# The Evolution of Skin Pigmentation and Hair Texture in People of African Ancestry

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**KEYWORDS**

• Melanin • Eumelanin • Ultraviolet radiation • *MC1R* • Afro-textured hair • Thermoregulation • African American

**KEY POINTS**

- Variability in skin pigmentation phenotypes in African and African-admixed populations has not been well documented or genetically characterized.
- Afro-textured hair is a shared characteristic of most African and African-admixed people, and may represent an adaptation to protect the brain against thermal stress.
- Vitamin D deficiency is a risk for darkly pigmented people because of the natural sunscreening properties of eumelanin and the increased prevalence of indoor living.
- Use of race categories is ill-advised because of the genetic heterogeneity and socially constructed nature of races.

Our species, *Homo sapiens*, evolved in Africa, and humanity's highest levels of genetic diversity are maintained there today.[1] Underlying genetic diversity combined with the great range of solar regimes and climatic conditions found in Africa has contributed to a wide range of human integumentary phenotypes within the continent. Millions of Africans have moved, both voluntarily and involuntarily, to other continents in the past 2000 years, and the range of integumentary phenotypes among admixed African diaspora populations is enormous. In this contribution, we do not catalog this variation, but provide basic evolutionary background as to how it developed in the first place.

## DIVERSITY OF INTEGUMENTARY PHENOTYPES WITHIN AFRICA

Africa has been a crucible of human diversification because of the length of human habitation there, and because of the continent's great size, environmental history, and past and present ecological diversity. Africa is the only continent that spans nearly 70° of latitude, thus containing an enormous range of solar radiation regimes. The continent's modern environmental mosaic first emerged about 20,000 years before present (BP) with the onset of more arid conditions across the continent. Formation and expansion of sand dunes along the southern margin of the Sahara and dramatic reductions in areas occupied by tropical forests proceeded until about 12,000 years BP.[2] Phases of increased wetness ("lacustrine phases") followed, from about 10,000 to 4000 years BP, during which the Sahara shrank and tropical forests rebounded.[2] Africa today exhibits a long and high elevational rise to the east along the Rift Valley that modifies the predominant global westerly humid air flow and creates a short seasonal monsoon. The specific effects of these environmental changes on

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human populations in Africa are not understood fully, but there is little doubt that they created opportunities for human biologic and cultural diversification by erecting and then eliminating geographic barriers to north-south and east-west migration. These changes alternately increased opportunities for the action of genetic drift and gene flow, such as across the Sahel corridor,[1] and created conditions under which biologic and cultural adaptations to rapid environmental change were promoted. Together, these factors contributed to the evolution of a large African population with a highly subdivided genetic structure.[3] The migration event that contributed most significantly to the establishment of the modern genetic landscape of Africa, including gene flow between once-isolated populations, was the expansion across Africa of the Bantu-language–speaking agriculturalists from near the Nigerian/Cameroonian highlands beginning approximately 3000 years BP.[1,3] This series of movements has resulted in overprinting of the original latitudinal cline of skin pigmentation, specifically, in the movement into southern Africa of equatorial peoples who are more darkly pigmented than the original moderately pigmented inhabitants.

Skin pigmentation is visibly different and measurably variable across Africa (**Fig. 1**). Diversity of environmental conditions, especially of ultraviolet radiation (UVR) regimes, along with population histories (including migrations) are the ultimate evolutionary causes of this diversity, but the specific and proximate genomic causes have not been elucidated fully. Studies of the genetics of skin pigmentation have focused on the significance of the virtual lack of variation in the sequence of the melanocortin 1 receptor (*MC1R*) locus in Africa,[4–7] compared with the extensive variation among African populations found elsewhere in the genome.[8] Between populations and individuals of African or African-admixed ancestry, differences in skin tone and the relative darkness of skin are due primarily to differences in the ratio of eumelanin to pheomelanin in the skin[9,10] that are regulated in part by the 8818G allele of the agouti signaling protein (*ASIP*) gene.[11] Subtle differences in skin tone are due to complex mixtures of melanin polymers and to the size and reflectance properties of the melanosomes in which the pigments are packaged.[12] Phenotypic differences in skin tone among and between people of African ancestry are incompletely known (see **Fig. 1**) and their genetic basis is inadequately understood.

Skin conditions affecting pigmentation produce highly visible disease states in normally darkly pigmented people. Of these, oculocutaneous albinism of the tyrosine-positive type (*OCA2*) is the most common that afflicts Africans and that has a genetic component. *OCA2* has been reported to occur at a prevalence approaching 1 in 1000 in some groups in Zimbabwe and South Africa, because of consanguinity and founder effects.[13,14] Individuals affected by albinism experience all the harmful effects of UVR exposure, including skin cancer, and face significant social ostracism, even death, because of their condition.[13–16] It has recently been suggested that the deleterious *OCA2* allele may be maintained in African populations as a balancing polymorphism, with the common deletion allele possibly conferring resistance to susceptibility to leprosy.[17]

Little is known about the evolution and diversification of human scalp hair phenotypes,[18] including the diversity that exists within Africa. Differences in hair color within Africa are minor and may represent pleiotropic effects of skin pigmentation genes.[12,19] Slight differences in hair form, growth characteristics, and susceptibility to breakage exist but have not been documented systematically. Sub-Saharan Africans generally exhibit tightly curled or Afro-textured hair and northern populations exhibit less tightly or loosely curled hair, but in all African populations, the hair shaft is elliptical in cross-section. The curliness of the hair shaft is caused by retrocurvature of the hair bulb, which gives rise to an asymmetrical S-shape of the hair follicle.[18] The continent-wide distribution of Afro-textured hair indicates that this is the ancestral condition for modern humans. Hrdy, who was one of the first to systematically characterize the morphology of human hair, speculated that hair form was determined by multiple genes, and that the tightly curly hair form had evolved convergently in African and Melanesian populations.[20,21] Progress has been made since then in the morphologic characterization of hair form,[22] but the genetic basis of hair form is still largely unknown. Symmetric hair follicles and generally straighter scalp hair shafts characterize Eurasian populations; the straight and thick hair shafts common to most East Asians are caused by a variant of the ectodysplasin receptor, *EDARV370A*.[23]

## THE INFLUENCE OF NATURAL SELECTION ON INTEGUMENTARY PHENOTYPES

Throughout most of the history of the genus *Homo*, roughly 2 million years, naked skin has been the primary interface between our bodies and the environment.[24] The major speciation events leading to the emergence of *Homo sapiens* occurred at or near the equator in Africa, where levels of UVR are high throughout the year. Within