Review

Author for correspondence:
Nina G. Jablonski
e-mail: ngj2@psu.edu

The colours of humanity: the evolution of pigmentation in the human lineage

Nina G. Jablonski and George Chaplin

Department of Anthropology, The Pennsylvania State University, 409 Carpenter Building, University Park, PA 16802, USA

NGJ, 0000-0001-7644-874X

Humans are a colourful species of primate, with human skin, hair and eye coloration having been influenced by a great variety of evolutionary forces throughout prehistory. Functionally naked skin has been the physical interface between the physical environment and the human body for most of the history of the genus *Homo*, and hence skin coloration has been under intense natural selection. From an original condition of protective, dark, eumelanin-enriched coloration in early tropical-dwelling *Homo* and *Homo sapiens*, loss of melanin pigmentation occurred under natural selection as *Homo sapiens* dispersed into non-tropical latitudes of Africa and Eurasia. Genes responsible for skin, hair and eye coloration appear to have been affected significantly by population bottlenecks in the course of *Homo sapiens* dispersals. Because specific skin colour phenotypes can be created by different combinations of skin colour-associated genetic markers, loss of genetic variability due to genetic drift appears to have had negligible effects on the highly redundant genetic 'palette' for the skin colour. This does not appear to have been the case for hair and eye coloration, however, and these traits appear to have been more strongly influenced by genetic drift and, possibly, sexual selection.

This article is part of the themed issue 'Animal coloration: production, perception, function and application'.

1. Introduction

Discussions of the cardinal features of the human lineage usually focus on bipedalism, relative brain size, language and technology, and ignore the remarkable distinctions of the integument and eyes that have figured importantly in human evolution. In this paper, we explore the diversity of skin, hair and eye coloration in the human lineage, and seek explanations for the evolution of pigmentation traits in relation to the history of human dispersals and population history. Our focus is primarily on the evolution of pigmentary traits in anatomically modern *Homo sapiens*, but brief consideration of integumentary coloration in non-human primates and during pre-*sapiens* phases of human evolution is necessary for understanding the starting point for *Homo sapiens*.

2. Human coloration in context

Like most mammals, primates have hair covering most of their bodies. Most non-human primates have coats consisting of brown or grey agouti hairs, but lavish variation exists. The trunk and limbs of most primates exhibit darker dorsal and lighter ventral pelage, probably for both concealment and thermoregulation [1–4]. Striking patterns of coat colours are found in some lineages [1,5–7], with the most conspicuous patterns found on both the bodies and faces of forest-dwelling diurnal primates such as marmosets (e.g. *Mico* species), guenons (*Cercopithecus*) [8], and doucs and snub-nosed monkeys (*Pygathrix* and *Rhinopithecus*). Nocturnal strepsirrhines such as lorises and galagos, and the only nocturnal haplorhine, the night monkey *Aotus*, are remarkable for cryptic body coloration combined with mask-like patterns of facial hair, which have almost certainly evolved primarily to facilitate species and mate recognition

under markedly reduced light conditions [1]. Compared with other catarrhines, the apes (gibbons, orangutans, chimpanzees and gorillas) lack agouti banding, and the large apes mostly lack regional patterning on their coats and colourful facial markings.

In some platyrrhines and all catarrhines, the skin of the face, and sometimes also the perineum, is not covered with hair and instead is glabrous and, sometimes, spectacularly coloured. The facial masks and perineal regions of the mandrill and golden snub-nosed monkey, to take two extreme examples, exhibit highly modified naked skin. Zones of red coloration are produced by a rich capillary bed perfused with haemoglobin-carrying red blood cells, while the zones of blue are structural colours produced by coherent scattering of light from oriented arrays of dermal collagen [9]. In some female catarrhines, the perineal skin turns pink or red near the time of ovulation as blood and interstitial fluid infuses the region as an advertisement of oestrus [10,11]; in some macaques, these changes are also accompanied by darkening of the facial skin, presumably also caused by perfusion of the region by blood [12]. In Old World monkeys and apes, the intensity of coloration of glabrous skin is under hormonal control and is considered a sign of fertility in females and competitive ability in males [12–14].

