interpreted as reflecting the crucial role of UV radiation in determining skin color. Until this time, accurate tests of this relationship were not possible because accurate data on UVMED levels at the Earth's surface were not available. Because these data are now available (Herman & Celarier, 1996), we were able to apply them to two critical analyses: (1) in the determination of the geographic distribution of the potential for previtamin D_3 synthesis; and (2) in assessment of the relationship between surface UV radiation levels and skin color reflectances for indigenous populations.

Methods

Skin reflectance data

A database of skin reflectance data was compiled from the literature. The database comprises samples designated as male, female, and both sexes, for reflectance at

425 nm (blue filter), 545 nm (green filter) and 685 nm (red filter), for the upper inner arm site. In many primary reports, intermediate wavelength reflectance readings were also provided, but these were not used. The complete skin reflectance data set with bibliographic sources is presented in the Appendix. The vast majority of these data had been collected with the E.E.L. (Evans Electric Limited) reflectometer. Readings for Colombian natives were the only ones taken using the Photovolt abridged spectrophotometer. These measurements were converted to E.E.L.-comparable values by using the regression equation for Belize Creoles developed by Lees & Byard (1978) designated in the Appendix. As is obvious from an inspection of the collated data, the skin reflectance data set is far from complete and is strongly skewed toward representation of indigenous human populations from the Old World. The inherent deficiencies of this database limited the scope of analyses that could be undertaken.

Indigenous populations were defined for purposes of this study as those which had existed in their current locations for a long time prior to European colonization. The names by which areas or groups were identified were taken from the original citations. Populations known to have high levels of admixture or to have recently migrated to their current locations were excluded. Some populations were represented by males only, others by males and females, and others where the values for the two sexes had been averaged by the original workers. In some cases, the sex of the subjects was not stated in the original report. Because more skin reflectance data exist for males than for females, analyses of skin reflectance in which data for the sexes were combined are slightly biased toward male reflectance values. In cases where more than one skin reflectance was measured for a specific population, either for each sex or by multiple workers, the means for each sex were averaged, except in the cases noted below where the reflectance values for the sexes were analyzed separately.

Reflectance data were specified in original reports at varying levels of geographic accuracy. Those specified to a small geographic area such as township or county could be matched to a small number of average UVMED cell values. For those specified at the regional or country level, a single skin reflectance value was associated with multiple UVMED cell values, depending on the size of the region. These varied from one cell (e.g., Germany, Mainz; India, Goa) to 453 cells (Zaire). To overcome the problem of cell replication and artificial exaggeration of variance, the UVMED data for each specified area was averaged for that area to produce a single value. This data reduction exercise made it possible for a single skin reflectance value to be evaluated relative to a single average UVMED value.

Because Relethford (1997) has suggested that a different relationship between UV radiation and skin reflectance exists between the northern and southern hemispheres, separate analyses were performed for both hemispheres together and for each hemisphere separately. (The only analysis in which this was not done was that comparing the significance of differences in skin reflectance between the sexes. See below.) Although the annual UVMED is equal for both hemispheres, the seasonal distribution of UV radiation is different (Chaplin & Jablonski, 1998). The hemispheres also differ in their respective land surface area (Chaplin & Jablonski, 1998) and degree of land mass connectivity. It is impossible, for instance, for non-seafarers to move around the globe in the southern hemisphere. Lastly, the proportion of different vegetation zones between the hemispheres is different, with the northern hemisphere exhibiting more extensive areas of forest, desert and mountains.

Calculation of annual average UVMED

The annual average values for UVMED were derived from readings taken from the NASA Total Ozone Mapping Spectrometer (TOMS) which was flown aboard the Nimbus-7 satellite between 1978 and 1993 (Herman & Celarier, 1996). The data represent the relative daily areal exposure of UV radiation effective in causing skin irritation, computed at each 1·25 degree longitude by one degree latitude pixel, between 65°S and 65°N; the solar flux was measured at noon (Herman & Celarier, 1996). These readings were computed to account for the total ozone column and scene reflectivities (cloud and snow cover) in the same latitude–longitude pixel. These measurements were then combined with the results of radiative transfer calculations, terrain height, solar zenith angle and the model action spectrum of erythemal sensitivity for caucasoid skin (Herman & Celarier, 1996). The wavelength range of 280–400 nm sampled by the TOMS ensured that all significant contributions to the erythemal exposure were included in the UVMED. Because the action spectrum is defined up to an arbitrary multiplicative constant, the basic UVMED data are of arbitrary dimensions.

The original dataset was very large (over 190,000 data points representing 37,400 readings taken each day from 1979–1992). Therefore, an abridged dataset (the annual average UVMED) was produced by taking an average for all years of the average of the 21st to the 23rd days of each month.

All data analyses in this study were undertaken using S-Plus® 2000 and ArcView®, reprojected in Mercator projection.

Analysis and visualization of the potential for vitamin D_3 synthesis

The rate of previtamin D_3 synthesis in lightly pigmented human skin exposed to natural sunlight has been experimentally determined (Webb *et al.*, 1988). Working in Boston, Massachusetts in 1986, Webb *et al.* (1988) found that the earliest occurrence in the year of previtamin D_3 synthesis in neonatal caucasoid foreskin samples was on 17 March. Because the actual UVMED for that place and time was available from the NASA TOMS dataset, values representing the potential for vitamin D_3 synthesis relative to annual average UVMED could be calculated for all locations included in the NASA TOMS dataset. It was then possible to define distinct geographic zones representing the differing potentials for vitamin D_3 synthesis for light-skinned individuals. The annual average UVMED and average skin reflectance measurement for each zone were then calculated and compared. The skin reflectance data used for this analysis comprised data for indigenous people (males, females, both sexes and unspecified sex), averaged by country and then by zone.

We also sought to demonstrate the potential for vitamin D_3 synthesis in the skin of dark-skinned human populations. The length of time required for endogenous vitamin D_3 biosynthesis increases with increasing melanin concentration in the skin (Clemens *et al.*, 1982; Holick *et al.*, 1981). Thus, the data showing the time of exposure to UV radiation necessary to maximize previtamin D_3 formation in different human groups were used to calculate the geographical zones in which annual UVMED was not sufficient, averaged over the year, to catalyze previtamin D_3 synthesis in moderately and highly melanized skin.

Sexual differences in skin reflectance

In order to test the hypothesis that females and males of the same populations differ in their average skin reflectance, we selected data from specific population where skin reflectance measurements had been taken and reported separately for males and females. A standard two-sample *t*-test was used to determine the significance of the differences between the sexes at the same locality. Separate analyses for the northern

and southern hemispheres were not undertaken because the small sizes of the datasets that met the above criteria would have rendered hemisphere-specific analyses meaningless. Further, our objective here was not to test the hypothesis that there is a difference between the hemispheres in the degree of differentiation between the two sexes in skin reflectance.

The relationship of annual average UVMED to skin reflectance

A correlation matrix was used to test the strength of the relationships between annual average UVMED, latitude and skin reflectance. This analysis was undertaken specifically to determine the strength of the correlation of skin reflectance to UVMED relative to its correlation with latitude. The skin reflectance data used in this analysis comprised those from indigenous populations, all-sex samples combined, averaged by country. For this analysis, latitude was transformed to absolute latitude, i.e., the absolute value of the latitude, which expresses the angle of a location from the Equator rather than relative north and south. It is unclear from previous studies of human skin pigmentation as to whether workers utilized conventional latitude or absolute latitude for purposes of correlation or regression analyses. Transformation of latitude to absolute latitude is necessary because of the nonlinear relationship between solar insolation and latitude. The transformation to absolute latitude renders this relationship more linear, and thus yields much higher correlations.

The relationship between UVMED and skin color reflectance was explored in greater detail using a least squares regression. For this analysis, the skin reflectance data used were the same as those employed in the correlation matrix analysis described above. Separate regressions were developed for data from each hemisphere, for each widely used skin reflectance filter (425, 545 and 685 nm).

Predicted vs. *observed skin reflectances*

In order to compare predicted *vs.* observed values for the skin reflectances of indigenous peoples, the largest available dataset for observed skin reflectance (at 685 nm) was used. It is important to note again that some populations were represented by males only, as both sexes combined, or as unspecified sex, as discussed. Although these variations in sexual classification of the raw data added to the expected variance of the pooled dataset, this problem could not be avoided. Significant outliers from the regression line were then identified.

In order to construct a map of predicted skin colors for modern terrestrial environments, a regression was computed between annual average UVMED and the observed skin reflectance. The observed reflectances for indigenous populations were based on all available data for a particular area or group. A regression equation derived from a larger data set including values for males, females, both sexes and samples of unknown sex was used:

$$\text{Predicted skin color} = \text{annual average UVMED} (\times -0{\cdot}1088) + 72{\cdot}7483.$$

Results

Analysis and visualization of the potential for vitamin D_3 synthesis

Three zones representing different potentials for UV-induced vitamin D_3 synthesis in light-skinned humans were identified (Figure 1). The annual average UVMED and average skin reflectance measurement for each zone are presented in Table 1. Zone 1 was delimited as the area in which the average daily UVMED was sufficient to catalyze previtamin D_3 synthesis throughout the year. This zone comprises the area from

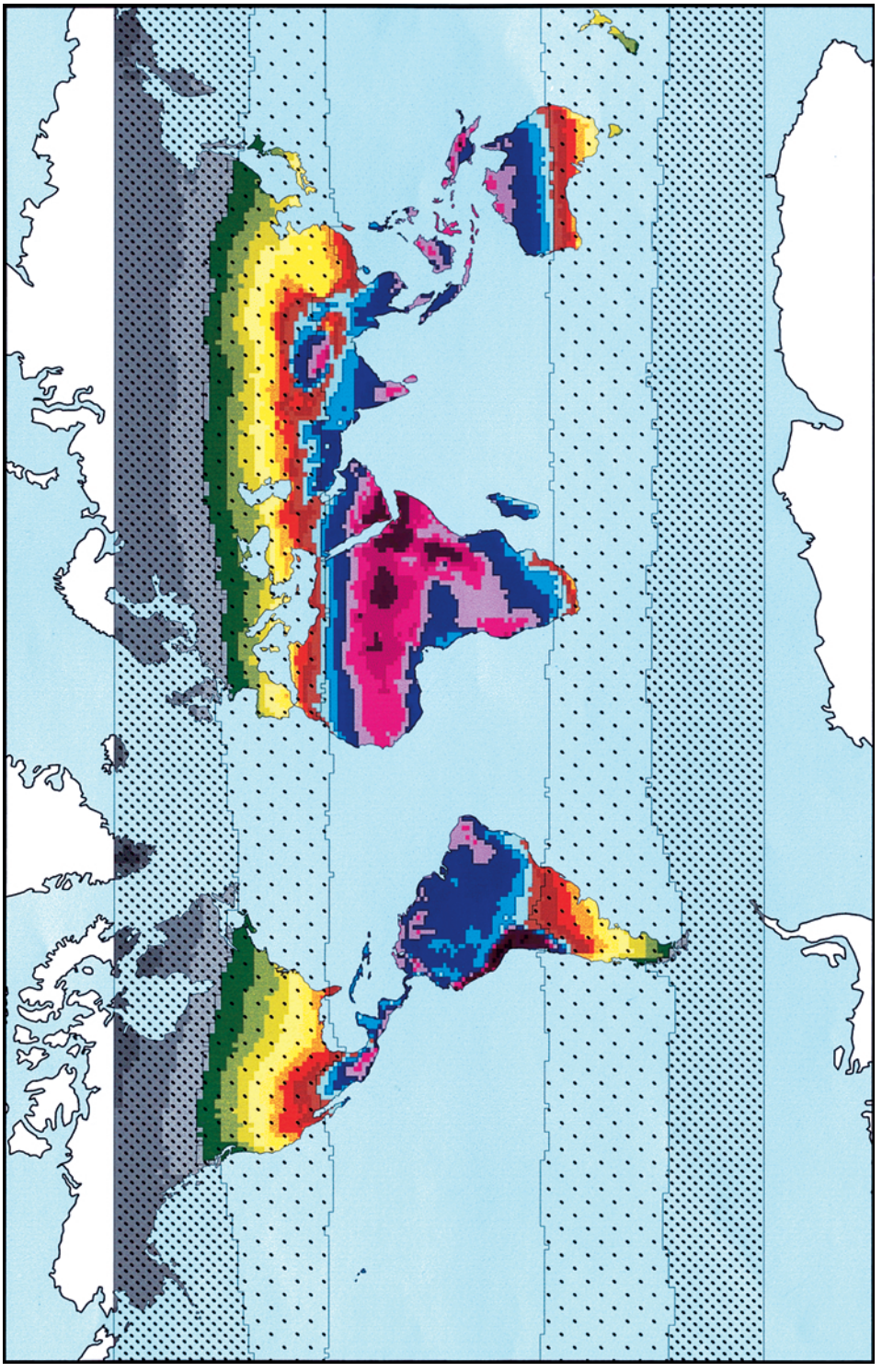

Figure 1. The potential for synthesis of previtamin D_3 in lightly pigmented human skin computed from annual average UVMED. The highest annual values for UVMED are shown in light violet, with incrementally lower values in dark violet, then in light to dark shades of blue, orange, green and gray (64 classes). White denotes areas for which no UVMED data exist. Mercator projection. In the tropics, the zone of adequate UV radiation throughout the year (Zone 1) is delimited by bold black lines. Light stippling indicates Zone 2, in which there is not sufficient UV radiation during at least one month of the year to produce previtamin D_3 in human skin. Zone 3, in which there is not sufficient UV radiation for previtamin D_3 synthesis on average for the whole year, is indicated by heavy stippling.

