Human Skin Pigmentation as an Example of Adaptive Evolution[1]

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HUMAN SKIN is remarkable and, in several ways, unique. It is mostly naked, it is sweaty, it is tough yet sensitive, and it comes in a range of colors. The plentiful sweat glands in human skin secrete watery fluid that evaporates and helps to cool us when we are hot, and the outer surface of our skin is rich in specialized keratin proteins that help the skin to resist physical and chemical insults while remaining exquisitely sensitive to touch. The pigmentation of human skin is of greatest interest here. The array of colors found in human skin is greater than that seen in any other mammalian species.

People with darkly and lightly colored skin differ in their skin reflectance, the amount of visible light that is actually reflected from the surface of their skin. This difference can be visually striking and has spurred questions for several centuries as to how variation in skin color came about. One of the problems in studying the evolution of human skin is that it is absent from the fossil record. It generally decays soon after death, leaving no traces of its composition or color behind. Evolutionary biologists seeking to understand the evolution of skin must thus resort to other means, including comparative anatomy, physiology, and molecular genetics.

The range of skin colors found in humans contrasts with the condition seen in our closest primate relatives, which have light skin covered by dark hair. This condition is typified by our closest living relatives, chimpanzees (fig. 1), which are born with uniformly pale skin. Glabrous skin on the face and hands darkens after exposure to the sun so that, after a few years of life, the infant's face becomes mottled and eventually becomes uniformly dark like that of its mother. The skin of the rest of its body, protected from the sun by hair, remains pale. The

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FIGURE 1. Mother and infant chimpanzees differ in the skin pigmentation of their faces. Infants are born with pale skin and, through sun exposure, develop darker skin on the exposed areas of their faces and hands. The skin underlying their dark body hair remains pale throughout life. Photograph by and with permission of Leanne Nash.

ability to produce melanin pigment in specialized cells called melanocytes in the skin in response to ultraviolet radiation (UVR) is a characteristic shared by humans and their closest relatives, the apes and Old World monkeys (Jablonski and Chaplin 2000). We can infer that this condition was present in the common ancestor of chimpanzees and humans six million years ago (Ma).

Reconstruction of the nature and likely appearance of the skin of the fossil relatives of humans—generically referred to as hominins—is possible using a wide range of methods and techniques available to

comparative biologists, including comparative and functional genomics. One of the best-known hominin species is *Australopithecus afarensis*, a species that lived in eastern and northeastern Africa between 3.6 and 2.9 Ma and became widely known through the well-preserved fossil partial skeleton nicknamed "Lucy" (AL 288-1) from the site of Hadar in Ethiopia. Reconstruction of the posture and locomotion of the species from its limb proportions and joint anatomy indicates that, although bipedal, *A. afarensis* was more of a deliberate walker and climber than a long-distance strider and runner (Jungers 1988). Its normal range of activities was probably closer to that of modern chimpanzees than to that of modern humans, and this generally would not have resulted in individuals' building up excess heat as the result of prolonged activity. We can infer that members of this species possessed skin similar in anatomy and appearance to that of modern chimpanzees (fig. 2). The timing of the loss of body hair in hominins can be inferred by similar means: examination of the skeleton and reconstruction of the mode and intensity of locomotion. The uncommonly well-preserved skeleton of an early member of the genus *Homo* from the site of West Turkana (WT-15000), aged about 1.5 Ma, indicates that functional modernity in gait and activity pattern had been achieved by this time, specifically, that they were engaging in extended bouts of vigorous exercise, which would have resulted in the build-up of excess body heat (Bramble and Lieberman 2004). These hominins lived in hot equatorial environments, and had to cope with high external heat loads in addition to those generated by elevated metabolism. Body heat is a concern for primates because they have relatively large brains, which function optimally within a narrow thermal range. Temperatures over 40°C can be life-threatening and thus the evolution of an efficient cooling mechanism to prevent hyperthermia was essential. Primates dissipate excess body heat primarily through radiation and evaporation, with the evaporation of sweat being more important at high ambient temperatures (Frisancho 1995). Heavy body hair or fur slows the evaporation of sweat, retarding body cooling (Folk and Semken 1991). It can be deduced, therefore, that early members of the genus *Homo* had undergone the loss of functional body hair and an increase in the density of eccrine (watery) sweat glands in order to facilitate sweating by the time that WT-15000 traversed the woodland grassland habitats of the Lake Turkana Basin about 1.5 Ma (Jablonski 2004).