The genetic and developmental processes that produce the complex topographical arrangements of coloration on the face, trunk and limbs are not well understood [15], and are still mostly a matter of conjecture. The fact that many patterns follow presumed pathways of migration of the neural crest-derived melanocytes into the face and trunk during development warrants further study [5].

Humans are distinguished from their non-human relatives by an absence of most fur and an almost complete lack of regional patterning in hair coloration, except for male facial hair in some populations [16]. Most of the surface area of human skin is covered with almost invisible vellus hairs and is often referred to as 'functionally naked'. The remnants of the primate hair coat are the localized concentrations of non-agouti terminal hairs of similar colour that occur on the scalp, and of a different type in the axillae and pubic region. The evolution of hair loss in the human lineage has been discussed extensively in the literature and is reviewed elsewhere [17]. Because skin is mostly not preserved in the fossil record, arguments about the evolutionary causation of hair loss have relied on critical examination and integration of pertinent comparative anatomical, physiological, palaeoecological and climatological evidence. This evidence is consistent with an explanation based on natural selection for enhanced thermoregulation during high physical activity levels under conditions of high environmental heat load [18–20]. Under these conditions, most body hair was lost and a high density and broad somatic coverage of eccrine sweat glands was gained in order to increase the capacity for heat dissipation by evaporation from the surface of the skin [21–23]. Loss of body hair was accompanied by disadvantages, notably, loss of some protection against abrasion and ultraviolet radiation (UVR). Compensatory changes evolved quickly in hominin skin, as evidenced by genomic comparisons between humans and our closest relative, the chimpanzee. These have revealed that the human lineage is characterized by accelerated evolution of keratinization and epidermal differentiation genes that contribute to enhanced barrier functions of the epidermis [24–26].

While these changes were occurring, others affecting constitutive pigmentation were also taking place. Decades before genomic evidence became available, the timing of the origin of permanent darkly pigmented skin over the entire hominin body surface had been deduced from anatomical, physiological and climatological evidence [27]. Since genomic evidence has become available, comparative study of the human melanocortin 1 receptor (MC1R) locus demonstrated that the timing of evolution of permanent, dark, eumelanin-rich, skin pigmentation coincided with the evolution of functional hairlessness and increased density of eccrine sweat glands early in the history of the genus Homo, approximately 1.2 Ma or earlier [28]. Adaptive evolution for sun-resistant alleles of the MC1R locus appears to have occurred, therefore, when early members of the genus Homo became mostly hairless and highly physically active inhabitants of open savannah environments in Africa. For members of the Homo lineage evolving since then in sub-Saharan Africa—including the earliest modern people, Homo sapiens—the absence of functional polymorphism has been maintained by purifying selection [29,30]. Protective, eumelanin-rich constitutive pigmentation has persisted because of its contribution towards the survival and successful reproduction of populations living under high UVR at low latitudes.