Table 1 Annual average UVMED and average observed skin reflectance measurements at 685 nm (red filter) for each of the zones depicted in Figure 1 and described in the text

Zone	Annual average UVMED	Average observed skin reflectance at 685 nm
1	313·2	37·2
2	158·3	55·0
3	68·1	68·9

UVMED is measured in units of arbitrary dimension (Herman & Celarier, 1996).

approximately 5° north of the Tropic of Cancer to approximately 5° south of the Tropic of Capricorn. Here, previtamin D_3 could be synthesized in lightly pigmented skin as a result of casual exposure to UVB throughout all months of the year. Zone 2 was defined as the area in which the average daily UVMED for at least one month was not sufficient to produce previtamin D_3 in lightly pigmented skin. (This zone is indicated by light stippling in Figure 1.) Large areas of the northern hemisphere fall within this zone. Zone 3 was defined as the area in which the daily UVMED, averaged over the whole year, was not sufficient to catalyze previtamin D_3 synthesis in lightly pigmented skin. That is, it was the zone in which previtamin D_3 synthesis resulting from UVB exposure, as averaged over the course of a year, was not sufficient to meet minimum physiological requirements. (This zone is indicated by heavy stippling in Figure 1.) Although there were some months around the summer solstice during which there was sufficient UV radiation to bring about cutaneous previtamin D_3 synthesis in Zone 3 (and the attendant potential for vitamin D storage), the average daily dose, when averaged over the course of a year, was not sufficient to catalyze the reaction. In other words, insufficient ambient UV radiation is available on a year by year (or long-term) basis to permit adequate cutaneous biosynthesis of previtamin D_3.

It is important to note that the zones defined in Figure 1 were calculated on the basis of the potential for previtamin D_3 synthesis in light skin. No comparable data were available for dark skin. Data concerning the times of exposure necessary to maximize previtamin D_3 synthesis in skin samples with different melanin concentrations are known, however. These were used to calculate the geographical zones in which annual UVMED was not sufficient, averaged over the year, to catalyze previtamin D_3 synthesis in moderately and highly melanized skin (Table 2; Figure 2). Figure 2 is a comparison of the estimated positions of Zone 3 from Figure 1 for human populations with lightly, moderately and deeply melanized skin. The fact that formation of previtamin D_3 takes more than five times as long in highly melanized (Type VI) skin as it does in lightly melanized (Type III) skin means that the continental areas that are ''vitamin D safe'' for darker skins are considerably smaller than they are for lighter skins (Figure 2).

Sexual differences in skin reflectance

Females were found to be significantly lighter (i.e., displaying higher reflectance values) than males regardless of the filter used to measure the reflectance (Table 3).

The relationship of annual average UVMED to skin reflectance

When the relationship between annual average UVMED and values of skin reflectance for the combined all-sexes dataset was examined using a correlation matrix it was found that, for skin reflectance at all wavelengths, the correlation with annual average UVMED and absolute latitude were both high (Table 4). The correlation between skin reflectance and annual average UVMED was stronger than the correlation between skin reflectance and absolute

Table 2 The effect of melanin concentration on the estimated annual average UVMED values that, averaged for the year, are not sufficient to catalyze previtamin D_3 synthesis in human skin

Skin type (human population)	Time of exposure to maximize pre D_3 formation (h) (range and mean)	Multiplier for amount of time relative to skin Type IIIa, calculated from mean time of exposure	Estimated annual average UVMED necessary to catalyze pre D_3 formation
Type IIIa (European)	0·50–0·75 (0·625)	1	68·1
Type V (Asian)	0·75–1·50 (1·125)	1·8	122·6
Type VI (African American)	3·00–3·50 (3·25)	5·2	354

The annual average UVMED value for Zone 3 in Table 1 (for lightly pigmented skin) was multiplied by a factor representing the increased number of hours necessary to catalyze previtamin D_3 synthesis in more heavily pigmented skin types, based on the results of Holick and colleagues (Holick *et al.*, 1981). This yielded an estimate of the minimum annual average UVMED necessary to catalyze previtamin D_3 synthesis in darker skin types. The designations of skin type and human population are from the original source.

latitude in three instances: for the 545 nm (green) filter reflectance for the separate hemispheres and for the 685 nm (red) filter reflectance for the southern hemisphere. The correlation between skin reflectance and annual average UVMED was only slightly weaker than the correlation between skin reflectance and absolute latitude in a further four instances: for the 425 nm (blue) filter reflectance for the southern hemisphere and both hemispheres combined, for the 545 nm (green) filter reflectance for both hemispheres combined, and for the 685 nm (red) filter reflectance for both hemispheres combined. In only two cases [425 nm (blue) for the northern hemisphere and 685 nm (red) for the northern hemisphere] was the correlation between skin reflectance and absolute latitude much higher than that between skin reflectance and annual average UVMED. The correlation between annual average UVMED and absolute latitude based on data from both hemispheres combined was found to be $-0{\cdot}935$, much higher than the correlation with untransformed latitude, $-0{\cdot}741$.

When the relationship between annual average UVMED and values of skin reflectance was examined using a least squares regression model (Table 5), the highest r^2 values were associated with green (545 nm) filter reflectance.

Predicted vs. *observed skin reflectances*

The differences between observed and predicted skin reflectance values at 685 nm for indigenous populations were generally small (Table 6; Figures 3 and 4), and the difference between the average observed and predicted values was not significant ($P=0{\cdot}9983$; two-sample *t*-test), and did not detract from the validity of the predictive model.

Discussion

The results presented here strongly support the theory that the degree of melanin pigmentation in human skin is an adaptation for the regulation of penetration of UV radiation into the epidermis.

The geographic distribution of the potential for vitamin D_3 synthesis

Skin pigmentation is determined as much by the requirements of previtamin D_3 synthesis as by photoprotection. Within Zone 1 as defined in this study, a clinal distribution of skin reflectance relative to annual average UVMED can be detected from inspection of the values presented in Table 5. A cline

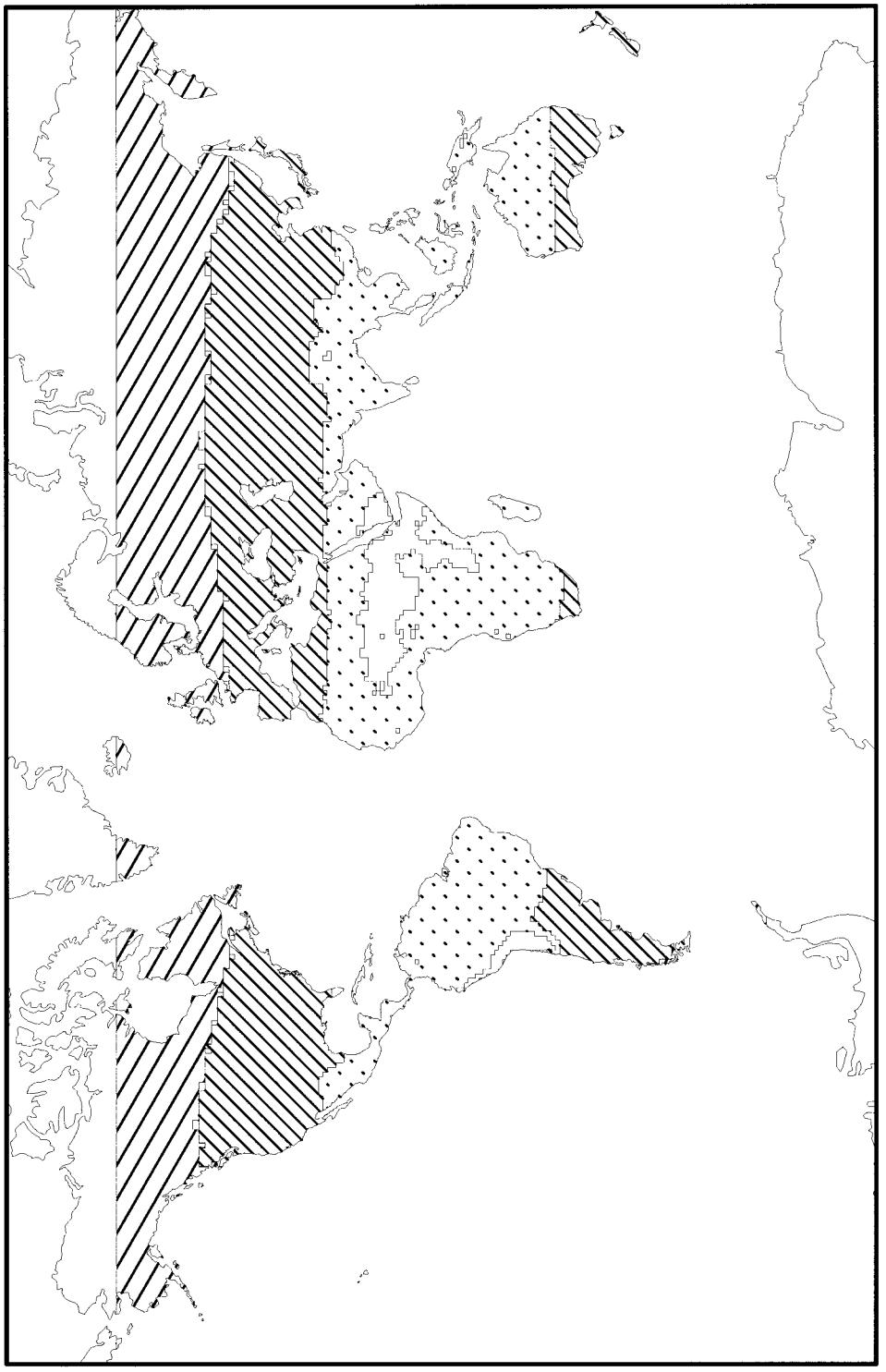

Figure 2. A comparison of the estimated areas in which annual UVMED is not sufficient, averaged over the year, to catalyze previtamin D_3 synthesis in lightly, moderately and highly melanized skin. All zones were defined by the values for previtamin D_3 synthesis potential presented in Table 2. Widely spaced oblique hachure covers the northernmost region of the Northern Hemisphere in which there is not sufficient UV radiation, averaged over the entire year, to catalyze the formation of previtamin D_3 in lightly pigmented (Type IIIa) human skin (Zone 3 from Figure 1). Narrowly spaced oblique hachure denotes the area, *in addition to that shown by widely spaced oblique hachure*, in which there is not sufficient UV radiation to catalyze the formation of previtamin D_3 in moderately melanized (Type V) skin. The large circum-Equatorial area denoted by stippling covers the area, *in addition to the previous two*, in which there is not sufficient UV radiation averaged over the entire year to catalyze the formation of previtamin D_3 in highly melanized (Type VI) skin.

Table 3 Difference between the means of female and male skin reflectances for a combined data set of indigenous human populations, based on samples from individual populations for which separate data for males and females were available

Filter nm	Female mean reflectance	Male mean reflectance	Two-sample *t*-test *P*-value
425 (blue)	19·20	16·88	0
545 (green)	23·93	22·78	0·0089
685 (red)	47·20	45·09	0

For reflectances at all wavelengths, females were found to be lighter (exhibiting higher reflectance values) than males.

Table 4 Results of the correlation matrix performed to examine the relationships between skin reflectance (at three wavelengths), absolute latitude and annual average UVMED

Filter nm by hemisphere (NH, SH or both)	Absolute latitude	Annual average UVMED
425 (blue), NH	0·974	− 0·714
425 (blue), SH	0·694	− 0·668
425 (blue), both	0·966	− 0·954
545 (green), NH	0·908	− 0·917
545 (green), SH	0·620	− 0·967
545 (green), both	0·964	− 0·957
685 (red), NH	0·844	− 0·632
685 (red), SH	0·423	− 0·498
685 (red), both	0·827	− 0·809

Table 5 The results of a least squares regression model in which the relationship between skin reflectance values for indigenous human populations and average annual UVMED was examined, by hemisphere

Filter nm, by hemisphere (NH, SH or both)	Intercept	Slope	r^2
425 (blue), NH	34·032	− 0·059	0·4572
425 (blue), SH	25·517	− 0·045	0·3402
545 (green), NH	45·046	− 0·083	0·7747
545 (green), SH	44·193	− 0·092	0·7013
685 (red), NH	65·575	− 0·073	0·3995
685 (red), SH	66·908	− 0·103	0·2485
685 (red), both	72·797	− 0·109	0·6551

For the 685 nm (red) filter reflectance, a value is also presented for combined hemispheric skin reflectance and UVMED data; this value was used to generate the predicted skin color values in Table 6 and Figure 3, and to compare with those published in previous studies (see Discussion).

of depigmentation is more noticeable in Zone 2, where increasing depigmentation has helped to ensure maintenance of adequate vitamin D_3 production in the skin throughout most months of the year. Although individuals in this zone do not receive enough UVB during at least one month each year to catalyze previtamin D_3 synthesis, intake of vitamin D_3-containing foods and the ability of the body to store vitamin D_3 mitigates this short lapse in previtamin D_3 biosynthesis. For humans living in this zone, however, the adoption of more housebound lifestyles with low UV radiation exposure combined with inadequate vitamin D_3 intake in recent years has resulted in a high prevalence of hypovitaminosis D (Thomas *et al.*, 1998). This problem is exacerbated if the human inhabitants of Zone 2 are relatively dark-skinned. The high prevalence of hypovitaminosis D, rickets, osteomalacia and osteoporosis among populations recently migrated from the Indian subcontinent to the U.K. is higher than that for the light-skinned general population, and shows a marked north–south gradient consistent with UV-radiation dosage dependence (Hodgkin *et al.*, 1973; Henderson *et al.*, 1987).

