Throughout the world, human skin color has evolved to be dark enough to prevent sunlight from destroying the nutrient folate but light enough to foster the production of vitamin D.

Among primates, only humans have a mostly naked skin that comes in different colors. Geographers and anthropologists have long recognized that the distribution of skin colors among indigenous populations is not random: darker peoples tend to be found nearer the equator, lighter ones closer to the poles. For years, the prevailing theory has been that darker skins evolved to protect against skin cancer. But a series of discoveries has led us to construct a new framework for understanding the evolutionary basis of variations in human skin color. Recent epidemiological and physiological evidence suggests to us that the worldwide pattern of human skin color is the product of natural selection acting to regulate the effects of the sun's ultraviolet (UV) radiation on key nutrients crucial to reproductive success.

From Hirsute to Hairless

THE EVOLUTION OF SKIN PIGMENTATION is linked with that of hairlessness, and to comprehend both these stories, we need to page back in human history. Human beings have been evolving as an independent lineage of apes since at least seven million years ago, when our immediate ancestors diverged from those of our closest relatives, chimpanzees. Because chimpanzees have changed less over time than humans have, they can provide an idea of what human anatomy and physiology must have been like. Chimpanzees' skin is light in color and is covered by hair over most of their bodies. Young animals have pink faces, hands, and feet and become freckled or dark in these areas only as they are exposed to sun with age. The earliest humans almost certainly had a light skin covered with hair. Presumably hair loss occurred first, then skin color changed. But that leads to the question, When did we lose our hair?

The skeletons of ancient humans--such as the well-known skeleton of Lucy, which dates to about 3.2 million years ago--give us a good idea of the build and the way of life of our ancestors. The daily activities of Lucy and other hominids that lived before about three million years ago appear to have been similar to those of primates living on the open savannas of Africa today. They probably spent much of their day foraging for food over three to four miles before retiring to the safety of trees to sleep.

By 1.6 million years ago, however, we see evidence that this pattern had begun to change dramatically. The famous skeleton of Turkana Boy--which belonged to the species Homo ergaster--is that of a long-legged, striding biped that probably walked long distances. These more active early humans faced the problem of staying cool and protecting their brains from overheating. Peter Wheeler of John Moores University in Liverpool, England, has shown that this was accomplished through an increase in the number of sweat glands on the surface of the body and a reduction in the covering of body hair. Once rid of most of their hair, early members of the genus Homo then encountered the challenge of protecting their skin from the damaging effects of sunlight, especially UV rays.

Built-in Sunscreen
IN CHIMPANZEES, the skin on the hairless parts of the body contains cells called melanocytes that are capable of synthesizing the dark-brown pigment melanin in response to exposure to UV radiation. When humans became mostly hairless, the ability of the skin to produce melanin assumed new importance. Melanin is nature's sunscreen: it is a large organic molecule that serves the dual purpose of physically and chemically filtering the harmful effects of UV radiation; it absorbs UV rays, causing them to lose energy, and it neutralizes harmful chemicals called free radicals that form in the skin after damage by UV radiation.

Anthropologists and biologists have generally reasoned that high concentrations of melanin arose in the skin of peoples in tropical areas because it protected them against skin cancer. James E. Cleaver of the University of California at San Francisco, for instance, has shown that people with the disease xeroderma pigmentosum, in which melanocytes are destroyed by exposure to the sun, suffer from significantly higher than normal rates of squamous and basal cell carcinomas, which are usually easily treated. Malignant melanomas are more frequently fatal, but they are rare (representing 4 percent of skin cancer diagnoses) and tend to strike only light-skinned people. But all skin cancers typically arise later in life, in most cases after the first reproductive years, so they could not have exerted enough evolutionary pressure for skin protection alone to account for darker skin colors. Accordingly, we began to ask what role melanin might play in human evolution.

The Folate Connection

IN 1991 ONE OF US (Jablonski) ran across what turned out to be a critical paper published in 1978 by Richard F. Branda and John W. Eaton, now at the University of Vermont and the University of Louisville, respectively. These investigators showed that light-skinned people who had been exposed to simulated strong sunlight had abnormally low levels of the essential B vitamin folate in their blood. The scientists also observed that subjecting human blood serum to the same conditions resulted in a 50-percent loss of folate content within one hour.

The significance of these findings to reproduction—and hence evolution—became clear when we learned of research being conducted on a major class of birth defects by our colleagues at the University of Western Australia. There Fiona J. Stanley and Carol Bower had established by the late 1980s that folate deficiency in pregnant women is related to an increased risk of neural tube defects such as spina bifida, in which the arches of the spinal vertebrae fail to close around the spinal cord. Many research groups throughout the world have since confirmed this correlation, and efforts to supplement foods with folate and to educate women about the importance of the nutrient have become widespread.

We discovered soon afterward that folate is important not only in preventing neural tube defects but also in a host of other processes. Because folate is essential for the synthesis of DNA in dividing cells, anything that involves rapid cell proliferation, such as spermatogenesis (the production of sperm cells), requires folate. Male rats and mice with chemically induced folate deficiency have impaired spermatogenesis and are infertile. Although no comparable studies of humans have been conducted, Wai Yee Wong and his colleagues at the University Medical Center of Nijmegen in the Netherlands have recently reported that folic acid treatment can boost the sperm counts of men with fertility problems.

Such observations led us to hypothesize that dark skin evolved to protect the body's folate stores from destruction. Our idea was supported by a report published in 1996 by Argentine pediatrician Pablo Lapunzina, who found that three young and otherwise healthy women whom he had attended gave birth to infants with neural tube defects after using sun beds to tan themselves in the early weeks of pregnancy. Our evidence about the breakdown of folate by UV radiation thus supplements what is already known about the harmful (skin-cancer-causing) effects of UV radiation on DNA.

