

# Skin: Its Biology in Black and White

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Human skin comes in a range of colours, grading from very dark brown near the equator to near ivory near the poles. This colour gradient resulted from the action of natural selection. The original skin tone for members of the *Homo* lineage, including *Homo sapiens*, was dark brown. Diversification of skin colouration occurred as some *Homo sapiens* populations dispersed to regions of lower ultraviolet radiation (UVR), mostly outside of Africa. Humans who began to inhabit higher latitudes faced reduced opportunities to make vitamin D in the skin because of lower and more seasonal levels of UVB from ambient sunlight. Depigmented skin evolved under these conditions, and genetic evidence indicates that mutations leading to loss of melanin pigmentation occurred multiple times in hominin history when groups invaded regions of lower UVB. Because similar skin colours have evolved multiple times under the same environmental conditions, classification of humans according to skin colour is fraught with problems. The colour-based races defined in the 18th century are congeries of physical and behavioural traits that do not exist. The persistence and propagation of these concepts has caused serious problems in many places, and can only be countered by effective education.

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Human skin comes in a wide range of sepia tones, from darkest brown to near ivory, but not in black or white. The sepia rainbow of skin colours grades from dark to light, from the equator to the poles. The geographic distribution of skin pigmentation has been known and studied by many people over nearly three centuries, but only in the last 20 years have new kinds of data become available that allow skin colour variation to be well understood. Skin pigmentation is a topic where 'the rubber meets the road' because it is at the meeting point of evolutionary biology and human experience. Scientists and the general public alike are engaged by skin colour diversity, and the social sensitivity that once inhibited both scientific research and social discourse on the topic has now ebbed. People want to know how skin colour evolved and why it has come to have the meaning it has in modern societies.

One of the biggest challenges in studying the evolution of skin is that there is very little actual preserved ancient human skin to study. There is no fossilized human skin yet confirmed, only the skin associated with mummified, frozen, or bog-preserved corpses dating to no more than a few thousand years old (Jablonski 2006). The study of skin and skin colour evolution in humans thus relies on evidence from comparative study of the anatomical and physiological characteristics of the skin of living people and primates, along with the comparative study of the genes that determine these characteristics. A lot of information has been inferred about the nature of the skin and hair in the last common ancestor (LCA) of humans and chimpanzees, for instance, by examining these features and some of the genes associated with them in humans, apes, and monkeys (Jablonski 2004). This examination shows that the LCA probably had dark hair covering lightly pigmented skin, very much like a modern chimpanzee. Exposed skin on the face and hands would have darkened by tanning when the skin was exposed to strong sunlight, but the skin covered by hair would have remained untanned. We can extend the same inference to the appearance of the skin in one of the best known the

early fossil hominin species, *Australopithecus afarensis*, known from middle Pliocene sites in Ethiopia and Tanzania. The skeletal evidence of *A. afarensis* indicates that, although the species was habitually bipedal, it was not an energetic bipedal strider and runner. Rather, the species had ape-like body proportions, retained abilities to climb trees, and probably was not a long-distance runner or fast walker. These aspects of hominin lifestyles are important because body temperature is elevated during vigorous exercise, and problems of dissipation of heat can become critical especially when hominins are exercising in hot environments. The likely cause of the loss of most functional body hair in hominins was the need for more efficient cooling from evaporation of sweat from the surface of the body (Jablonski 2004). Evaporation of expressed sweat works extremely well if the skin is naked, but not well if the skin is covered with dense hair (Folk & Semken 1991). When the skeletons of early members of the genus *Homo* are compared with those of *Australopithecus*, the differences between the two in the likely modes of locomotion are immediately apparent (Crompton *et al.* 1998; Ruff 2008; Ruff 1991). Unlike *Australopithecus*, early *Homo* was a bipedal strider and runner (Bramble & Lieberman 2004). These activities raised metabolic levels and generated body heat that had to be liberated from the body's surface. Dissipation of excess body heat probably was accomplished primarily by evaporation of sweat, and the sweat was produced by a high density of eccrine sweat glands on the body's surface (Jablonski 2004). Keeping cool is of particular importance in highly encephalized primates: the brain is sensitive to elevated core temperature. Eccrine sweat evaporating on nearly naked skin creates a whole-body cooling system that helps to maintain the brain's thermal homeostasis during intense exercise (Caputa & Cabanac 1988; Shibasaki & Crandall 2010), and enhanced body cooling through sweating no doubt released a physiological constraint that made

possible increased brain size in the human lineage (Jablonski 2010a).