Humans inhabiting Zone 3 are at highest risk of severe vitamin D_3 deficiency. Successful, long-term human habitation of this zone has depended upon two key factors: the evolution of a depigmented integument capable of permitting maximum cutaneous previtamin D_3 synthesis under conditions of available UV radiation and the consumption of foodstuffs naturally high in vitamin D_3 (such as fish and marine mammals). Recent migrants to high latitude regions, such as Greenlanders, appear to be only very slowly

undergoing depigmentation because of their vitamin D_3-rich diet.

Robins (1991) has challenged the theory that depigmentation in high latitude human populations is due to the requirements of endogenous vitamin D_3 synthesis. He has concluded that, for early *Homo sapiens* on the Eurasian or North American landscapes of the Pleistocene, "there is not a scintilla of paleontological or experimental evidence that rickets (or osteomalacia) ever did or would have manifested, regardless of skin colour [sic]" (Robins, 1991:208). The paleoenvironmental and clinical evidence now at hand militates against this interpretation.

Populations of *Homo sapiens* (*sensu stricto*) have been established above the 40th parallel, in areas of low annual UV radiation, for, approximately, only the last 50,000 years. (It is important to note in this connection that there is no equivalent land mass in the southern hemisphere available for human habitation.) The period from approximately 50,000 to 10,000 years ago comprises the Last Glaciation, and includes the Last Glacial Maximum (LGM) at 18,000 B.P. During this period, human habitation north of the Tropic of Cancer and, particularly, north of 40°N was limited by low temperatures and the proximity of ice sheets. Climatic oscillations were frequent and sudden, and had profound impacts on the distributions of humans and the mammals they depended upon (Williams *et al.*, 1993). The minimum distance of habitation sites from the southern margin of the ice sheets was approximately 400–600 km (Madeyska, 1992). During the LGM, the areas of Europe habitable by humans were characterized by extreme cold, with annual mean air temperatures 8°C colder than present day, widespread decreases in precipitation, and fierce dust storms (Frenzel, 1992*a*,*b*). Accurate reconstruction of patterns of human activity north of the 40th parallel from the period of 50,000 to 10,000 B.P. is not possible. It can be safely said, however, that human populations—especially around the LGM—here would have worn more protective clothing and would have needed to seek shelter from the elements more than they do today. The latter would have been particularly true of females and young children.

Abundant clinical evidence attests to the fact that moderately to deeply pigmented humans suffer from various manifestations of hypovitaminosis D_3 (including rickets, osteomalacia and osteoporosis) when their opportunities for endogenous vitamin D_3 synthesis are restricted as a result of changes in lifestyle or geographical relocation. Manifestations of vitamin D_3 deficiency in such populations can be attributed to lifestyle changes such as more indoor living in urban environments and the wearing of concealing garments outdoors (Bachrach *et al.*, 1979; Haworth & Dilling, 1986; Henderson *et al.*, 1987; Gullu *et al.*, 1998; Wauters & Soesbergen, 1999). The phenomenon is equally true of populations who have recently relocated from an area of high annual UV radiation to one of lower UV, and who have otherwise maintained all aspects of their original lifestyle (Hodgkin *et al.*, 1973; Fogelman *et al.*, 1995). Pregnant or lactating women and small children undergoing rapid bone growth are most susceptible to changes of UV radiation regime (Bachrach *et al.*, 1979; Fogelman *et al.*, 1995; Gessner *et al.*, 1997; Namgung *et al.*, 1998; Waiters *et al.*, 1999). Vitamin D_3 deficiencies are also common among the elderly, where they render individuals more susceptible to osteoporosis and its sequelae (Davies *et al.*, 1986; Thomas *et al.*, 1998). The key point here is that overwhelming clinical evidence demonstrates that even a relatively minor decrease in endogenous synthesis of vitamin D_3 as a result of reduced annual UV radiation exposure can trigger vitamin D_3 deficiencies in moderately to deeply pigmented people. These

Table 6 **Observed *vs.* predicted values for human skin reflectance at 685 nm based on the results of a linear regression model between observed reflectance for all available groups of indigenous humans and country averages of annual average UVMED**

Country and population or area and hemisphere designation (NH or SH)	Observed reflectance at 685 nm	Predicted reflectance at 685 nm
Afghanistan/Iran (NH)	55·70	45·55
Algeria (Aures) (NH)	58·05	47·91
Australia (Darwin) (SH)	19·30	36·24
Belgium (NH)	63·14	65·66
Botswana (San) (SH)	42·40	39·45
Brazil (Caingan) (SH)	49·40	48·53
Brazil (Guarani) (SH)	47·20	45·29
Burkina Faso (Kurumba) (NH)	28·60	34·23
Cambodia (NH)	54·00	38·99
Cameroon (Fali) (NH)	21·50	34·37
Chad (Sara) (NH)	24·60	34·77
China (Southern) (NH)	59·17	50·49
China (Tibet) (NH)	54·70	41·78
Ethiopia (NH)	31·70	32·70
Ethiopia (Highland) (NH)	33·55	31·35
Germany (Mainz) (NH)	66·90	65·21
Greenland (Southern) (NH)	55·70	70·31
India (NH)	44·60	48·85
India (Bengal) (NH)	49·73	44·33
India (Goa) (NH)	46·40	38·93
India (Nagpur) (NH)	41·30	41·53
India (Northern) (NH)	53·26	44·23
India (Orissa) (NH)	32·05	41·52
India (Punjab) (NH)	54·24	47·89
India (Rajasthan) (NH)	52·00	42·19
India (Southern) (NH)	46·70	37·60
Iraq/Syria (Kurds) (NH)	61·12	51·50
Ireland (Ballinlough) (NH)	65·20	67·11
Ireland (Carnew) (NH)	64·50	65·84
Ireland (Longford) (NH)	65·00	66·99
Ireland (Rossmore) (NH)	64·75	66·73
Israel (NH)	58·20	48·67
Japan (Central) (NH)	55·42	58·51
Japan (Hidakka) (NH)	59·10	63·58
Japan (Northern) (NH)	54·90	61·34
Japan (Southwest) (NH)	53·55	56·68
Jordan (NH)	53·00	45·36
Kenya (NH)	32·40	34·21
Lebanon (NH)	58·20	50·74
Liberia (NH)	29·40	40·52
Libya (Cyrenaica) (NH)	53·50	44·19
Libya (Fezzan) (NH)	44·00	41·31
Libya (Tripoli) (NH)	54·40	48·83
Malawi (SH)	27·00	38·67
Mali (Dogon) (NH)	34·10	34·54
Morocco (NH)	54·85	49·09
Mozambique (Chopi) (SH)	19·45	43·84

Observed *vs.* predicted values were not found to be significantly different ($P=0·9983$), based on a standard two-sample *t*-test between the combined means for the observed (46·449) and predicted (46·445) 685 nm (red) filter skin reflectance values.

Table 6 (*Continued*)

Country and population or area and hemisphere designation (NH or SH)	Observed reflectance at 685 nm	Predicted reflectance at 685 nm
Namibia (SH)	25·55	38·29
Namibia (Okavango) (SH)	22·92	38·63
Namibia (Rehoboth Baster) (SH)	32·90	36·49
Nepal (Eastern) (NH)	50·42	46·31
Netherlands (NH)	67·37	65·94
Nigeria (Ebo) (NH)	28·20	41·86
Nigeria (Yoruba) (NH)	27·40	39·62
Pakistan (NH)	52·30	44·15
Papua New Guinea (SH)	35·30	37·26
Papua New Guinea (Goroka) (SH)	33·30	34·20
Papua New Guinea (Karker) (SH)	32·00	37·25
Papua New Guinea (Lufa) (SH)	31·20	36·88
Papua New Guinea (Mt Hagan) (SH)	35·35	31·56
Papua New Guinea (Port Moresby) (SH)	41·00	35·45
Peru (Maranon) (SH)	43·05	42·28
Peru (Nunoa) (SH)	47·70	34·89
Philippines (Manila) (NH)	54·10	41·53
Russia (Chechen) (NH)	53·45	59·04
Saudi Arabia (NH)	52·50	38·65
South Africa (SH)	42·50	45·67
South Africa (Cape) (SH)	50·96	50·71
South Africa (Hottentot) (SH)	46·80	43·91
South Africa (San Central) (SH)	43·75	41·14
Spain (Basques) (NH)	65·70	62·38
Spain (Leon) (NH)	64·66	60·80
Sudan (NH)	35·50	33·45
Swaziland (SH)	35·60	44·62
Tanzania (Nyatura) (SH)	25·80	34·12
Tanzania (Sandewe) (SH)	28·90	32·13
Tunisia (NH)	56·30	52·03
Turkey (NH)	59·15	55·56
United Kingdom (Cumberland) (NH)	66·75	66·99
United Kingdom (London) (NH)	62·30	65·84
United Kingdom (Northern) (NH)	66·10	67·49
United Kingdom (Wales) (NH)	65·00	66·15
Vietnam (NH)	55·90	43·59
Zaire (NH)	33·20	37·46
Zaire (Konda) (SH)	29·40	39·43
Average	46·18	46·52

deficiencies are more marked in reproductive females, growing children and the elderly. Because moderately to deeply pigmented people require from two to six times as much UV radiation as lightly pigmented individuals to catalyze the synthesis of an equivalent amount of previtamin D_3 (Table 2; Figure 2) (Holick *et al.*, 1981; Clemens *et al.*, 1982), they are highly susceptible to vitamin D_3 deficiencies caused by a change of UV radiation regime. We therefore conclude, contrary to Robins, that moderately to deeply pigmented modern human populations are optimally tuned for endogenous synthesis of vitamin D_3 under the specific UV radiation regimes under which they evolved. This fine-tuning is easily disrupted by changes of lifestyle or locale. This

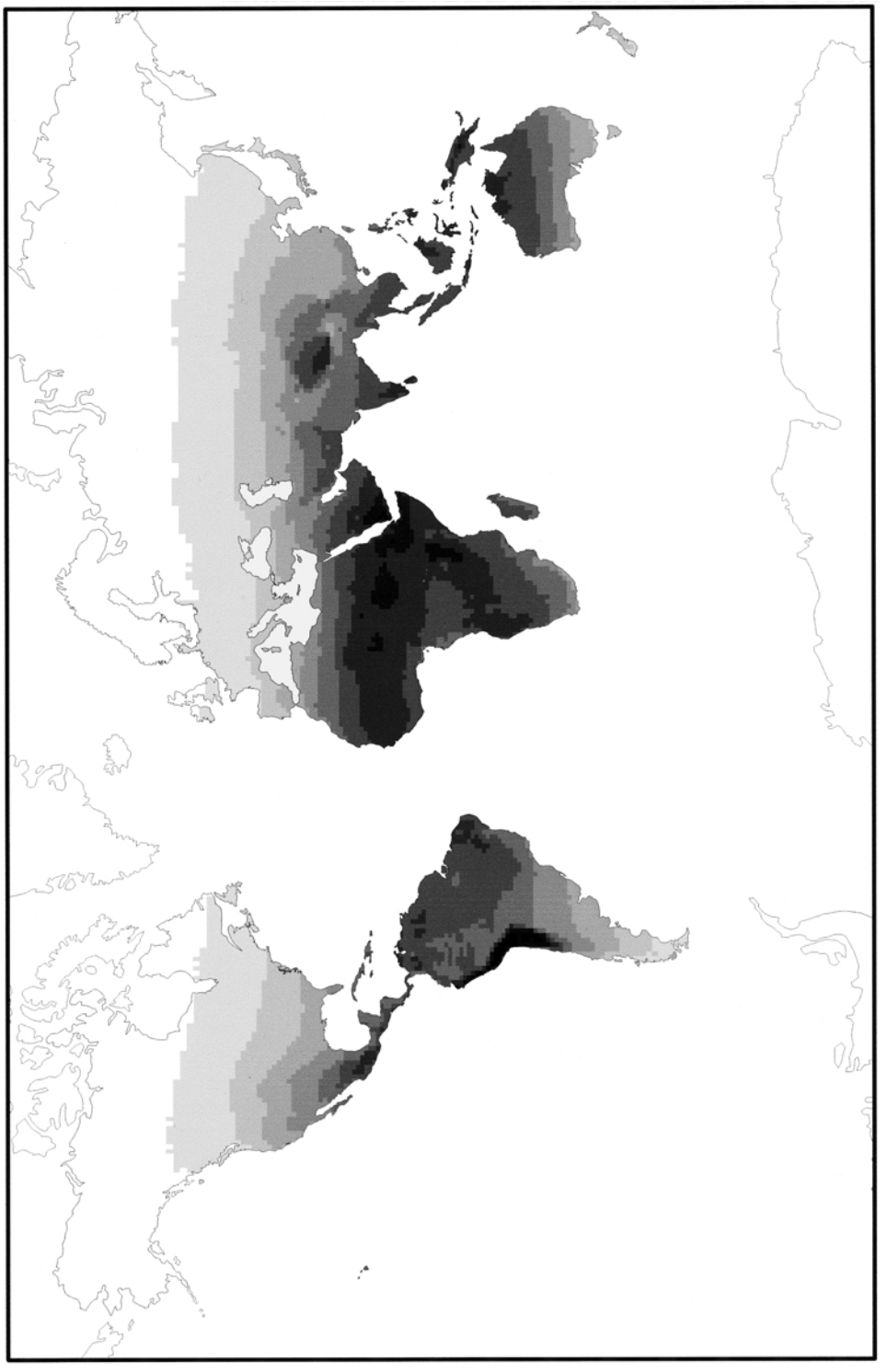

Figure 3. Predicted shading of skin colors for indigenous humans based on the results of a linear regression model in which skin reflectance (at 685 nm) for indigenous peoples in both hemispheres was allowed to respond to annual average UVMED for both hemispheres. The predicted skin reflectance values were first divided into 50 equal intervals and then graphically represented in gray shades ranging from darkest gray (greatest melanization) to lightest gray (least melanization). Darker shades of gray represent a higher degree of skin melanization and do not represent actual predicted skin colors. Mercator projection.