3. Variation in human skin coloration is mostly a product of natural selection

Skin colour (as measured by skin reflectance) and levels of UVR are highly correlated. Biologically effective UVR is often described in units of minimal erythemal dose or MED, which expresses the amount of UVR radiation that will produce minimal erythema (sunburn or redness caused by engorgement of capillaries) in lightly pigmented human skin within a few hours following UVR exposure. Skin colour can be almost fully modelled as an effect of autumn UVMED alone ($r = 0.927$; $p < 0.0001$) [21,31]. If this relationship developed under natural selection, plausible causation must demonstrate real or probable enhanced reproductive success for specific skin pigmentation phenotypes under specific UVR conditions. Many adaptive explanations for the evolution of variation in human skin colour have been put forward in the last century, as reviewed elsewhere [17], and most have suffered from a lack of evidence for likely differences in survivorship and reproduction of different skin colour phenotypes under the same UVR conditions. Such was the fate of the 'skin cancer hypothesis', recently revived [32], that has invoked dark pigmentation as an evolutionary adaptation against sunburn, DNA damage and skin cancer. Skin cancers rarely cause death or adversely affect reproductive success during the peak reproductive years [33], so this explanation was dismissed long ago as being a primary cause of the evolution of dark skin pigmentation. The recent argument that ancestral hominins had pale, cancer-prone skin similar to that of individuals with OCA2 albinism and that evolution of dark skin spared the human lineage from skin cancer–related mortality lacks support [34]. Other explanations have insufficient explanatory power. These include the hypothesis that the eumelanin was most important in affording protection against tropical parasites and tropical skin diseases because of its potent antimicrobial properties [35–37], an idea that fails to explain the near-absence of eumelanin on the

primary environmental interfaces of the volar surfaces of the hands and feet and the lips. More recently, mooted is the hypothesis that the primary function of eumelanin was augmentation of epidermal barrier function by increasing the skin's resistance to desiccation under arid conditions, and that depigmentation did not occur under positive selection for vitamin D production [38–40]. This hypothesis has been disproved by multiple lines of evidence, including the fact that tanning occurs in the presence of UVR, not desiccation [41], and that positive selection for depigmented skin capable of producing vitamin D under low and highly seasonal UVB conditions is now well established [42].

The strongest hypothesis for the evolution of dark skin colour is that it afforded protection against photodegradation of cutaneous and systemic folate under high UVR conditions for early members of the genus *Homo*. The physiological effects of photodegradation of folate were explored long before the full extent of folate's roles in DNA biosynthesis, repair, DNA methylation, amino acid metabolism and melanin production were appreciated [43]. Because folate (in its main form of 5-methyltetrahydrofolate or 5-MTHF) is sensitive to photodegradation [44–47], protective eumelanin-rich pigmentation evolved in early *Homo* primarily to prevent reduction of fertility due to loss of folate in cutaneous blood vessels and the systemic circulation [21,48]. Folate deficiencies are associated with potentially fatal birth defects such as neural tube defects and male infertility [49–52]. Folate metabolism is regulated by genes and epigenomic factors, which have evolved to favour conservation of folate under conditions of longer day length and greater potential UVR-related folate loss [53,54]. Recent physiological evidence also indicates the importance of folate (in the form of 5-MTHF) in thermoregulation, via its effect on controlling nitric oxide-mediated cutaneous vasodilation [55–58]. Maintaining the integrity of folate metabolism is important with respect to evolution because it directly affects reproductive success and survival early in life [21,59]. Natural selection has, thus, affected varied genetic and physiological mechanisms in order to protect folate and 5-MTHF in the face of high UVR. The primary role of constitutive dark skin colour in hominin and modern human evolution is that of a natural sunscreen to conserve folate. Protection of epidermal DNA against strand breaks was the important secondary role played by dark skin colour.

The genus *Homo* and the species *Homo sapiens* emerged in equatorial Africa under conditions of intense and relatively invariant sunlight and UVR. Dispersal of hominins into non-equatorial Africa, Eurasia and the Americas involved movements into habitats with more seasonally variable patterns and differing wavelength mixtures of UVR [60]. In this review, we shall confine our discussion to the consequences for skin colour of dispersal of *Homo sapiens* into Eurasia and the Americas, a process which began around 55 000 years ago [61]. Dispersing populations were small and bottlenecks further reduced available genetic variation in populations crossing major geographic boundaries [62]. Note also that there is no evidence that dispersing archaic *Homo sapiens* used sewn clothing or other methods of full-coverage protection against the sun and elements. Non-sewn animal skins probably afforded some protection, but for the most part people were subjected to the full force of UVR apart from the times when they sought natural shelter. Skin was thus the primary interface with the environment for most of human evolution.