The evolution of functional nakedness was not the only major change that occurred in the early evolution of the genus *Homo*. Naked skin was vulnerable to the damaging effects of ultraviolet radiation, and so we reasoned from first principles that permanent dark pigmentation in the skin would have had to have evolved in early *Homo* at the same time as hairlessness in order to protect individuals from these effects (Jablonski & Chaplin 2000). This inference was later supported by genetic evidence indicating that the form of the *MC1R* pigmentation that produces permanent dark pigmentation in darkly pigmented Africans today had been invariant for as long as 1.2 million years (Rogers *et al.* 2004). Early members of the genus *Homo* living under equatorial or near-equatorial sunlight containing abundant ultraviolet radiation (UVR) were, thus, hairless and darkly pigmented (Jablonski & Chaplin 2000).

The pigment melanin, specifically, the intensely dark brown form of melanin called eumelanin, is a natural sunscreen that confers superior protection against the damaging effects of UVR (Brenner & Hearing 2008; Kollias *et al.* 1991). The intensity of UVR at the earth's surface is related to latitude and humidity, with arid areas near the equator having the highest levels (Chaplin 2004). Outside of the tropics, UVR levels decline significantly, and the amount of UVR that falls on any particular area depends on the energy of the radiation emitted by the sun. The most biologically significant types of UVR that fall on the earth are long wavelength UVR called UVA and medium wavelength UVR called UVB. The more energetic of these is UVB and it is readily absorbed and scattered by oxygen and ozone in the atmosphere. Outside of the tropics, when the sunlight passes obliquely through the atmosphere during the winter months, little or no UVB reaches the earth's surface, while most UVA passes through the atmosphere with visible light (Madronich *et al.* 1998). Ultraviolet radiation is mostly harmful to living systems because it damages DNA, cell membranes, and connective tissues, and biological systems have evolved elaborate mechanisms to repair damage caused by UVR (Cleaver & Crowley 2002; Rothschild 1999). For vertebrate animals, one of the most effective means of preventing damage from UVR is eumelanin pigment in the integument. When incorporated into the epidermis of the skin, eumelanin absorbs and scatters most UVB, thereby sparing damage to deeper layers including the blood flowing through the cutaneous blood vessels (Brenner & Hearing 2008; Tadokoro *et al.* 2003; Zmudzka *et al.* 2006).

It was long thought that dark, eumelanin-rich pigmentation originally evolved in humans in order to protect against skin cancer caused by damage to DNA in the skin. When it was demonstrated that this was unlikely because most skin cancers afflict people after their reproductive years (Blum 1961), a rethinking of the role of eumelanin was required. A key discovery was published in 1978, when it was shown that the B vitamin folate was sensitive to ultraviolet radiation (Branda & Eaton 1978). Folate is a vitamin that is obtained from green leafy vegetables,

citrus fruits, and whole grains, and is of critical importance to health because it is necessary for making and repairing DNA (Lucock & Daskalakis 2000). Folate sufficiency is important for normal reproduction because it is a precondition for healthy sperm production in men and for normal development of early embryos in women (Bower & Stanley 1992; Fleming & Copp 1998; Mathur *et al.* 1977). Folate deficiency is one of the main causes of the family of birth defects called neural tube defects (Bower & Stanley 1992; Fleming & Copp 1998). Because of the important role played by folate and related compounds in successful reproduction, we reasoned that protection of these important biomolecules was the primary cause for the evolution of permanent eumelanin protection in the skin (Jablonski & Chaplin 2000). Eumelanin-rich skin protected all members of the genus *Homo*, from the species of the Early Pleistocene through *Homo sapiens*. The evolution of the *Homo* lineage leading to anatomically modern humans, *Homo sapiens*, occurred in Africa, and all members of this lineage were darkly pigmented (Jablonski & Chaplin 2000). The question then arises as to how and when the modern pattern of skin colour diversity arose. For the answer to this question, we must examine the pattern of dispersals of modern people outside of tropical Africa, and the UVR conditions that obtained in these environments.

Modern humans, *Homo sapiens*, evolved in Africa between 200 000 and 120 000 years ago, and the first half of our species existence was spent only in Africa. During this time, populations expanded and dispersals into the extremities of the continent proceeded, accompanied by extensive genetic diversification (Tishkoff *et al.* 2009). The changes that occurred in human populations during this period would have included subtle changes in pigmentation, as populations adapted to local UVR conditions or experienced genetic bottlenecks due to small population sizes. The genetic basis for evolutionary changes in pigmentation among modern people living in Africa is not well understood. Approximately 80 000 years ago, small populations of modern people left Africa, taking with them a small fraction of the continent's genetic diversity. These people were culturally sophisticated and their movements – into southeast and east Asia first, then later into Europe – occurred quickly by sea and over land (Stringer 2000). These movements saw people entering highly diverse solar regimes, including those with very low levels of UVR. A large fraction of the land mass of Eurasia lies at high latitudes which receive low UVR, and particularly low UVB (Chaplin & Jablonski 1998). As people entered these lands, they were subjected to lower and more strongly seasonal levels of UVR than they had ever experienced, and this had profound effects on human health (Chaplin & Jablonski 2009).