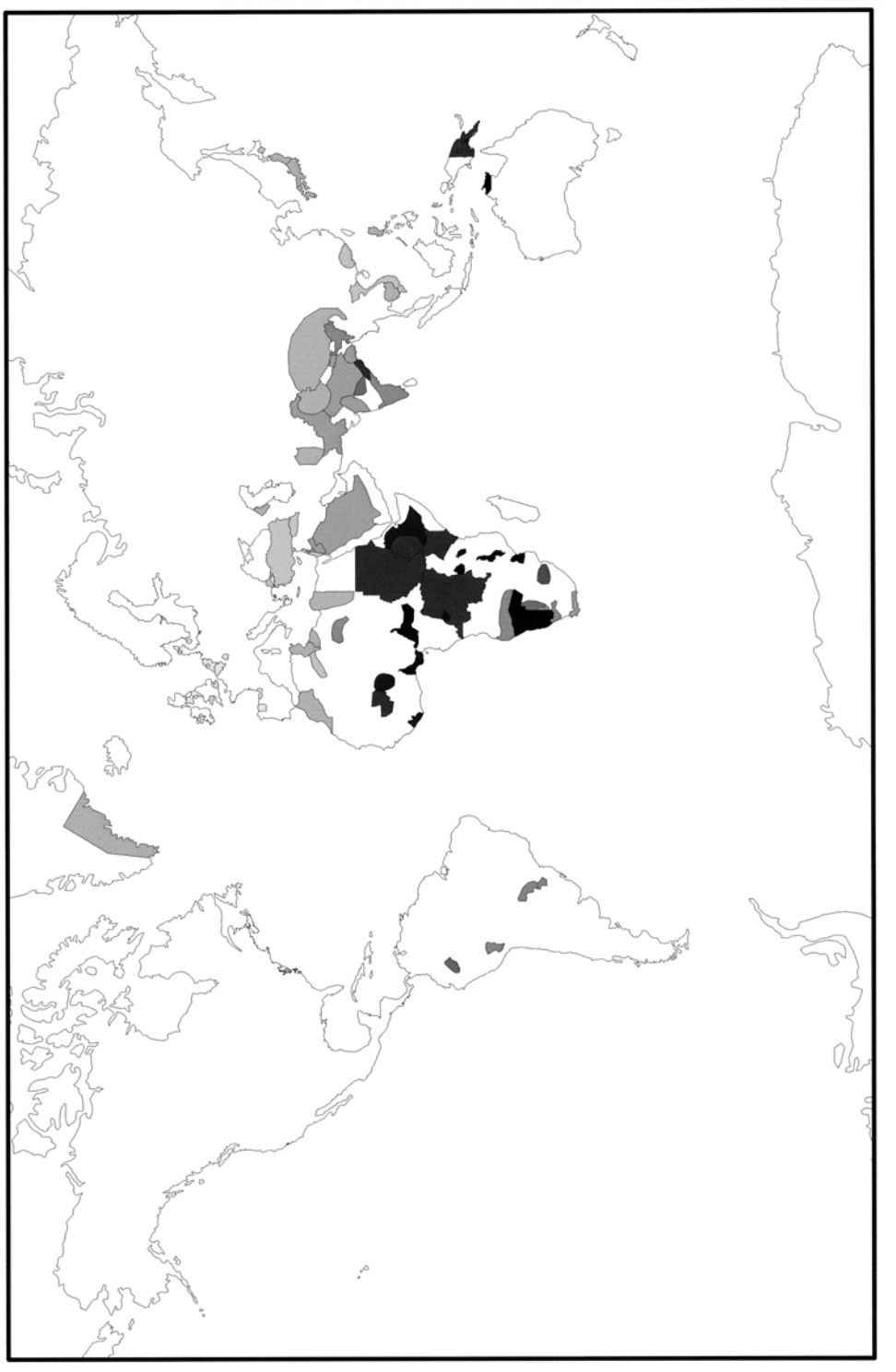

Figure 4. Gradation of skin colors for known indigenous human populations, represented by shading from darkest to lightest gray (greatest to least melanization, as in Figure 3), based on observed skin reflectances at 685 nm reported in Table 6. Mercator projection.

situation applies equally to populations of early *Homo sapiens* that undertook migrations from eastern Africa into the circum-Mediterranean region and Europe. Their original levels of pigmentation would have precipitated vitamin D_3 crises in their new environments, especially among females and infants, and these crises would have been more severe the farther north the populations ventured. Clinical evidence indicates that the ability of humans to store vitamin D_3 and its metabolites for long periods of time in fat and skeletal muscle is dependent on their pre-existing stores of the vitamin (Mawer *et al.*, 1972). Individuals receiving large doses of vitamin D_3 by injection for the first time showed rapid elimination of vitamin D_3 metabolites within 7–10 days; those who had previously received them showed a much more protracted schedule of elimination (Mawer *et al.*, 1972). Thus, the potential for vitamin D_3 storage is great if the intake or the endogenous synthesis is high; otherwise it is not. Robins' arguments against the depigmentation hypothesis are, therefore, not supported.

Sexual differences in skin reflectance

Comparison of skin reflectances between the sexes confirmed previous observations that human females are consistently lighter than males (Byard, 1981; Robins, 1991). Although female skin coloration darkens through adolescence and adulthood and only lightens after 45 (Wiskemann & Wisser, 1956; Byard, 1981), females are still significantly lighter (that is, show a higher value for skin reflectance) than males for populations in which males and females are represented from the same location. This suggests that the lighter skin pigmentation of females is needed to permit relatively greater UV light penetration of the integument for previtamin D_3 synthesis. The extra calcium needs of females during pregnancy and lactation are met by increasing plasma concentrations of 1.25-dihydroxyvitamin D, which in turn enhances calcium absorption in the intestine (Wilson *et al.*, 1990; Whitehead *et al.*, 1981). Skin pigmentation in human females thus represents a complex compromise between the exigencies of photoprotection and previtamin D_3 synthesis.

The documentation of lighter skin in females than in males for all populations raises a serious question concerning the validity of the hypothesis that human skin coloration is in large part determined by sexual selection (Diamond, 1988, 1991). Were this so, one would have to postulate that there was a universal preference of males for females slightly lighter than themselves, even in populations purported to prefer dark skin (e.g., Tasmanians; Diamond, 1988, 1991). Avoidance of the sun by females is practiced in some cultures and is probably maintained as a custom in those cultures in part by mate choice. It is unlikely, however, that this acquired custom would have any effect on constitutive pigmentation through time unless inherently more lightly pigmented females who also avoided the sun were more reproductively successful than more darkly pigmented females who followed the same practice. We suggest that lighter pigmentation in human females began as a trait directly tied to increased fitness and was subsequently reinforced and enhanced in many human populations by sexual selection.

Annual average UVMED and skin reflectance

Previous studies of the relationship between skin reflectance and environmental variables (Roberts & Kahlon, 1976; Tasa *et al.*, 1985), undertaken before remote sensing data on UV radiation were available, found highest correlations between 685 nm filter skin reflectance and latitude (r=0·835 by Roberts & Kahlon, 1976, and r=0·82 by Tasa *et al.*, 1985). Relative to these values, calculations based on the larger skin reflectance dataset amassed for this study showed a very similar correlation (r=0·827). The

generally very high correlations between skin reflectance at all wavelengths and annual average UVMED speaks of the close relationship of UV radiation to skin color (*contra* Diamond, 1991).

The generally small differences found between observed and expected values for skin coloration appear to reflect differences between populations in duration of habitation in their respective areas. Populations believed to have inhabited their current area of distribution for 10–20,000 years (e.g., Spanish Basques) conform most closely to predicted values for skin reflectance. Those which are thought to have migrated into their current locations more recently (e.g., Aboriginal Australians from Darwin who are migrants from the Central Desert) conform less closely to predicted values.

Cultural practices have had significant effects on rates of change of integumentary pigmentation in human populations that have undergone migrations, especially in the last 20,000 or so years. The first modern human inhabitants of Tibet, for instance, were clad, not naked. The skin of modern Tibetans is lighter than would be predicted from the annual average UVMED alone probably because of the relative recency of their migration and because the obligate wearing of clothes has meant that the areas of skin available for previtamin D_3 synthesis (such as the face) had to remain relatively unpigmented. By the same token, immigrants to the New World who inhabit tropical forests are also relatively lightly pigmented. This is probably again because of the relative recency of their immigration, but also because of their habitual shade-seeking behavior (Hames, 1992), which mitigates the photolytic effects of UV radiation.

The specific role of melanin in human skin

Melanin has general absorption from the infrared to the ultraviolet, but the absorption maxima of other integumentary pigments are more specific. Although it is subject to the effects of melanin, the absorption from oxyhemoglobin can be sampled with a green (545 nm) filter. UV absorption at this value is greater in lightly pigmented individuals and produces a greater erythemal response (Daniels & Imbrie, 1958; Daniels, 1964). The strongest statistical correlations between skin reflectance and UVMED are observed for the 545 nm filter (Tables 4 and 5), suggesting that the main role of melanin pigmentation in humans is regulation of the effects of UV radiation on the contents of cutaneous blood vessels located in the dermis. This finding supports the proposition that skin reflectance, particularly in the wavelength approximating the absorption maximum of oxyhemoglobin (545 nm), has been optimized by natural selection to balance the conflicting requirements of prevention of folate photolysis (photoprotection) and previtamin D_3 synthesis (requiring UV penetration). We would predict that the relationship between annual average UVMED and green filter reflectance would be even stronger in females than in males because of their need to optimize the endogenous synthesis of previtamin D_3. Unfortunately, because insufficient sex-specific reflectance data exist for each hemisphere, this hypothesis could not be conclusively tested.

Conclusions

The results presented here demonstrate that skin coloration in humans is highly adaptive and has evolved to accommodate the physiological needs of humans as they have dispersed to regions of widely varying annual UVMED. The dual selective pressures of photoprotection and vitamin D_3 synthesis have created two clines of skin pigmentation. The first cline, from the equator to the poles, is defined by the significantly greater need for photoprotection at the equator in particular and within the tropics in general. Deeply melanized skin protects against folate photolysis and helps to prevent

UV-induced injury to sweat glands (and subsequent disruption of thermoregulation). The second cline, from approximately 30°N to the North Pole, is defined by the greater need in high latitudes to accommodate as much previtamin D_3 synthesis as possible in areas of low annual UVMED. Humans inhabiting regions at the intersection of these clines demonstrate a potential for developing varying degrees of facultative pigmentation (tanning) (Quevedo *et al.*, 1975). Moderately melanized skin would appear to be at risk of vitamin D_3 deficiency and rickets under conditions where UV radiation is restricted as a result of latitude, cultural practices or both.

The results of this study suggest that skin pigmentation is relatively labile, and that adaptations to local UVMED conditions can occur over relatively short periods of geological time. Thus, it is likely that some human lineages through time may have gone through alternating periods of depigmentation and pigmentation (or vice versa) as they moved from one UVMED regime to another. As the pace of human migrations has quickened in recent centuries, more and more populations are finding themselves living under UV irradiation regimes to which they are inherently poorly adapted (e.g., the English who settled in Australia in the nineteenth and twentieth centuries, and the Indians and Pakistanis who have moved to northern England in recent decades), with major public health consequences (Kaidbey *et al.*, 1979; Henderson *et al.*, 1987). Cultural practices such as sun-bathing and purdah have in some cases exacerbated these conditions and mitigated others. Because of its high degree of responsiveness to environmental conditions, skin pigmentation is of no value in assessing the phylogenetic relationships between human groups.