The loss of most body hair left the surface of the skin increasingly vulnerable to a battery of environmental assaults, including high UVR. It was at this juncture in evolution that the human lineage developed permanent dark pigmentation over the entire body by way of protection from the many harmful effects of UVR (Jablonski and Chaplin

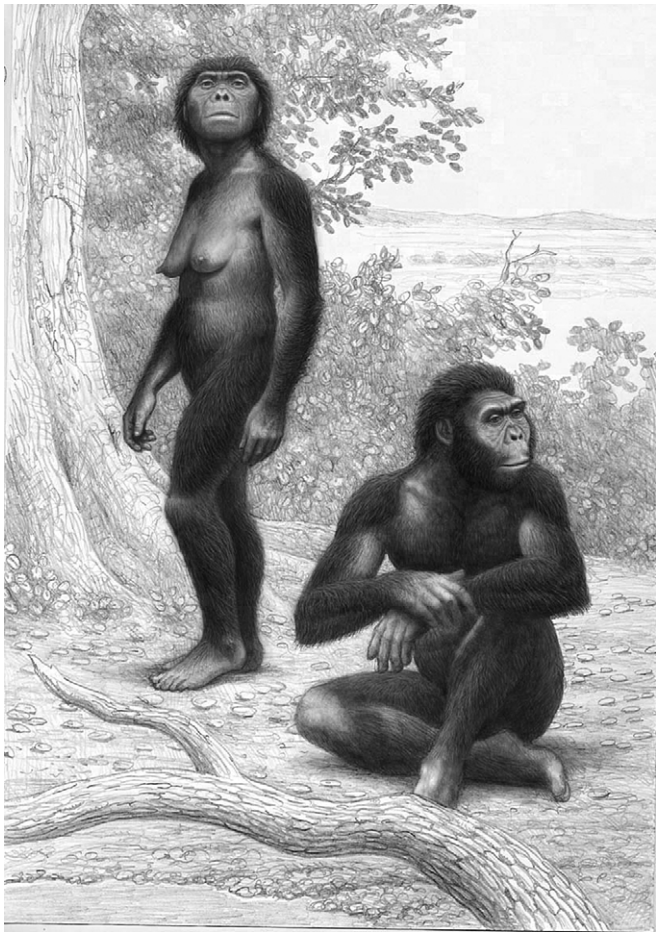

FIGURE 2. Reconstruction of *Australopithecus afarensis* by Mauricio Antón

2000). The deductions about hair loss and pigmentation that we made on the basis of functional anatomy and thermophysiology were supported independently by the results of a genetic analysis indicating that lack of variation in a gene that is critical to the production of melanin pigment, the melanocortin 1 receptor locus (or *MC1R*) could be traced back possibly as early as 1.2 Ma (Rogers, Iltis, and Wooding 2004). This implies that, by this time, the evolutionary pressure for protective melanin pigmentation was so high that variation in the MC1R gene had disappeared through the action of purifying natural selection. The members of the genus *Homo* living in Africa around 1 Ma, from which all modern humans evolved, thus probably had mostly naked and darkly pigmented skin (fig. 3).

FIGURE 3. Reconstruction of early *Homo erectus* from Africa by Mauricio Antón

Melanin is a remarkable pigment. It is the dark brown form, eumelanin, colloquially known as melanin, that imparts most of the color to human skin. Eumelanin is a long and complex polymeric molecule capable of absorbing and scattering highly energetic forms of solar and other radiation. It is particularly good at absorbing UVR, and so skin that is rich in eumelanin readily absorbs UVR, sparing underlying tissues from much of the damage caused by high-energy photons. Eumelanin also chemically neutralizes damaging chemicals created by UVR bombardment, such as reactive oxygen species that can damage DNA (Brenner and Hearing 2008; Kollias 1995; Meredith 2006). These unique properties make eumelanin a superior natural sunscreen, and explain why the pigment has been recruited in evolution as a coloring and protective agent many times in the history of life on the earth.