Ultraviolet radiation is not a universally malign influence. Its single most important positive action is initiation of the process of vitamin D formation in the skin by UVB. This process occurs in all terrestrial vertebrates and is essential for life (Holick 2003). Vitamin D is necessary because it permits absorption of calcium from the diet. Vitamin D deficiency is a serious problem that leads to skeletal malformation and weakness that manifests itself

as rickets in children and osteomalacia in adults (Dimitri & Bishop 2007). Serious and persistent rickets in young women leads to pelvic deformities that impair or prevent natural childbirth, so vitamin D deficiency can directly impact reproductive success. Because vitamin D is also responsible for maintenance of the health of the immune system, vitamin D deficiencies are related to increased susceptibility to infectious diseases, certain cancers, and autoimmune disorders (Holick 2005; Ponsonby *et al.* 2005) (Holick 2007; Holick & Chen 2008).

On the continent of Africa, the region experiencing the lowest and most seasonal levels of UVB is the southern coast of South Africa. At and near the winter solstice, there is no UVB in the sunlight over this region, and no vitamin D production can take place in human skin, regardless of skin colour (Jablonski & Chaplin, unpubl. obs.). The absence or attenuation of UVB reaching middle and high latitudes during the winter months had profound influences for the evolution of skin pigmentation. Because eumelanin is a superior sunscreensing agent, and because UVB is necessary to make vitamin D in the skin, it would have been beneficial for people living under conditions of weak and highly seasonal sunlight to have less eumelanin in their skin (Jablonski 2004; Jablonski & Chaplin 2000; Loomis 1967; Murray 1934). In any given period of time, more vitamin D precursor can be in lightly pigmented skin than in darkly pigmented skin, and so lighter skin was favoured by natural selection under low UVB conditions (Norton *et al.* 2007; Webb & Holick 1988). Light skin is actually depigmented skin, and genetic mutations leading to depigmentation evolved independently in the ancestors of modern east Asians and modern western Europeans (Lamason *et al.* 2005; Norton *et al.* 2007). The importance of vitamin D production in the skin is attested by the fact that genetic fixation of the pigmentation gene mutations leading to loss of pigmentation occurred through selective sweeps resulting from positive selection (Norton *et al.* 2007). Loss of eumelanin pigmentation has also been inferred to have occurred earlier and independently in *Homo neanderthalensis*, the distant cousin of *Homo sapiens* that inhabited low and moderate UVB environments Europe and the circum-Mediterranean (Lalueza-Fox *et al.* 2007).

The convergent evolution of light pigmentation on at least three occasions in hominin history – in the ancestors of modern western Europeans, modern east Asians, and Neanderthals is remarkable, and has important consequences for the use of skin colour as a feature in human classification. Similarly, the evolution of repigmentation is equally important. As people have moved around in the last 20 000 years, some depigmented populations have re-entered regions with strong UVR and have undergone genetic mutations leading to enhanced tanning abilities and darker baseline pigmentation. This has been demonstrated for some New World populations (Quillen 2010) and is strongly suspected for some groups that now inhabit southern reaches of the Indian subcontinent.

Through time, people have become increasingly mobile as the result of innovations in transportation technology, spurred on by interests in distant resources and trade.

This has resulted in people moving around over longer distances at faster speeds, especially in the last 500 years. The mismatches between skin pigmentation and environmental UVR that have arisen because of these rapid movements have resulted in profound and mostly negative effects on health (Chaplin & Jablonski 2009; Jablonski & Chaplin 2012). People living in earlier times were less mobile, and would not have been exposed to solar regimes significantly different from those experienced by their ancestors. But this situation is common for modern people, whether they are vacationing or are living permanently in a region distant from their ancestral homeland. Even for people who have not moved far in recent millennia, there is often a mismatch between skin pigmentation and sun exposure because of indoor lifestyles in cities and a lack of sun exposure. Lightly pigmented people living in high UVR environments face significantly elevated risk of skin cancer (De Gruijl 1999; Rees 2000; Rigel 2008). Darkly pigmented people living under low or seasonal UVB conditions face an elevated risk of vitamin D deficiency (Brunvand & Haug 1993; Fogelman *et al.* 1995; Fonseca *et al.* 1984). Vitamin D deficiencies are also increasingly common among city dwellers of all skin colours who spend most of their time indoors, or among people who routinely wear concealing clothing and chemical sunscreen when outdoors (Chatfield *et al.* 2007; Davies *et al.* 1986; Forrest & Stuhldreher 2011; Le Goaziou *et al.* 2011). Although relatively few epidemiological studies on vitamin D status have been conducted in South Africa, preliminary indications are that vitamin D deficiency is common and has serious consequences for disease susceptibility (Martineau *et al.* 2011).