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Appendix

Original skin reflectance data for indigenous human populations as defined in the text

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Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
Afghanistan/Iran	Afghanistan	Afghani/Iranian		M
Algeria Aures	Algeria	Aures	Chaouias from Bouzina	M
Algeria Aures	Algeria	Aures	Chaouias from Bouzina	F
Australia Darwin	Australia	Darwin	Aborigines	M
Belgium	Belgium	Belgians 3	Belgians	B
Belgium	Belgium	Brussels	Belgians	M
Belgium	Belgium	Brussels	Belgians	F
Belgium	Belgium	Brussels	Belgians (except 2 Greeks, 1 Iraqi)	M
Belgium	Belgium	Brussels	Belgians (except 2 Greeks, 1 Iraqi)	F
Botswana San	Botswana	Kalahari Desert	Central Bushmen	M
Botswana San	Botswana	Kalahari Desert	Central Bushmen	F
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Lone Tree, Central San	M
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Lone Tree, Central San	F
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Takashwani, Central San	M
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Takashwani, Central San	F
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Ghanzi, Central San	M
Botswana San	Botswana	Kalahari Desert	Yellow Bushmen at Ghanzi, Central San	F
Brazil Caingan	Brazil	Parana	Caingang Indians	M
Brazil Caingan	Brazil	Parana	Caingang Indians	F
Brazil Guarani	Brazil	Parana	Guarini Indians	F
Brazil Guarani	Brazil	Parana	Guarini Indians	M
Burkina Faso Kurumba	Burkina Faso	Formerly Upper Volta	Kurumba from Roanga	F
Burkina Faso Kurumba	Burkina Faso	Formerly Upper Volta	Kurumba from Roanga	M
Cambodia	Cambodia		Khmers	M
Cameroon Fali	Cameroon	(Northern)	Fali Tinguelin	M
Cameroon Fali	Cameroon	(Northern)	Fali Tinguelin	F
Cameroon Fali	Cameroon	(Northern)	Fali Kangou	M

Sex designations: F=female; M=male; B=both. All data are from published sources except for those indicated to be from "OSU-Beal's Database", which were kindly provided by Dr Kenneth Beals. Skin reflectances for filters of different wavelength are identified by the wavelength only rather than their filter number. (For instance, the 609 filter which measures skin reflectance at 685 nm is identified only as 685 nm.) The only original measurements converted from Photovolt to E.E.L. values were those from Colombia, which were converted using the formula for Belize Creoles of Lees & Byard, 1978.

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
Cameroon Fali	Cameroon	(Northern)	Fali Kangou	F
Chad Sara	Chad	Ndila	Sara Madjingay	M
Chad Sara	Chad	Ndila	Sara Madjingay	F
China Southern	China			M
China Southern	China	Hong Kong	Chinese	M
China Tibet	Tibet	India Mussoorie	Tibetans	M
China Tibet	Tibet	India Mussoorie	Tibetans	F
Colombia	Americas	Region De Planos	Guahibos	M
Ethiopia	Ethiopia		Residents of Adi-Arkai (1500 m altitude)	M
Ethiopia	Ethiopia		Residents of Adi-Arkai (1500 m altitude)	F
Ethiopia Highland	Ethiopia	Highlands	Residents of Debarech (3000 m altitude)	M
Ethiopia Highland	Ethiopia	Highlands	Residents of Debarech (3000 m altitude)	F
Germany Mainz	Germany	Mainz	German and American Whites	M
Greenland Southern	Greenland	Greenland East	Eskimo Ammassalimiut	M
India	India		Angami Nagas	B
India Bengal	India	Bengal	Low Caste	M
India Bengal	India	Bengal	Kayastha	M
India Bengal	India	Bengal	Brahman	M
India Bengal	India	Bengal	Vaidya	M
India Bengal	India	Calcutta	Rarhi Brahman	M
India Goa	India	Goa	Goans	M
India Nagpur	India	Nagpur and Kamptee	Mahar	M
India Northern	India	North India	Baniya	M
India Northern	India	North India	Jat Sikhs	M
India Northern	India	North India	Haryana Jats	M
India Northern	India	North India	Khatris	M
India Northern	India	North India	Brahmans	M
India Northern	India	North India	Aroras	M
India Northern	India	North India	Aroras	F
India Northern	India	North India	Khatris	F
India Northern	India	Delhi	Saxena Kayastha (husband–wife–children)	F
India Northern	India	Delhi	Saxena Kayastha (husband–wife–children)	M
India Northern	India	Delhi	Saxena Kayastha (husband–wife–children)	B
India Northern	India	Delhi	Aggarwal	M
India Northern	India	Delhi	Aggarwal	F
India Northern	India	England	North Indians (Higher Castes)	M

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
India Orissa	India	Koraput Town, Orissa	Bareng Paroja	M
India Orissa	India	Koraput Town, Orissa	Bado Gadaba	M
India Punjab	India	Delhi	Punjabi Indians (mother)	F
India Punjab	India	Delhi	Punjabi Indians (father)	M
India Punjab	India	Delhi	Punjabi Indians (son)	M
India Punjab	India	Delhi	Punjabi Indians (daughter)	F
India Punjab	India	England	Sikhs (husband–wife–children)	F
India Punjab	India	England	Sikhs (husband–wife–children)	M
India Punjab	India	England	Sikhs (husband–wife–children)	F
India Punjab	India	England	Sikhs (husband–wife–children)	M
India Punjab	India	Punjab	Khatris Punjab	M
India Punjab	India	Sikhs 2	Sikhs	B
India Rajasthan	India	North India	Rajputs	M
India Southern	India	South India		M
Iran Nowshahr	Iran	Iran (Northern)	Nowshahr City	M
Iran Nowshahr	Iran	Iran (Northern)	Nowshahr City	F
Iraq Syria Kurds	Syria	Mainz	Syrians and Iranians	M
Iraq Syria Kurds	Iraq	Iraqi/Syrian		M
Iraq Syria Kurds	Iraq	Iraqi/Syrian		F
Ireland Balinlough	Ireland (Eire)	Ballinlough		M
Ireland Balinlough	Ireland (Eire)	Ballinlough		F
Ireland Carnew	Ireland (Eire)	Carnew		F
Ireland Carnew	Ireland (Eire)	Carnew		M
Ireland Longford	Ireland (Eire)	County Longford		B
Ireland Longford	Ireland (Eire)	County Longford		M
Ireland Longford	Ireland (Eire)	County Longford		F
Ireland Rossmore	Ireland (Eire)	Rossmore		F
Ireland Rossmore	Ireland (Eire)	Rossmore		M
Israel	Palestine	Palestine		M
Israel	Palestine	Palestine		F
Japan Central	Japan	Japan (Central)	Japanese	M
Japan Central	Japan	Japan (Central)	Japanese	F
Japan Central	Japan	Central Japanese	Central Japanese	B
Japan Central	Japan	Tokyo	Japanese	M
Japan Hidaka	Hokkaido	Hidaka	Ainu	M
Japan Hidaka	Hokkaido	Hidaka	Ainu	F

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
Japan Northern	Japan	Japan (North)	Japanese	M
Japan Northern	Japan	Japan (North)	Japanese	F
Japan Southwest	Japan	Southwest	Southwest	M
Japan Southwest	Japan	Southwest	Southwest	F
Jordan	Jordan	Jordan	Non-village Arabs	M
Jordan	Jordan	Jordan	All Arabs	M
Jordan	Jordan	Jordan		M
Jordan Azzarqa	Jordan	Jordan Azraq depression	Arab villager, child	F
Jordan Azzarqa	Jordan	Jordan Azraq depression	Arab villagers	M
Kenya	Kenya	Kenya		M
Kurdish Jews	Iraq	Ne Baghdad	Kurdish Jews	M
Kurdish Jews	Iraq	Ne Baghdad	Kurdish Jews	M
Lebanon	Lebanon		Lebanese	M
Lebanon	Lebanon		Lebanese	F
Liberia	Liberia	Germany Mainz	Africans from Ghana and Liberia	M
Libya Cyrenaica	Libyia	Cyrenaica		M
Libya Cyrenaica	Libyia	Cyrenaica		F
Libya Fezzan	Libyia	Fezzan		M
Libya Tripoli	Libyia	Tripolitania		M
Libya Tripoli	Libyia	Tripolitania		F
Malawi	Malawi		Mainly Cewa	M
Mali Dogon	Mali	Sanga and Boni	Dogon	M
Mali Dogon	Mali	Sanga and Boni	Dogon	F
Morocco	Morocco	Moraccans	Morocans	B
Morocco	Morocco	Morocco		M
Mozambique Chopi	Mozambique	Sofala	Chopi	M
Mozambique Chopi	Mozambique	Sofala	Chopi	F
Namibia	Namibia	Kurungkuru Kraal	Kurungkuru Kraal	B
Namibia	Namibia	Tondoro	Tondoro	B
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, Kuangali	M
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, Kuangali	F
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, Kuangali	M
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, Kuangali	F
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, M'bukushu at Bagani	F
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, M'bukushu at Bagani	M
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, M'bukushu at Bagani	M
Namibia Okavango	Namibia	Bordering on Angola	Okavango Bantu, M'bukushu at Bagani	F

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
Namibia Rehoboth Baster	Namibia	Bordering on Angola	Black Bushmen at Bagani	M
Namibia Rehoboth Baster	Namibia	Bordering on Angola	Black Bushmen at Bagani	F
Namibia Rehoboth Baster	Namibia	Bordering on Angola	Black Bushmen at Bagani	M
Namibia Rehoboth Baster	Namibia	Bordering on Angola	Black Bushmen at Bagani	F
Namibia Rehoboth Baster	Namibia	Rehoboth	Basters	M
Namibia Rehoboth Baster	Namibia	Rehoboth	Basters	F
Nepal Eastern	Nepal	Eastern	Jirel	B
Nepal Eastern	Nepal	Eastern	Sunwar	B
Nepal Eastern	Nepal	Eastern	Sherpa	B
Nepal Eastern	Nepal	Eastern	Tamang	B
Nepal Eastern	Nepal	Eastern	Brahman	B
Nepal Eastern	Nepal	Eastern	Chetri	B
Nepal Eastern	Nepal	Eastern	Average	B
Nepal Eastern	Nepal	Eastern	Jirel	M
Nepal Eastern	Nepal	Eastern	Jirel	F
Netherlands	Netherlands		Dutch	B
Netherlands	Netherlands		Dutch (mainly resident in Utrecht)	M
Netherlands	Netherlands		Dutch (mainly resident in Utrecht)	F
Nigeria Ibo	Nigeria	Southern (Ibadan)	Ibo	M
Nigeria Yoruba	Nigeria	Southern (Ibadan)	Yoruba	M
Nigeria Yoruba	Nigeria	Southern (Ibadan)	Yoruba	F
Nigeria Yoruba	Nigeria	Lagos	Africans	M
Pakistan	Pakistan	Pakistan		M
Pakistan	Pakistan	Pakistan		F
Pakistan	Pakistan			M
Papua Karker	Papua-New Guinea	Karkar Island	Karker Islanders	F
Papua Lufa	Papua-New Guinea	Western Highlands	Lufa villagers	M
Papua Lufa	Papua-New Guinea	Western Highlands	Lufa villagers	F
Papua Mt Hagan	Papua-New Guinea	Mount Hagan	Western Highlands	M
Papua Mt Hagan	Papua-New Guinea	Mount Hagan	Western Highlands	F
Papua New Guinea	Papua-New Guinea	Papuans	Papuans	B
Papua Port Moresby	Papua-New Guinea	Port Moresby	Hanuabada	B
Peru Maranon	Peru	Maranon Valley	Aguarana Indians	M
Peru Maranon	Peru	Maranon Valley	Aguarana Indians	F
Peru Nunoa	Peru	Nunoa	Az	B
Philippines Manila	Philippines	Manila	Filipino	M

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
Russia Chechen	Russia	Chechnia	Chechen	F
Russia Chechen	Russia	Chechnia	Chechen	M
Saudi Arabia	Saudi	Saudi		M
South Africa	South Africa	Johannesburg	S. A. Negroes (73% Tswana and Xhosa)	M
South Africa	South Africa	Johannesburg	S. A. Negroes (73% Tswana and Xhosa)	F
South Africa	South Africa		Bantu (96% Xhosa)	M
South Africa	South Africa		Bantu (96% Xhosa)	F
South Africa Cape	South Africa	Cape Province	Cape Coloureds	M
South Africa Cape	South Africa	Cape Province	Cape Coloureds	F
South Africa Cape	South Africa	Cape Province	Cape Coloureds	M
South Africa Cape	South Africa	Cape Province	Cape Coloureds	F
South Africa Hottentot	South Africa	Namaqualand	Hottentot	M
South Africa Hottentot	South Africa	Namaqualand	Hottentot	F
South Africa San Central	Namibia	Warmbath	Hottentot	M
South Africa San Central	Namibia	Warmbath	Hottentot	F
Spain Basques	Spain	Guipuzcoa	Basques	F
Spain Basques	Spain	Guipuzcoa	Basques	M
Spain Basques	Spain	Vizcaya	Basques	F
Spain Basques	Spain	Vizcaya	Basques	M
Spain Basques	Spain	Biscay	Basque and non-Basques	M
Spain Leon	Spain	Leon	Meseta	M
Spain Leon	Spain	Leon	Cabrera	M
Spain Leon	Spain	Leon	Bierzo	M
Spain Leon	Spain	Leon	Montana	M
Spain Leon	Spain	Leon	Maragateria	M
Sudan	Sudan	Sudan		M
Swaziland	South Africa	Johannesburg and Swaziland	Swazis	M
Swaziland	South Africa	Johannesburg and Swaziland	Swazis	F
Syria Druze	Jordan	Jordan Azraq Depression	Druze	M
Tanzania Nyatura	Tanzania		Nyatura	M
Tanzania Nyatura	Tanzania		Nyatura	F
Tanzania Sandewe	Tanzania		Sandawe	M
Tanzania Sandewe	Tanzania		Sandawe	F
Tunisia	Tunisia	Tunisians	Tunisians	B
Turkey	Turkey	Turkey		M
Turkey	Turkey	Turkey		F