Members of the human lineage evolving continuously in Africa from the earliest members of the genus *Homo* through the early members of the modern human species, *Homo sapiens*, had dark skin pigmentation because it afforded protection against the multifarious harmful effects of UVR. The specific harmful effects that led to diminished

reproductive success are those that demand attention in the context of evolutionary discussions. The role of UVR in causing skin cancer, for instance, is mostly not relevant in this context because most such cancers develop after reproductive age and, in any case, do not affect a person's ability to bear offspring (Blum 1961). Equatorial latitudes receive high doses of medium- and long-wavelength UVR, known as UVB and UVA, respectively, throughout the year. Low doses of UVB reach the earth's surface—even at the equator—due to the attenuating effects of atmospheric oxygen and ozone, while most UVA (along with visible light) traverses the atmosphere unimpeded. The numerous harmful effects of UVA on biological systems are related to its ability not only to traverse the atmosphere, but to penetrate through the superficial layers of skin and damage DNA and the collagen and elastin molecules that are responsible for the skin's strength and elasticity. This damage is cumulative and leads to skin cancer, skin thickening, and wrinkles (de Gruijl 1998; Freeman et al. 1962; Leiter and Garbe 2008); hence the frequent injunctions we receive to protect skin from direct sun exposure. The effects of UVB are somewhat different because it cannot penetrate the skin as deeply, but it also can bring about serious damage to the DNA in the skin that can lead to skin cancer. While serious, none of these sequelae was able to significantly affect the reproductive success of our ancestors. Even for the most serious type of skin cancer, cutaneous malignant melanoma, which is often fatal and can afflict individuals of reproductive age, the overall incidence and mortality rates prior to the mid-twentieth century were so low (<5 per 100,000) (Diepgen and Mahler 2002) that melanoma probably never was a significant selective factor in the evolution of skin pigmentation.

Our research has revealed that the most evolutionarily significant effects of UVR are those that have to do with folate metabolism. Folate is a B vitamin necessary for the production and repair of DNA, and for modulating gene expression. Folate is not made in the body; rather, it comes from leafy green vegetables, whole grains, and citrus fruits in the diet. Circulating levels of the vitamin (and its active metabolite, 5-Methyltetrahydrofolate or 5MTHF) vary according to many parameters, including the body's needs at any given time and the effects of environmental stressors. One of the most potent of these stressors is UVR, which lowers levels of circulating folate and 5MTHF through direct photo-degradation and probably also by directing available folate toward the repair of UVR-damaged DNA in the skin (Steindal et al. 2008; Tam et al. 2009; Jablonski and Chaplin 2010). We have theorized that direct and indirect depletion of folate by UVR creates acute folate deficiency, which can be most serious when DNA replication and cell division affect the production of germ cells or the formation of

organ systems in the rapidly differentiating embryo. These include periods of sperm formation in men, and the critical intervals in women when the embryonic neural tube, the precursor of the central nervous system, is developing in early pregnancy. Folate deficiency contributes to male infertility and to increased prevalence of neural tube defects, one of the most common classes of birth defects to affect the early embryo (Bower and Stanley 1992; Copp, Fleming, and Greene 1998; MRC Vitamin Study Research Group 1991; Wallock et al. 2001). Maintaining sufficient levels of folate thus emerges as one of the keys to successful reproduction, and the safeguarding of folate becomes an evolutionary mandate. The evolution of permanent dark skin pigmentation, which is at its darkest in the middle of the human reproductive career (Quevedo 1969; Ortonne 1990), was one of the most effective and economical means whereby this protection could be achieved.

Having established a plausible and testable framework for understanding the evolution of dark skin pigmentation, the questions remaining surround the evolution of light pigmentation and the mechanisms and timing involved in the production of the conspicuous gradient of human skin pigmentation from dark at the equator to light at the poles. The previous discussion on the effects of UVR emphasized harmful effects. The one positive effect of UVR is its ability to begin the process of making vitamin D in the skin. This is accomplished only by UVB photons (in the 290–315 nm range), which cause the transformation of provitamin D_3 (7-dehydrocholesterol) to previtamin D_3. The other steps necessary to produce biologically active vitamin D occur over the space of 48 hours in the liver and kidney. An individual with darkly pigmented skin living at the equator begins the process of vitamin D manufacture in the skin following sun exposure, but this process occurs relatively slowly because of the natural sunscreening effects of eumelanin (Webb and Holick 1988; Holick, MacLaughlin, and Doppelt 1981). Attenuation of most UVB by the atmosphere means that biologically significant doses of UVR able to catalyze vitamin D production reach the earth's surface when the sun is nearly directly overhead. At the equator this is most of the time, maximally at the equinoxes, but outside of the tropics the UVB maximum occurs only once a year at the summer solstice. The higher the latitude, the more attenuated the UVB (fig. 4). The potential for cutaneous photosynthesis of previtamin D_3 is minimal in the winter at latitudes greater than 37°, and on an annual basis people living north of 50° cannot produce enough previtamin D_3 to satisfy their physiological needs (Webb, Kline, and Holick 1988; Jablonski and Chaplin 2000, 2010).