Skin is the interface between the body and the physical environment, and skin pigmentation evolved to regulate the penetration of UVR into body under different environmental conditions. The gradient of skin pigmentation seen in modern people, from darker tones near the equator to lighter ones closer to the poles, is the product of two competing clines, one favouring photoprotection in areas of high UVR, the other favouring photosynthesis of vitamin D in areas of low UVR (Chaplin & Jablonski 2009; Jablonski 2010b; Jablonski & Chaplin 2010). People with moderate pigmentation living in middle latitudes (between about 23° and 37°) generally have good abilities to tan, thereby gaining a measure of increased protection from summer sun. Skin pigmentation is a superb example of natural selection acting on the human body, and should be used as a model system for teaching evolution at all levels of the curriculum.

What skin colour does not provide is a unique marker of ancestry for purposes of classification of people into groups. Visibly identical skin phenotypes have evolved from distinct genotypes that arose from independent mutations. This means that skin colour itself cannot be used as a unique indicator of genetic ancestry or as a characteristic for sorting people into races because the same colour is associated with multiple ancestries and races. We recognize this now, but this fact was not known to the naturalists who composed the first classifications of humans and the philosophers who first defined races.



When Carolus Linnaeus created the first scientific classification of humans, he placed them into four groups, sorted by skin colour and continent. The variations of *Homo* he named in 1748 in the 6th edition of his *Systema Naturae* were *Europaeus albus* (white), *Americanus rubescens* (red), *Asiaticus fuscus* (brown), and *Africanus niger* (black). Linnaeus had limited information on which to base a classification of humankind, and so this simple classification must not be judged too harshly. What is significant is what happens in subsequent editions of the *Systema Naturae*. By the 10th edition of 1758, Linnaeus had changed his classification to include more characteristics of each group. Physical traits other than skin colour, such as eye colour and hair texture were added, but he also included behavioural attributes. Europeans were *sanguineus* (sanguine), [Native] Americans were *cholericus* (choleric), Asians were *melancholicus* (melancholy), and Africans were *phlegmaticus* (phlegmatic). He also characterized the four varieties of people according to *regitur* or how they were governed, so that Europeans were described as being ruled by *ritibus* (rites), Americans by *consuetudine* (custom), Asians by *opinionibus* (opinion), and Africans by *arbitrio* (will). Linnaeus was a naturalist and *Systema Naturae* was considered the first 'scientific' classification of living things. It was extraordinary, therefore, that Linnaeus departed from his usual custom of describing organisms on the basis of only their physical attributes to describe people on the basis of dispositions and cultural behaviour as well as physical traits (Broberg 1983). The mixing of physical and behavioural traits that Linnaeus introduced heralded a new era in human classification, and presaged the first description of races.

Linnaeus's classifications of humans were widely read and discussed by scholars of his day. Other naturalists and philosophers took up the challenge of human diversity, and by the late 18th century, no less a figure than Immanuel Kant had published his own classification of humans. Kant was the first person to place people into races (*Rassen* in German), which were defined by skin colour and place of origin (Bernasconi 2001; Shell 2006). Kant placed great importance on place of origin because climate (and sun exposure) had purposeful influences on physical traits – notably skin colour – and on the collective motivation exhibited by a race and the level of civilization it could attain (Bernasconi 2006). Kant considered races and racial characteristics to be fixed and immutable, and on this point he clashed with many of his contemporaries (Bernasconi 2006). He was also the first to rank races clearly and unambiguously: 'Humanity is at its greatest perfection in the race of the whites. The yellow Indians do have a meagre talent. The Negroes are far below them and at the lowest point are a part of the American peoples' (Bernasconi 2002).

The most significant aspect of Linnaeus's and Kant's taxonomies in the context of this paper is that both Linnaeus and Kant considered that the colours of skin they recognized were unique to geographical groups of humans, and that skin colour was unerringly connected with other physical and behavioural traits. They conceived of defined varieties or races of humans as discrete pack-

ages of biosocial attributes. These conceptions have lasted and have been propagated, despite the accumulation of two centuries of evidence showing that discrete races do not exist. The study of skin pigmentation evolution has revealed that similar skin colours evolved independently many times in hominin history, and that pigmentation is not, for the most part, genetically connected to other physical traits. Further, there is no genetic relationship between physical, behavioural, and cultural traits. Thus, the original conception of colour-based human races which many societies have operated under for over 200 years is flawed and baseless.

Skin colour is a trait of great biological significance that illustrates action of evolution by natural selection on the human body. It is also a trait that has been used, incorrectly and persistently, for classifying people into groups which were considered to be elevated or diminished in status because of colour. This unfortunate state of affairs can be changed, if there is motivation and a commitment to change through education. We are one people, and skin colour unites us, not divides us, through the process of evolution.

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