Appendix (*Continued*)

Population designation (as in Table 5)	Country or region	Subregion or city	Population name given in study	Sex
United Kingdom Cumberland	United Kingdom	Cumberland		F
United Kingdom Cumberland	United Kingdom	Cumberland		M
United Kingdom London	United Kingdom	London	Europeans	F
United Kingdom London	United Kingdom	London	Europeans	M
United Kingdom Northern	United Kingdom	Northumberland	Holy Island	M
United Kingdom Northern	United Kingdom	Northumberland	Holy Island	F
United Kingdom Northern	United Kingdom	Liverpool	Europeans	B
United Kingdom Northern	United Kingdom	Northumberland	North Northumberland	F
United Kingdom Northern	United Kingdom	Northumberland	North Northumberland	M
United Kingdom Northern	United Kingdom	Northumberland	South-east Northumberland	F
United Kingdom Northern	United Kingdom	Northumberland	South-east Northumberland	M
United Kingdom Wales	United Kingdom	British Isles	Isle of Man	F
United Kingdom Wales	United Kingdom	British Isles	Isle of Man	M
United Kingdom Wales	United Kingdom	Wales	Merthyr Tydfil	F
United Kingdom Wales	United Kingdom	Wales	Merthyr Tydfil	M
United Kingdom Wales	United Kingdom	Wales (Southwest)	North Pembrokeshire	F
United Kingdom Wales	United Kingdom	Wales (Southwest)	North Pembrokeshire	M
United Kingdom Wales	United Kingdom	Wales (Southwest)	South Pembrokeshire	F
United Kingdom Wales	United Kingdom	Wales (Southwest)	South Pembrokeshire	M
Vietnam	Vietnam		Vietnamese	M
Vietnam	Vietnam		Veitnamese	B
Zaire	Zaire	Zaire 2	Zaire	B
Zaire	Zaire		Congolese except 3 Cameroon females	M
Zaire	Zaire		Congolese except 3 Cameroon females	F
Zaire Konda	Zaire	Konda 0·9–18·2	Oto	M
Zaire Konda	Zaire	Konda 0·9–18·2	Twa	M

Appendix

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
Afghanistan/Iran	E		24·2						31·7	
Algeria Aures	E									
Algeria Aures	E									
Australia Darwin	E									
Belgium	E									
Belgium	E	36·5	37·7	33·5	44·7	46·7	46·7	38·6	44·8	42·7
Belgium	E	35·7	36·5	32·7	43·5	45·3	45·7	38·2	44·6	42·3
Belgium	E	37·1	39·1	33·8	45·5	46·6	46·1	38·6	43·8	42·5
Belgium	E	36·3	38·2	32·8	43·7	44·5	44·8	38·1	43·2	41·9
Botswana San	E	12·7	12·7	9·3	15·5	16·2	17·2	13·8	18·1	19·1
Botswana San	E	13·2	13·7	9·7	16·6	17·4	18·2	14·4	19·0	20·0
Botswana San	E		14·4							
Botswana San	E		15·2							
Botswana San	E		16·2							
Botswana San	E		17·2							
Botswana San	E		15·6							
Botswana San	E		16·4							
Brazil Caingan	E		16·5						22·9	
Brazil Caingan	E		18·4						26·1	
Brazil Guarani	E		17·2						23·4	
Brazil Guarani	E		16·8						23·6	
Burkina Faso Kurumba	E	8·6	10·8	6·3	12·0	11·0	11·0	8·4	11·6	12·2
Burkina Faso Kurumba	E	8·8	11·4	6·4	12·5	11·6	11·4	8·6	12·0	12·5
Cambodia	E									
Cameroon Fali	E	6·5	7·3	5·0	7·4	7·4	7·6	5·7	7·9	7·7
Cameroon Fali	E	6·7	7·7	5·1	7·6	7·6	7·9	5·9	8·2	8·1
Cameroon Fali	E	6·7	7·4	5·2	7·7	7·7	8·0	6·0	8·4	8·1
Cameroon Fali	E	7·2	8·1	5·3	8·0	8·0	8·5	6·3	8·7	9·0
Chad Sara	E									
Chad Sara	E									
China Southern	E									
China Southern	E									
China Tibet	E									
China Tibet	E									
Colombia	P									
Ethiopia	E		8·3						11·0	
Ethiopia	E		9·8						13·1	

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
Ethiopia Highland	E		9·5						12·7	
Ethiopia Highland	E		10·3						14·3	
Germany Mainz	E	37·5	40·3	34·6	45·5	47·4	47·1	39·8	45·2	43·6
Greenland Southern	E		22·4						29·9	
India	E									
India Bengal	E	13·6	13·9	10·1	17·0	18·2	19·9	15·1	20·4	20·2
India Bengal	E	16·4	16·3	12·9	19·7	21·1	22·8	19·0	24·3	23·3
India Bengal	E	17·1	17·2	13·4	20·4	21·7	24·0	19·6	24·3	24·1
India Bengal	E	17·6	18·4	14·1	21·3	24·0	25·4	20·8	25·3	25·2
India Bengal	E	17·1	18·3	13·4	20·3	21·9	23·2	19·8	24·5	24·2
India Goa	E									
India Nagpur	E	12·3	13·3	9·2	14·8	15·7	16·9	13·4	18·2	18·7
India Northern	E		14·3						22·0	
India Northern	E		15·4						23·6	
India Northern	E		15·7						24·0	
India Northern	E		16·5						25·1	
India Northern	E		17·2						26·0	
India Northern	E		20·7							
India Northern	E		21·1							
India Northern	E		21·7							
India Northern	E	14·9	13·9	11·6	17·1	18·9	19·6	17·3	21·5	21·2
India Northern	E	17·0	16·8	13·4	20·3	22·8	23·5	20·1	24·8	24·4
India Northern	E	15·6	14·5	12·1	18·0	19·9	20·9	18·2	22·3	22·4
India Northern	E									
India Northern	E									
India Northern	E	18·6	21·4	14·9	25·2	26·5	28·0	22·2	27·9	26·6
India Orissa	E	9·6	9·8	7·0	10·3	10·7	11·5	9·6	12·4	13·7
India Orissa	E	9·7	10·3	7·1	10·7	11·2	11·8		12·7	14·1
India Punjab	E	18·2	17·9	14·4	22·0	24·4	25·9	21·6	26·2	26·4
India Punjab	E	18·6	18·8	14·8	23·3	25·5	27·0	22·2	27·0	27·0
India Punjab	E	18·2	17·8	14·4	22·4	24·5	26·0	21·7	26·2	26·4
India Punjab	E	18·7	18·6	14·9	23·0	25·5	27·0	22·4	27·2	27·3
India Punjab	E	20·1	23·4	16·6	27·5	28·3	30·5	24·4	30·9	29·6
India Punjab	E	19·5	23·1	16·0	27·0	27·7	29·5	23·6	29·7	28·5
India Punjab	E	19·3	21·8	15·8	26·0	26·7	28·7	23·2	29·3	28·2
India Punjab	E	18·4	20·5	15·0	24·2	25·0	27·0	22·0	27·4	26·8

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
India Punjab	E		21·3							
India Punjab	E									
India Rajasthan	E		16·2						24·7	
India Southern	E									
Iran Nowshahr	E	17·9	18·2	14·6	21·6	24·4	26·6	21·1	27·2	25·8
Iran Nowshahr	E	22·8	28·0	19·4	32·9	35·6	37·3	28·5	37·6	33·6
Iraq Syria Kurds	E	35·7	38·9	32·4	41·2	42·7	43·3	38·1	43·0	41·6
Iraq Syria Kurds	E		27·4						34·1	
Iraq Syria Kurds	E		31·2						39·1	
Ireland Balinlough	E		35·4						40·9	
Ireland Balinlough	E		36·2						41·9	
Ireland Carnew	E		37·2						42·1	
Ireland Carnew	E		34·9						39·4	
Ireland Longford	E	35·0	36·7	32·2	41·0	44·8	44·6	37·0	41·4	40·8
Ireland Longford	E									
Ireland Longford	E									
Ireland Rossmore	E		35·7						41·8	
Ireland Rossmore	E		34·6						40·7	
Israel	E		26·4						33·6	
Israel	E		29·6						37·3	
Japan Central	E	18·8		15·1	24·4	26·3	27·0	22·6	27·7	27·3
Japan Central	E	20·7		17·1	28·6	30·4	32·1	25·2	32·9	30·2
Japan Central	E				26·7				30·5	
Japan Central	E									
Japan Hidaka	E	20·6		16·7	29·2	30·8	31·9	25·2	31·7	29·9
Japan Hidaka	E	22·9		19·0	33·3	35·1	36·8	28·3	37·6	31·6
Japan Northern	E	19·4		15·7	26·1	27·8	28·8	23·4	29·5	28·2
Japan Northern	E	21·0		17·5	29·7	31·2	33·1	25·6	33·6	30·6
Japan Southwest	E	18·1		14·5	23·0	24·3	25·7	21·4	26·9	26·3
Japan Southwest	E	20·6		17·1	29·7	31·4	31·0	25·6	33·7	30·3
Jordan	E		22·4						30·4	
Jordan	E		21·6						29·3	
Jordan	E		23·7						31·1	
Jordan Azzarqa	E		16·7						24·2	
Jordan Azzarqa	E		20·3						27·6	
Kenya	E		11·9						14·0	

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
Kurdish Jews	E		21·1						29·2	
Kurdish Jews	E		24·2						33·7	
Lebanon	E		27·0						34·4	
Lebanon	E		28·7						36·6	
Liberia	E	9·0	13·6	7·2	12·1	12·2	13·3	8·8	13·7	13·1
Libya Cyrenaica	E		19·0						26·6	
Libya Cyrenaica	E		24·3						32·3	
Libya Fezzan	E		14·9						20·7	
Libya Tripoli	E		19·8						27·4	
Libya Tripoli	E		24·7						33·6	
Malawi	E		9·0	1·2					10·0	
Mali Dogon	E				11·5	11·0	11·4	12·9	11·9	14·0
Mali Dogon	E				11·8	11·2	11·5	13·1	11·9	14·4
Morocco	E									
Morocco	E		21·2						28·1	
Mozambique Chopi	E		7·3							
Mozambique Chopi	E		7·7							
Namibia	E									
Namibia	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Okavango	E									
Namibia Rehoboth Baster	E									
Namibia Rehoboth Baster	E									
Namibia Rehoboth Baster	E									
Namibia Rehoboth Baster	E									
Namibia Rehoboth Baster	E		17·2							
Namibia Rehoboth Baster	E		20·6							
Nepal Eastern	E		16·5						25·2	
Nepal Eastern	E		17·7						26·3	
Nepal Eastern	E		19·7						29·5	

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
Nepal Eastern	E		15·9						24·4	
Nepal Eastern	E		19·0						28·4	
Nepal Eastern	E		17·7						26·1	
Nepal Eastern	E		17·4						26·1	
Nepal Eastern	E		16·2						24·8	
Nepal Eastern	E		19·5						23·9	
Netherlands	E									
Netherlands	E	37·8	39·7	34·7	46·8	48·3	47·8	39·3	44·7	43·3
Netherlands	E	36·4	37·7	33·1	44·6	45·8	45·8	38·0	43·2	42·0
Nigeria Ibo	E	8·7	8·7	6·5	9·2	9·3	10·7	8·6	11·2	11·7
Nigeria Yoruba	E	7·7	8·0	5·9	8·3	8·1	9·7	7·4	10·1	9·7
Nigeria Yoruba	E	8·4	8·5	6·3	8·9	8·9	10·5	8·3	11·1	11·0
Nigeria Yoruba	E	9·9	12·8	7·7	12·6	13·1	14·1	10·1	14·9	14·4
Pakistan	E		20·5						26·9	
Pakistan	E		21·9						28·4	
Pakistan	E									
Papua Karker	E		10·1						15·0	
Papua Lufa	E		9·1						13·3	
Papua Lufa	E		9·3						13·8	
Papua Mt Hagan	E									
Papua Mt Hagan	E									
Papua New Guinea	E									
Papua Port Moresby	E									
Peru Maranon	E								24·5	
Peru Maranon	E								24·7	
Peru Nunoa	E									
Philippines Manila	E									
Russia Chechen	E		21·2						29·1	
Russia Chechen	E		27·4						33·6	
Saudi Arabia	E		21·0						28·0	
South Africa	E	12·4	15·3	9·2	17·9	17·0	18·1	13·1	18·2	18·8
South Africa	E	13·3	16·5	10·0	19·3	18·7	20·0	14·5	20·6	20·5
South Africa	E	10·1	10·6	7·6	12·3	12·4	12·8	10·5	13·7	14·7
South Africa	E	11·6	12·6	8·6	14·5	14·8	15·5	12·3	16·8	17·4
South Africa Cape	E	16·1	15·8	12·5	19·4	20·5	21·5	18·7	22·7	23·1
South Africa Cape	E	17·9	18·5	14·3	22·4	24·3	25·4	21·3	27·0	26·0