As hominins dispersed outside of tropical latitudes, availability of UVB for the production of vitamin D was a problem, which was

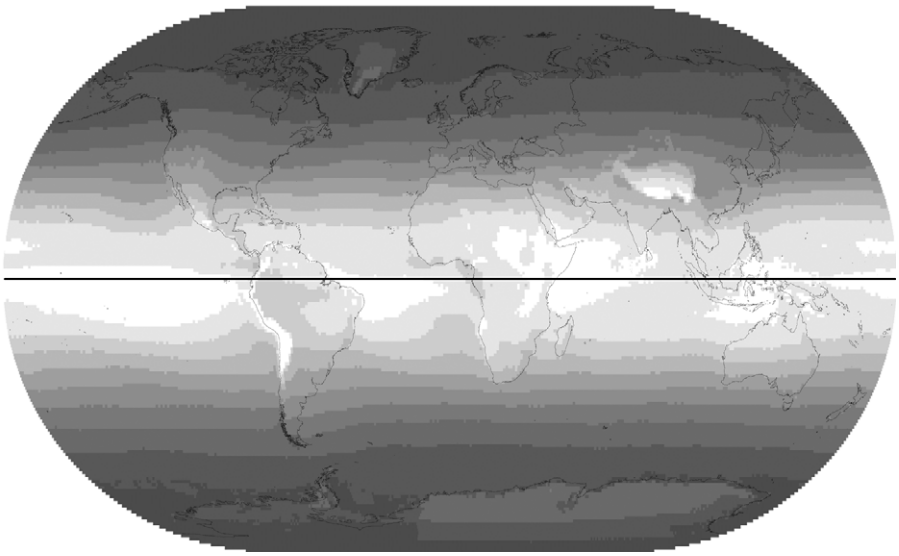

FIGURE 4. The average distribution of UVB (305 nm). Intensity is indicated by gradations from white (high) to black (low), varying from 135 to 1 Jm^{-2} in ten steps with oceans partially grayed out. Map by George Chaplin based on NASA data.

compounded by dark skin pigmentation. Two major dispersals of hominins out of the African tropics occurred. The first involved early members of the species generally known as *Homo erectus* and began around 1.9 Ma, and the second involved modern *Homo sapiens* and began around 80,000 years ago. We know much more about the latter dispersal because it occurred more recently and because the descendants of that event are the modern people living all over the world today. The dispersal of *Homo sapiens* occurred over a relatively short period of time, evolutionarily speaking, and was propelled by advances in human culture and technology. Modern humans began living outside of the tropics more than 60,000 years ago and in high latitudes (>50°) about 40,000 years ago. Among the many challenges humans faced in these new environments was that of making sufficient vitamin D in their skin to satisfy their physiological and reproductive needs. Vitamin D has long been known to be important for the absorption of calcium and the production and maintenance of a healthy skeleton, but research in recent years has revealed that it is essential for maintenance of healthy immune and cardiovascular systems (Cantorna and Mahon 2005; Norman 2008). Chronic vitamin D deficiencies are associated with rickets in children and difficulties in childbearing due to related pelvic deformities, weakening of the skeletal system in adults, increased risk of developing autoimmune disease, lowered resistance of infectious disease, and the