The UVR regimes faced by dispersing hominins were a major selective pressure affecting the evolution of skin pigmentation. Outside of the tropics, consideration of the pattern of UVB is relevant because only some wavelengths of UVB (between 270 and 300 nm, with peak synthesis between 295 and 297 nm) catalyse production of vitamin D in the skin. Within the tropics, average UVB is high and has two equinoctial peaks, but outside of the tropics, average UVB levels are lower and exhibit but a single peak at the Summer Solstice [60]. Average UVB in northern Eurasia and North America is extremely low and highly variable. Because eumelanin in skin is a highly effective sunscreen, the potential for cutaneous vitamin D production is reduced by dark skin [21,63–66]. Darkly pigmented hominins dispersing out of equatorial Africa thus faced conditions that significantly affected their vitamin D physiology. Penetration of UVR into the skin is related to the amount and distribution of melanin; larger and more superficial melanosomes and 'melanin dust' present in the stratum corneum are highly effective at reducing UVB transmission [67]. Pre-vitamin D production occurs in skin of all colours, but in eumelanin-rich skin, low doses of UVB do not raise 25(OH)D levels to physiologically adequate levels at which storage can take place; higher doses over longer periods of time are required for this, and these conditions are not met outside of equatorial latitudes. For people with dark skin living outside of the tropics, and especially north or south of 43°, there is insufficient UVB available in the sunlight outside of the time immediately around the summer solstice to satisfy the body's vitamin D requirement [21,41,60,68,69]. Long-term occupation of non-tropical latitudes, thus, would not have been possible without loss of some constitutive eumelanin pigmentation in order to prevent the serious sequelae of vitamin D deficiency [21]. At extreme high latitudes, year-round occupation is not possible without a diet that is centred on consumption and storage of vitamin-D rich foods such as oily fish, marine mammals, or caribou and reindeer, which concentrate vitamin D in their muscle meat and fat [21,70].

Most people living in the tropics and subtropics (at latitudes below 38°) gain eumelanin pigment in their skin as the result of seasonal high UVR exposure in a process referred to as the tanning response. Melanin produced by the tanning response is the outcome of UV-induced stress and is regulated by melanocortins in the skin [71]. Melanocortins in the skin reduce the production of reactive oxygen species, enhance repair of DNA damage caused by UVR and inaugurate eumelanin synthesis in individuals who carry specific, naturally expressed variants of *MC1R* [71]. Tanning is thus a response to damage caused by UVR. Contrary to popular belief, tanned skin affords little or no protection from damage from subsequent UVR exposure. Recent experimental studies have shown that a tan developed under suberythemal UVB exposure provides minimal photoprotection, but a tan developed under UVA-rich sunlamps such as those used in tanning salons provided no photoprotective benefit [72–74].

Depigmented skin evolved not once, but multiple times in human history, and was accomplished by different combinations of genetic mutations. For modern European populations, different signatures of selection on the *MC1R* and *SLC24A5* genes imply that both natural selection and genetic drift contributed to the evolution of depigmented skin. These genetic changes affected the amounts of melanin being produced in melanocytes and the size of the melanosomes in which the melanin was packaged [75]. For modern eastern

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Asian populations, depigmentation was not achieved through mutations at the *SLC24A5* locus [75], but via a different set of genetic changes, which are still incompletely known [76,77]. The fact that depigmented skin evolved independently in the ancestors of modern Europeans and East Asians suggests that at least two (and probably more) distinct genetic mutation events occurred and that multiple loci underwent positive selection in these two regions receiving relatively low levels of UVB [78–80]. The most likely reason for this was that it was associated with a loss of skin pigment that favoured vitamin D production under conditions of low UVB [69,78,81]. Depigmented skin also evolved independently in *Homo neanderthalensis* [82] probably for the same reason. The 'palette' of skin and hair colour genes is extensive and, especially outside of Africa, there is evidence that multiple genes of small effect have contributed to subtle differences in integumentary coloration [83].