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
South Africa Cape	E									
South Africa Cape	E									
South Africa Hottentot	E									
South Africa Hottentot	E									
South Africa San Central	E									
South Africa San Central	E									
Spain Basques	E	31·0	29·2	28·5	35·9	40·9	40·9	34·4	40·9	38·7
Spain Basques	E	31·6	30·0	28·7	37·0	41·2	40·9	34·1	39·6	38·3
Spain Basques	E	30·8	29·0	28·1	35·5	40·1	40·4	34·0	40·0	38·3
Spain Basques	E	31·5	30·0	28·7	36·6	41·1	40·7	34·2	39·6	38·4
Spain Basques	E	32·6	34·1	29·0	36·2	38·3	39·8	35·1	39·5	38·6
Spain Leon	E	31·1	29·0	14·3	36·4		39·0	24·4	36·8	
Spain Leon	E	29·3	26·3		33·4		36·5		36·1	
Spain Leon	E	30·0	27·4		34·4		37·1		35·5	
Spain Leon	E	30·8	28·5		36·0		37·8		35·1	
Spain Leon	E	28·4	25·1	12·7	31·8		34·8		33·4	
Sudan	E		12·2						14·7	
Swaziland	E	9·8	9·7	7·2	11·0	10·3	13·3	10·1	13·9	13·1
Swaziland	E	11·2	10·5	8·2	12·2	12·3	14·9	12·0	16·5	15·9
Syria Druze	E		22·5						30·0	
Tanzania Nyatura	E		7·8						10·2	
Tanzania Nyatura	E		8·6						10·6	
Tanzania Sandewe	E		8·8						11·1	
Tanzania Sandewe	E		9·1						11·7	
Tunisia	E									
Turkey	E		28·8						36·6	
Turkey	E		30·0						38·0	
United Kingdom Cumberland	E		36·9						42·4	
United Kingdom Cumberland	E		35·8						41·8	
United Kingdom London	E	34·4	34·3	30·8	41·4	43·1	43·9	35·6	40·5	39·7
United Kingdom London	E	33·3	32·8	29·5	39·7	41·4	41·6	34·0	37·9	38·1
United Kingdom Northern	E		34·1						39·8	
United Kingdom Northern	E		34·1						39·6	
United Kingdom Northern	E	35·0	36·1	31·4	41·6	43·0	43·7	36·5	41·0	40·4
United Kingdom Northern	E	35·3	36·5	32·8	42·1	45·8	46·4	38·5	44·8	42·5
United Kingdom Northern	E	33·9	34·2	31·3	40·0	43·8	45·3	37·3	43·8	41·4

Appendix (*Continued*)

Population designation (as in Table 5)	EEL (E) or photovolt (P)	420 nm	425 nm	450 nm	465 nm	485 nm	515 nm	525 nm	545 nm	550 nm
United Kingdom Northern	E	34·7	35·6	32·1	41·1	44·6	45·5	37·8	43·9	41·8
United Kingdom Northern	E	33·2	33·0	30·4	38·9	42·7	44·0	36·2	42·1	40·4
United Kingdom Wales	E		36·8						41·8	
United Kingdom Wales	E		36·6						41·9	
United Kingdom Wales	E		33·2						38·7	
United Kingdom Wales	E		32·8						38·7	
United Kingdom Wales	E		35·6						40·9	
United Kingdom Wales	E		34·2	16·4					40·8	
United Kingdom Wales	E		34·1						40·5	
United Kingdom Wales	E		33·7						39·6	
Vietnam	E									
Vietnam	E									
Zaire	E									
Zaire	E	9·0	7·4	6·6	8·6	9·0	9·7	8·9	10·4	12·3
Zaire	E	10·5	9·0	7·6	10·7	11·5	12·5	10·6	12·8	14·8
Zaire Konda	E			2·3						
Zaire Konda	E									

Appendix

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
Afghanistan/Iran						55·7	(Sunderland, 1979)	Original
Algeria Aures						57·4	(Chamla & Demoulin, 1978)	(Robins, 1991)
Algeria Aures						58·7	(Chamla & Demoulin, 1978)	(Robins, 1991)
Australia Darwin				12·9		19·3	(Walsh, 1963); red estimated	Original
Belgium						60·1	FOS73 from OSU-Beals s database	OSU-Beals s database
Belgium	48·9	59·5	45·6	65·7	66·5	67·3	(Leguebe, 1961)	(Robins, 1991)
Belgium	48·8	58·5	45·1	64·3	65·4	65·9	(Leguebe, 1961)	(Robins, 1991)
Belgium	47·5	57·4	45·0	62·9	65·1	64·5	(Van Rijn-Tournel, 1966)	(Robins, 1991)
Belgium	47·2	57·3	44·5	62·6	64·2	63·7	(Van Rijn-Tournel, 1966)	(Robins, 1991)
Botswana San	21·1	28·4	20·5	39·4	32·0	42·5	(Tobias, 1963)	(Robins, 1991)
Botswana San	22·5	30·2	21·3	40·8	33·0	43·6	(Tobias, 1963)	(Robins, 1991)
Botswana San						40·5	(Weiner *et al.*, 1964)	(Robins, 1991)
Botswana San						43·1	(Weiner *et al.*, 1964)	(Robins, 1991)
Botswana San						43·0	(Weiner *et al.*, 1964)	(Robins, 1991)
Botswana San						43·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Botswana San						43·0	(Weiner *et al.*, 1964)	(Robins, 1991)
Botswana San						44·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Brazil Caingan						48·1	(Harrison & Salzano, 1966)	(Robins, 1991)
Brazil Caingan						50·7	(Harrison & Salzano, 1966)	(Robins, 1991)
Brazil Guarani						46·5	(Harrison & Salzano, 1966)	(Robins, 1991)
Brazil Guarani						47·9	(Harrison & Salzano, 1966)	(Robins, 1991)
Burkina Faso Kurumba	13·0	17·1	12·2	27·1	21·7	27·9	(Huizinga, 1968)	(Robins, 1991)
Burkina Faso Kurumba	13·5	17·4	12·5	28·0	22·4	29·3	(Huizinga, 1968)	(Robins, 1991)
Cambodia				50·2		54·0	(Carbonnel & Oliver, 1966); red estimated	(Harrison, 1973)
Cameroon Fali	8·5	11·3	8·3	16·1	15·9	20·0	(Ritgers-Aris, 1973*b*)	(Robins, 1991)
Cameroon Fali	8·8	12·0	8·2	16·9	16·3	20·9	(Ritgers-Aris, 1973*b*)	(Robins, 1991)
Cameroon Fali	8·9	11·9	8·3	16·8	16·5	21·1	(Ritgers-Aris, 1973*b*)	(Robins, 1991)
Cameroon Fali	9·3	12·6	9·0	18·6	18·4	25·5	(Ritgers-Aris, 1973*b*)	(Robins, 1991)
Chad Sara						23·2	(Hiernaux, 1972)	(Robins, 1991)
Chad Sara						26·0	(Hiernaux, 1972)	(Robins, 1991)
China Southern				56·6		59·9	(Carbonnel & Oliver, 1966); red estimated	(Harrison, 1973)
China Southern				54·3		57·7	(Walsh, 1963); red estimated	Original
China Tibet						54·5	(Kalla & Tirwari, 1970)	(Robins, 1991)
China Tibet						54·9	(Kalla & Tirwari, 1970)	(Robins, 1991)
Colombia			24·6				(Diaz Ungria, 1965)	(Harrison, 1973)

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
Ethiopia						30·2	(Harrison *et al.*, 1969)	(Robins, 1991)
Ethiopia						33·2	(Harrison *et al.*, 1969)	(Robins, 1991)
Ethiopia Highland						31·4	(Harrison *et al.*, 1969)	(Robins, 1991)
Ethiopia Highland						35·7	(Harrison *et al.*, 1969)	(Robins, 1991)
Germany Mainz	50·1	60·6	46·3	66·7	66·9	66·9	(Ojikutu, 1965)	(Robins, 1991)
Greenland Southern						55·7	(Ducros *et al.*, 1975)	(Robins, 1991)
India						44·6	OSU-Beals s database	OSU-Beals s database
India Bengal	24·1	29·9	22·1	41·5	34·2	44·8	(Buchi, 1957)	(Robins, 1991)
India Bengal	27·4	35·6	28·1	45·3	43·7	48·6	(Buchi, 1957)	(Robins, 1991)
India Bengal	28·5	36·3	29·3	47·5	45·1	49·9	(Buchi, 1957)	(Robins, 1991)
India Bengal	30·2	37·9	30·0	47·2	45·9	50·7	(Buchi, 1957)	(Robins, 1991)
India Bengal	29·1	36·9	29·5	47·7	45·2	49·7	(Das & Mukherjee, 1963)	(Robins, 1991)
India Goa				42·0		46·4	(Walsh, 1963); red estimated	Original
India Nagpur	21·6	28·4	19·6	37·6	31·3	41·3	(Das & Mukherjee, 1963)	(Robins, 1991)
India Northern						48·6	(Jaswal, 1979)	(Robins, 1991)
India Northern						50·6	(Jaswal, 1979)	(Robins, 1991)
India Northern						51·5	(Jaswal, 1979)	(Robins, 1991)
India Northern						52·7	(Jaswal, 1979)	(Robins, 1991)
India Northern						52·8	(Jaswal, 1979)	(Robins, 1991)
India Northern						55·8	(Kalla, 1969)	(Robins, 1991)
India Northern						56·1	(Kalla, 1969)	(Robins, 1991)
India Northern						56·4	(Kalla, 1969)	(Robins, 1991)
India Northern	24·8	32·8	25·7	41·5	40·8	45·8	(Kalla, 1972)	(Robins, 1991)
India Northern	29·0	37·6	29·3	46·5	45·2	50·4	(Kalla, 1972)	(Robins, 1991)
India Northern	26·0	34·4	27·0	43·7	42·6	48·0	(Kalla, 1972)	(Robins, 1991)
India Northern						49·5	(Kalla, 1973)	(Robins, 1991)
India Northern						50·0	(Kalla, 1973)	(Robins, 1991)
India Northern	31·5	40·5	31·4	49·4	47·6	52·5	(Tiwari, 1963)	(Robins, 1991)
India Orissa	14·6	20·0	14·3	28·8	24·3	31·8	(Das & Mukherjee, 1963)	(Robins, 1991)
India Orissa	15·2	20·7	14·6	29·7	24·8	32·3	(Das & Mukherjee, 1963)	(Robins, 1991)
India Punjab	31·2	40·5	31·5	49·7	48·0	53·6	(Banerjee, 1984)	Original
India Punjab	31·8	41·4	32·2	50·8	48·8	54·5	(Banerjee, 1984)	Original
India Punjab	30·9	40·6	31·6	50·0	48·3	54·3	(Banerjee, 1984)	Original
India Punjab	32·3	41·8	32·5	51·0	49·2	54·9	(Banerjee, 1984)	Original
India Punjab	36·5	45·3	34·6	52·0	51·1	55·6	(Kahlon, 1973)	(Robins, 1991)
India Punjab	34·8	43·5	33·4	50·6	49·8	54·5	(Kahlon, 1973)	(Robins, 1991)