promotion of certain cancers (Thacher et al. 2006; Aranow 2011; Cannell et al. 2006; Lucas et al. 2008; Ponsonby, Lucas, and van der Mei 2005; Ramagopalan et al. 2011). The problem for hominins living under reduced and highly seasonal UVB conditions thus became how to maximize production of vitamin D when UVB was available. We deduced from physical evidence of hominins at high latitudes that loss of most of the protective eumelanin pigmentation would have been essential for year-round habitation under low UVB conditions (Jablonski and Chaplin 2000). This prediction has been supported by the results of a recent genomic study, which showed that a specific genetic mutation leading to production of depigmented skin occurred in the ancestors of modern western Europeans (Lamason et al. 2005). Because this mutation is not shared by lightly pigmented East Asians, it has been deduced that mutations leading to depigmented skin occurred independently in the ancestors of western Europeans and East Asians (Norton et al. 2007). In a related study, investigators examining the Neanderthal genome discovered evidence that European representatives of these distant and extinct cousins of modern humans also probably had lightly pigmented skin (Lalueza-Fox et al. 2007). Evidence indicating the independent evolution of lightly pigmented skin at high latitudes in three hominin populations (two modern human groups and central European Neanderthals) points to the action of strong natural selection, or positive selection, in selective sweeps that established depigmented skin as the normal appearance for skin at high latitudes.

The evidence of strong natural selection operating at low latitudes to maintain dark pigmentation under high UVR conditions and at high latitudes to establish and maintain light pigmentation under low UVR conditions indicates that skin pigmentation is a Darwinian adaptation, which is the product of evolution by natural selection. The stable gradient of skin colors observed from the equator to the poles is the product of two conflicting clines operating over a spatially varying optimum of UVR distribution. One of these emphasizes photoprotection by dark pigmentation near the equator, and the other emphasizes photosynthesis of vitamin D facilitated by light pigmentation near the poles. Moderately pigmented skin, which can develop a tan in the presence of high UVR in the summer and then lose melanin pigment again in the absence of strong UVR in the winter, is a characteristic of humans inhabiting middle latitudes and experiencing seasonal UVR regimes (Jablonski and Chaplin 2010). The most important implication of the independent evolution of similar skin tones under similar environmental circumstances is that skin color is not a useful trait for separating people into unique groups. Skin color was used for a long time to define human races, but this is inappropriate because skin tones are not unique. A corollary of this is

that because skin pigmentation evolved independently of other traits, the combining of anatomical, physiological, and even behavioral traits into so-called races under the banner of shared skin color is incorrect.

Modern humans today are distinguished by remarkable mobility and by sophisticated culture and technology, which buffer us against the exigencies of the environment. In the last 500 years, advances in transportation have made it possible for humans to traverse thousands of kilometers and dozens of degrees of latitude within hours. Humans often live in places remote from their ancestral homelands, or at least vacation in them. Also, the majority of the world's people today inhabit cities where they live and work mostly indoors, and do not experience the solar conditions and UVR regimes that their ancestors did. This has resulted in more humans' being mismatched to the UVR conditions of the environment in which they live, and suffering adverse health consequences because of it. Large populations of lightly pigmented people live or vacation in high UVR regions like the American Southwest or Australia, and large populations of darkly pigmented people live in low UVR areas such as the American Northeast or northern Europe. The health consequences of these changes in geography and lifestyle have been in some cases severe. On the one hand, the prevalence of skin cancers, including cutaneous malignant melanoma, in lightly pigmented people who live in sunny places, especially those who partake of recreational suntanning, is high (Leiter and Garbe 2008). On the other hand, the prevalence of vitamin D deficiencies in darkly pigmented people living in low-UVR environments and in all people living and working in indoor environments in cities is high, with the global disease burden caused by low UVR now exceeding that of high UVR (Lucas et al. 2008). Problems of vitamin D deficiency often are compounded by cultural practices such as the wearing of concealing garments or the routine application of chemical sunscreen, which prevent or retard vitamin D production in the skin. The importance of preventive public health measures to reduce the risk of diseases caused by inappropriate UVR exposure cannot be stressed enough.

In conclusion, two points warrant reiteration. The first is that skin pigmentation is the product of evolution by natural selection and is one of the best examples of evolution acting on the human body. Skin color is an ideal tool for teaching evolution, and should be used widely as such. The second is that similar skin tones have evolved multiple times independently in human history, and skin color does not define human races. This knowledge should be widely promulgated to help dispel racism and to discourage the repeated social reinvention of race as a concept. These activities will conduce to the weal of humanity and greatly improve human society.

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