There has been a cause and effect relationship between UVR and skin pigmentation in human evolution, and skin colour phenotypes have been modified under the action of natural selection to maintain an optimum balance between photoprotection and photosynthesis over spatially varying conditions of UVR. Skin colour thus evolved as the product of two opposing clines, one emphasizing dark pigmentation and photoprotection against high loads of UVA and UVB near the equator, the other favouring depigmented skin to promote seasonal, UVB-induced photosynthesis of vitamin D_3 nearer the poles [60]. Intermediate latitudes with seasonally high loads of UVB favoured the evolution of people with intermediate colour capable of tanning [84,85]. The most important points to reinforce here are that the geographical gradient of human skin colour evolved under the influence of natural selection, and that very similar skin colour phenotypes (dark, light and intermediate) have evolved independently numerous times under similar UVR conditions. Diverse combinations of skin colour genes occurred during the course of prehistory as the combined result of natural selection, gene flow due to migration, and founder effect or genetic drift due to population bottlenecks occurring in the course of dispersal events [62,86]. Indigenous populations of the New World have generally lighter skin colours than those of the Old World, probably because they have not resided in their homelands for as long a time and because their adaptations to the environment have been more strongly cultural than biological, as exemplified by the wearing of sewn clothing and the making of shelters [21,22,87].

Sexual selection does not appear to have been a major influence on the evolution of human skin coloration, but it probably did increase the degree of sexual dimorphism in skin colour in some populations [21,87]. The unexposed skin of females is lighter than that of males in most populations [21,83], possibly because of the greater need of females to produce vitamin D in the skin to absorb and mobilize calcium during pregnancy and lactation. A persistent, directional preference for lighter-coloured females as marriage partners has been recognized during historic times in some east- and south-Asian cultures, and it is likely that this has contributed to the greater sexual dimorphism in coloration observed [21,87].

4. Hair and eye coloration are not under strong natural selection

Like skin, the coloration of human hair and eyes is determined primarily by the amount and type of melanin produced and stored in melanosomes [88,89]. Iris pigmentation is also influenced by structural features within the eye itself and by the degree of pupillary dilation [90–92]. Although skin coloration varies according to the intensity and seasonality of UVR on a global scale, no such regular geographical pattern is observed with hair and eye coloration [93]. In fact, little variation in hair and eye coloration occurs in indigenous populations outside of Europe (for hair) and outside of Europe, North Africa, the Middle East, Central Asia and South Asia for eyes [88,89,94]. The lack of variation in hair and eye coloration in Africa has been assumed to be caused by the importance of eumelanin in affording protection, as it does in the case of skin coloration, but this has not been empirically established. Hair and eye coloration appear to have not been under as strong natural selection as skin coloration, and loss of genetic variation at one or more population bottlenecks probably contributed to the patterns of phenotypic variation observed in the hair and irises of modern people [95].

Scalp hair in most non-European populations is very dark brown, with little phenotypic variation [96]. Many genes appear to contribute to the dark brown hair colour phenotype [88,93], and the relative importance of different loci is not yet known. The relatively high prevalence of blond hair in Northern Island Melanesia has been traced to the 93C allele of the *TYRP1* gene [97,98], which has been dispersed throughout the region in the course of human colonization of the Southwest Pacific. In Europe, blond hair has been traced to establishment of variation in a regulatory enhancer of the *KITLG* gene, while red hair is produced by a specific range of variants of the *MC1R* locus [99–102]. Sexual selection is thought to have influenced the high prevalence of blond- and red-hair phenotypes in Europe [93], but this has not been established empirically.

The nature and coloration of human male facial hair— beards and moustaches—have been a matter of curiosity and speculation, but little formal research [16,103,104]. Male facial hair, manifested as moustaches, cheek hair (whiskers) and beards, occurs in some male primates and appears to represent secondary sexual characteristics that evolved as amplified visual signals of rank, dominance and attractiveness [8,105]. This supports claims that age-related changes in human beard and moustache coverage and colour on the male face serve as honest signals of age or social dominance [104], and that they evolved as products of contest competition between males [106]. Beards augment the effectiveness of human aggressive facial displays, but are rated as ambivalent or unattractive by females [107,108].