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
India Punjab	34·6	43·1	33·2	50·4	49·5	54·1	(Kahlon, 1973)	(Robins, 1991)
India Punjab	32·6	41·0	31·6	48·4	47·7	52·4	(Kahlon, 1973)	(Robins, 1991)
India Punjab						56·1	(Kalla, 1969)	(Robins, 1991)
India Punjab						54·0	ROB72 from OSU-Beals s database	OSU-Beals s database
India Rajasthan						52·0	(Jaswal, 1979)	(Robins, 1991)
India Southern				42·4		46·7	(Walsh, 1963); red estimated	Original
Iran Nowshahr	31·2	39·7	30·2	46·5	45·8	50·0	(Mehrai & Sunderland, 1990)	(Robins, 1991)
Iran Nowshahr	41·9	50·9	38·6	56·6	55·7	59·7	(Mehrai & Sunderland, 1990)	(Robins, 1991)
Iraq Syria Kurds	46·7	57·7	44·2	62·3	63·6	64·0	(Ojikutu, 1965)	(Robins, 1991)
Iraq Syria Kurds						57·4	(Sunderland, 1979)	Original
Iraq Syria Kurds						60·2	(Sunderland, 1979)	Original
Ireland Balinlough						65·3	(Sunderland *et al.*, 1973)	(Robins, 1991)
Ireland Balinlough						65·1	(Sunderland *et al.*, 1973)	(Robins, 1991)
Ireland Carnew						64·6	(Sunderland *et al.*, 1973)	(Robins, 1991)
Ireland Carnew						64·4	(Sunderland *et al.*, 1973)	(Robins, 1991)
Ireland Longford	46·2	58·2	43·7	63·1	64·7	64·9	(Lees *et al.*, 1979)	Original
Ireland Longford						64·9	(Lees *et al.*, 1979)	Original
Ireland Longford						65·2	(Lees *et al.*, 1979)	Original
Ireland Rossmore						64·8	(Sunderland *et al.*, 1973)	(Robins, 1991)
Ireland Rossmore						64·7	(Sunderland *et al.*, 1973)	(Robins, 1991)
Israel						57·6	(Sunderland, 1979)	Original
Israel						58·8	(Sunderland, 1979)	Original
Japan Central	33·0	42·8	32·4	50·5	48·7	53·3	(Hulse, 1967)	(Robins, 1991)
Japan Central	37·1	46·4	35·1	53·2	51·7	55·7	(Hulse, 1967)	(Robins, 1991)
Japan Central						54·6	(Harvey & Lord, 1978; Hulse, 1967)	Original
Japan Central				54·3		57·8	(Walsh, 1963); red estimated	Original
Japan Hidaka	35·6	46·0	35·0	54·3	52·1	57·4	(Harvey & Lord, 1978)	Original
Japan Hidaka	41·0	51·1	36·1	58·2	59·4	60·8	(Harvey & Lord, 1978)	Original
Japan Northern	34·0	44·1	33·2	51·4	49·5	54·1	(Hulse, 1967)	(Robins, 1991)
Japan Northern	37·9	46·8	35·5	53·5	52·0	55·7	(Hulse, 1967)	(Robins, 1991)
Japan Southwest	31·7	41·6	31·2	49·0	47·2	51·6	(Hulse, 1967)	(Robins, 1991)
Japan Southwest	37·9	47·0	35·5	53·4	51·9	55·5	(Hulse, 1967)	(Robins, 1991)
Jordan						52·7	(Sunderland & Coope, 1973)	Original
Jordan						52·2	(Sunderland & Coope, 1973)	Original
Jordan						54·1	(Sunderland, 1979)	Original

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
Jordan Azzarqa						48·0	(Sunderland & Coope, 1973)	Original
Jordan Azzarqa						51·5	(Sunderland & Coope, 1973)	Original
Kenya						32·4	(Sunderland, 1979)	Original
Kurdish Jews						54·9	(Lourie, 1973)	Original
Kurdish Jews						60·0	(Lourie, 1973)	Original
Lebanon						58·0	(Sunderland, 1979)	Original
Lebanon						58·4	(Sunderland, 1979)	Original
Liberia	15·6	21·2	12·5	25·4	22·3	29·4	(Ojikutu, 1965)	(Robins, 1991)
Libya Cyrenaica						53·0	(Sunderland, 1979)	Original
Libya Cyrenaica						54·0	(Sunderland, 1979)	Original
Libya Fezzan						44·0	(Sunderland, 1979)	Original
Libya Tripoli						53·6	(Sunderland, 1979)	Original
Libya Tripoli						55·2	(Sunderland, 1979)	Original
Malawi						27·0	(Tobias, 1974)	(Robins, 1991)
Mali Dogon	13·7	18·2	19·4	32·4	27·8	33·7	(Huizinga, 1968)	(Robins, 1991)
Mali Dogon	14·0	18·5	19·9	33·5	28·4	34·5	(Huizinga, 1968)	(Robins, 1991)
Morocco						56·4	FOS73 from OSU-Beals s database	OSU-Beals s database
Morocco						53·3	(Sunderland, 1979)	Original
Mozambique Chopi						17·8	(Weninger, 1969)	(Robins, 1991)
Mozambique Chopi						21·1	(Weninger, 1969)	(Robins, 1991)
Namibia						26·6	(Weiner *et al.*, 1964)	OSU-Beals s database
Namibia						24·5	(Weiner *et al.*, 1964)	OSU-Beals s database
Namibia Okavango						21·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						22·1	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						24·2	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						25·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						22·2	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						22·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						22·4	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Okavango						25·5	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						28·2	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						29·4	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						28·0	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						32·4	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						47·9	(Weiner *et al.*, 1964)	(Robins, 1991)
Namibia Rehoboth Baster						51·9	(Weiner *et al.*, 1964)	(Robins, 1991)

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
Nepal Eastern						48·9	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						51·5	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						53·6	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						48·7	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						52·1	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						50·0	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						50·1	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						49·5	(Williams-Blangero & Blangero, 1991)	Original
Nepal Eastern						55·7	(Williams-Blangero & Blangero, 1991)	Original
Netherlands						66·5	HRM64 from OSU-Beals s database	OSU-Beals s database
Netherlands	49·0	60·9	46·1	67·5	67·9	68·9	(Ritger-Aris, 1973)	(Robins, 1991)
Netherlands	47·4	58·7	44·8	65·3	66·0	66·7	(Ritger-Aris, 1973)	(Robins, 1991)
Nigeria Ibo	12·6	17·0	12·4	24·6	21·7	28·2	(Barnicot, 1958)	(Robins, 1991)
Nigeria Yoruba	10·9	14·3	10·4	20·6	18·8	23·6	(Barnicot, 1958)	(Robins, 1991)
Nigeria Yoruba	12·2	16·2	11·8	23·1	20·6	26·1	(Barnicot, 1958)	(Robins, 1991)
Nigeria Yoruba	16·9	22·5	14·4	28·3	24·7	32·5	(Ojikutu, 1965)	(Robins, 1991)
Pakistan						52·0	(Sunderland, 1979)	Original
Pakistan						51·3	(Sunderland, 1979)	Original
Pakistan				49·8		53·6	(Walsh, 1963); red estimated	Original
Papua Karker						33·2	(Harvey & Lord, 1978)	(Robins, 1991)
Papua Lufa						30·8	(Harvey & Lord, 1978)	(Robins, 1991)
Papua Lufa						31·6	(Harvey & Lord, 1978)	(Robins, 1991)
Papua Mt Hagan				29·5	21·9	34·8	(Walsh, 1963); red estimated	Original
Papua Mt Hagan				30·7	22·5	35·9	(Walsh, 1963); red estimated	Original
Papua New Guinea						35·3	HAR71 from OSU-Beals s database	OSU-Beals s database
Papua Port Moresby				36·2	25·3	41·0	(Walsh, 1963); red estimated	Original
Peru Maranon						42·8	(Weiner *et al.*, 1963)	(Robins, 1991)
Peru Maranon						43·3	(Weiner *et al.*, 1963)	(Robins, 1991)
Peru Nunoa						47·7	CON72 from OSU-Beals s database	OSU-Beals s database
Philippines Manila				50·3		54·1	(Walsh, 1963); red estimated	Original
Russia Chechen						51·9	(Sunderland & Coope, 1973)	Original
Russia Chechen						55·0	(Sunderland & Coope, 1973)	Original
Saudi Arabia						52·5	(Sunderland, 1979)	Original
South Africa	20·7	27·8	19·3	39·0	30·8	41·7	(Robins, 1991)	(Robins, 1991)
South Africa	23·4	31·2	21·1	41·5	33·1	44·3	(Robins, 1991)	(Robins, 1991)
South Africa	16·4	22·5	15·4	30·1	25·2	32·1	(Wasermann & Heyl, 1968)	(Robins, 1991)
South Africa	19·7	26·5	18·1	35·0	29·4	38·9	(Wasermann & Heyl, 1968)	(Robins, 1991)

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
South Africa Cape	26·8	36·1	27·9	45·2	43·7	49·2	(Wasermann & Heyl, 1968)	(Robins, 1991)
South Africa Cape	31·0	40·3	30·9	48·6	47·1	52·1	(Wasermann & Heyl, 1968)	(Robins, 1991)
South Africa Cape						50·1	(Weiner *et al.*, 1964)	(Robins, 1991)
South Africa Cape						51·3	(Weiner *et al.*, 1964)	(Robins, 1991)
South Africa Hottentot						45·5	(Weiner *et al.*, 1964)	(Robins, 1991)
South Africa Hottentot						48·1	(Weiner *et al.*, 1964)	(Robins, 1991)
South Africa San Central						41·9	(Weiner *et al.*, 1964)	(Robins, 1991)
South Africa San Central						45·6	(Weiner *et al.*, 1964)	(Robins, 1991)
Spain Basques	45·6	56·0	42·3	64·5	64·2	66·4	(Rebato, 1987)	(Robins, 1991)
Spain Basques	44·1	55·0	41·7	63·4	63·8	65·5	(Rebato, 1987)	(Robins, 1991)
Spain Basques	44·9	55·2	41·8	63·9	63·6	65·8	(Rebato, 1987)	(Robins, 1991)
Spain Basques	44·5	55·0	41·7	63·3	63·7	65·3	(Rebato, 1987)	(Robins, 1991)
Spain Basques	42·9	52·6	41·6	61·1	61·6	62·3	(Rebato, 1987)	Original
Spain Leon				62·8		66·1	(Caro, 1980)	(Robins, 1991)
Spain Leon				61·0		64·6	(Caro, 1980)	(Robins, 1991)
Spain Leon				60·6		64·3	(Caro, 1980)	(Robins, 1991)
Spain Leon				60·4		64·0	(Caro, 1980)	(Robins, 1991)
Spain Leon				59·5		62·7	(Caro, 1980)	(Robins, 1991)
Sudan						35·5	(Sunderland, 1979)	Original
Swaziland	14·5	18·4	14·3	27·6	24·3	32·4	(Roberts *et al.*, 1986)	(Robins, 1991)
Swaziland	18·1	22·7	17·3	32·8	28·8	38·8	(Roberts *et al.*, 1986)	(Robins, 1991)
Syria Druze						52·8	(Sunderland & Coope, 1973)	Original
Tanzania Nyatura						25·3	Weiner, 1969 cited in (Ritgers-Aris, 1973*b*)	(Robins, 1991)
Tanzania Nyatura						26·3	Weiner, 1969 cited in (Ritgers-Aris, 1973*b*)	(Robins, 1991)
Tanzania Sandewe						28·1	Weiner, 1969 cited in (Ritgers-Aris, 1973*b*)	(Robins, 1991)
Tanzania Sandewe						29·7	Weiner, 1969 cited in (Ritgers-Aris, 1973*b*)	(Robins, 1991)
Tunisia						56·3	FOS73 from Oregon data	OSU-Beals s database
Turkey						59·3	(Sunderland, 1979)	Original
Turkey						59·0	(Sunderland, 1979)	Original
United Kingdom Cumberland						67·0	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom Cumberland						66·5	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom London	43·9	54·3	42·6	61·5	63·3	63·1	(Barnicot, 1958)	(Robins, 1991)
United Kingdom London	41·4	52·4	40·9	59·9	62·0	61·5	(Barnicot, 1958)	(Robins, 1991)
United Kingdom Northern						63·4	(Cartwright, 1975)	(Robins, 1991)
United Kingdom Northern						62·3	(Cartwright, 1975)	(Robins, 1991)
United Kingdom Northern	45·2	54·8	43·1	61·7	63·2	62·3	(Harrison & Owen, 1964)	(Robins, 1991)

Appendix (*Continued*)

Population designation (as in Table 5)	575 nm	595 nm	600 nm	655 nm	670 nm	685 nm	Original reference	Source of data
United Kingdom Northern	50·0	59·6	45·7	66·7	66·9	68·9	(Hulse, 1973)	(Robins, 1991)
United Kingdom Northern	48·9	58·7	44·8	66·2	66·0	68·6	(Hulse, 1973)	(Robins, 1991)
United Kingdom Northern	48·9	59·1	45·0	65·9	66·1	68·3	(Hulse, 1973)	(Robins, 1991)
United Kingdom Northern	47·4	56·8	43·7	64·4	64·8	66·8	(Hulse, 1973)	(Robins, 1991)
United Kingdom Wales						67·0	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom Wales						65·9	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom Wales						63·5	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom Wales						62·8	(Smith & Mitchell, 1973)	(Robins, 1991)
United Kingdom Wales						63·1	(Sunderland & Woolley, 1982)	(Robins, 1991)
United Kingdom Wales						62·9	(Sunderland & Woolley, 1982)	(Robins, 1991)
United Kingdom Wales						62·7	(Sunderland & Woolley, 1982)	(Robins, 1991)
United Kingdom Wales						62·4	(Sunderland & Woolley, 1982)	(Robins, 1991)
Vietnam				51·3		55·0	(Carbonnel & Olivier, 1966); red estimated	(Harrison, 1973)
Vietnam						56·8	FOS73 from OSU-Beals s database	OSU-Beals s database
Zaire						33·9	FOS73 from OSU-Beals s database	OSU-Beals s database
Zaire	13·3	18·2	13·3	25·6	23·0	29·6	(Van Rijn-Tournel, 1966)	(Robins, 1991)
Zaire	15·4	21·7	16·0	30·1	26·6	36·1	(Van Rijn-Tournel, 1966)	(Robins, 1991)
Zaire Konda						28·8	(Hiernaux, 1977)	Original
Zaire Konda						30·0	(Hiernaux, 1977)	Original