Iris coloration in modern people is mostly brown, but this label is misleading because colours described as 'brown' vary greatly from light to dark [89]. Until very recently, studies of human iris coloration focused primarily on European populations, where the greatest range and variety of eye colours—from dark brown to pale blue—are found. Iris colour phenotypes are determined by amounts of melanin and by the ratio of eumelanin to phaeomelanin in the iris, with brown eyes having a higher ratio than light eyes [88,89]. Other categorical eye colours, such as blue, green and hazel, are common in Europe and parts of the Middle East, and Central and South Asia, with Europeans having the lightest eye colours [88]. The sets of genetic markers associated with variation in iris coloration in Europe, South Asia and East Asia are distinct, and relatively little is known of the

combination of evolutionary forces—including natural and sexual selection—that influenced their distribution [89]. Dark iris coloration is associated with less scattering of intraocular light, a trait that may be protective under conditions of bright sunlight and high UVR. Blue eye coloration, on the other hand, is associated with greater intraocular light scattering and a higher level of melatonin suppression, traits that may have been adaptive under highly seasonal sunshine regimes in northwestern Eurasia [109]. Blue-eyed women have been found to be preferred by blue-eyed men, possibly as a manifestation of a male adaptation for the detection of extra-pair paternity based on eye colour, as a phenotypically based assurance of paternity [110]. Arguments for the action of natural and sexual selection on iris colour need to be examined with great care as more data on the genetic basis of the trait are revealed. A recent study showing that the genetic markers associated with iris coloration are also associated with skin and hair pigmentation traits suggests that iris coloration was a pleitropic effect associated with selection on pigmentation genes whose primary effect was skin or hair pigmentation, not iris coloration [89].

The genetic basis of human coloration is complex because some genetic variants affect all pigmentary systems—skin, hair and eyes—through pleiotropic effects, while others affect only one type [111] and because different genes and gene combinations can create similar coloration phenotypes. Despite the technical difficulties of such studies, the fascination of humans with their own coloration phenotypes will certainly continue to propel research forward quickly.

5. Conclusion

Skin, hair and eye coloration in humans is variable, and has been influenced by different combinations of evolutionary forces. Skin coloration has been strongly influenced by natural selection, globally and throughout human prehistory, because of the importance of melanin as a natural sunscreen on naked skin. The role of natural selection in the evolution of hair and eye coloration appears to have been negligible, but genetic bottlenecks followed by sexual selection may have played more significant roles in establishing the patterns of variation recognized outside of Africa.

In recent centuries, humans have migrated faster and over longer distances than during any time in prehistory. Many of these movements have brought people into regions with markedly different solar regimes than their homelands. Many people now live under levels of solar radiation that are much stronger, or much weaker and more seasonal, than those under which their ancestors evolved. These rapid changes in living circumstances have created significant health problems resulting from too much UVR exposure (skin cancer, accelerated ageing of the skin) and from too little UVR exposure (vitamin D deficiency and its many sequelae) that have greatly impacted individual well-being and public health. Mitigating these problems is now the focus of considerable attention in many health professions [112–115]. Rapid, long-distance migrations have also brought people together from disparate and widely separated places, creating unprecedented and novel opportunities for gene flow. The twenty-first century world contains a sepia rainbow of human skin colours, created from old and new combinations of skin colour–related genetic markers. The effects of these new genetic admixtures on health are not known. More significant to health and overall human well-being, however, are the problems of social segregation and behavioural bias that are rooted in cultural constructions of skin colour–based race categories [87]. Humans are visually oriented primates, and our varied colours are badges of our recently shared evolutionary history. Our skin colours unite us, not divide us.

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