Human Skin on the Move

THE EARLIEST MEMBERS of Homo sapiens, or modern humans, evolved in Africa between 120,000 and 100,000 years ago and had darkly pigmented skin adapted to the conditions of UV radiation and heat that existed near the equator. As modern humans began to venture out of the tropics, however, they encountered environments in which they received significantly less UV radiation during the year. Under
these conditions their high concentrations of natural sunscreen probably proved detrimental. Dark skin contains so much melanin that very little UV radiation, and specifically very little of the shorter-wavelength UVB radiation, can penetrate the skin. Although most of the effects of UVB are harmful, the rays perform one indispensable function: initiating the formation of vitamin D in the skin. Dark-skinned people living in the tropics generally receive sufficient UV radiation during the year for UVB to penetrate the skin and allow them to make vitamin D. Outside the tropics this is not the case. The solution, across evolutionary time, has been for migrants to northern latitudes to lose skin pigmentation.

The connection between the evolution of lightly pigmented skin and vitamin D synthesis was elaborated by W. Farnsworth Loomis of Brandeis University in 1967. He established the importance of vitamin D to reproductive success because of its role in enabling calcium absorption by the intestines, which in turn makes possible the normal development of the skeleton and the maintenance of a healthy immune system. Research led by Michael Holick of the Boston University School of Medicine has, over the past 20 years, further cemented the significance of vitamin D in development and immunity. His team also showed that not all sunlight contains enough UVB to stimulate vitamin D production. In Boston, for instance, which is located at about 42 degrees north latitude, human skin cells begin to produce vitamin D only after mid-March. In the wintertime there isn't enough UVB to do the job. We realized that this was another piece of evidence essential to the skin color story.

During the course of our research in the early 1990s, we searched in vain to find sources of data on actual UV radiation levels at the earth's surface. We were rewarded in 1996, when we contacted Elizabeth Weatherhead of the Cooperative Institute for Research in Environmental Sciences at the University of Colorado at Boulder. She shared with us a database of measurements of UV radiation at the earth's surface taken by NASA's Total Ozone Mapping Spectrophotometer satellite between 1978 and 1993. We were then able to model the distribution of UV radiation on the earth and relate the satellite data to the amount of UVB necessary to produce vitamin D.

We found that the earth's surface could be divided into three vitamin D zones: one comprising the tropics, one the subtropics and temperate regions, and the last the circumpolar regions north and south of about 45 degrees latitude. In the first, the dosage of UVB throughout the year is high enough that humans have ample opportunity to synthesize vitamin D all year. In the second, at least one month during the year has insufficient UVB radiation, and in the third area not enough UVB arrives on average during the entire year to prompt vitamin D synthesis. This distribution could explain why indigenous peoples in the tropics generally have dark skin, whereas people in the subtropics and temperate regions are lighter-skinned but have the ability to tan, and those who live in regions near the poles tend to be very light skinned and burn easily.

One of the most interesting aspects of this investigation was the examination of groups that did not precisely fit the predicted skin-color pattern. An example is the Inuit people of Alaska and northern Canada. The Inuit exhibit skin color that is somewhat darker than would be predicted given the UV levels at their latitude. This is probably caused by two factors. The first is that they are relatively recent inhabitants of these climes, having migrated to North America only roughly 5,000 years ago. The second is that the traditional diet of the Inuit is extremely high in foods containing vitamin D, especially fish and marine mammals. This vitamin D-rich diet offsets the problem that they would otherwise have with vitamin D synthesis in their skin at northern latitudes and permits them to remain more darkly pigmented.

Our analysis of the potential to synthesize vitamin D allowed us to understand another trait related to human skin color: women in all populations are generally lighter-skinned than men. (Our data show that women tend to be between 3 and 4 percent lighter than men.) Scientists have often speculated on the reasons, and most have argued that the phenomenon stems from sexual selection—the preference of men for women of lighter color. We contend that although this is probably part of the story, it is not the original reason for the sexual difference. Females have significantly greater needs for calcium throughout their reproductive lives, especially during pregnancy and lactation, and must be able to make the most of the calcium contained in food. We propose, therefore, that women tend to be lighter-skinned than men to allow slightly more UVB rays to penetrate their skin and thereby increase their ability to produce vitamin D. In areas of the world that receive a large amount of UV radiation, women are indeed at the knife's edge of natural selection, needing to maximize the photoprotective function of their skin on the one hand and the ability to synthesize vitamin D on the other.
Where Culture and Biology Meet

AS MODERN HUMANS MOVED throughout the Old World about 100,000 years ago, their skin adapted to the environmental conditions that prevailed in different regions. The skin color of the indigenous people of Africa has had the longest time to adapt because anatomically modern humans first evolved there. The skin-color changes that modern humans underwent as they moved from one continent to another--first Asia, then Austro-Melanesia, then Europe and, finally, the Americas--can be reconstructed to some extent. It is important to remember, however, that those humans had clothing and shelter to help protect them from the elements. In some places, they also had the ability to harvest foods that were extraordinarily rich in vitamin D, as in the case of the Inuit. These two factors had profound effects on the tempo and degree of skin-color evolution in human populations.

Africa is an environmentally heterogeneous continent. A number of the earliest movements of contemporary humans outside equatorial Africa were into southern Africa. The descendants of some of these early colonizers, the Khoisan (previously known as Hottentots), are still found in southern Africa and have significantly lighter skin than indigenous equatorial Africans do--a clear adaptation to the lower levels of UV radiation that prevail at the southern extremity of the continent.

Interestingly, however, human skin color in southern Africa is not uniform. Populations of Bantu-language speakers who live in southern Africa today are far darker than the Khoisan. We know from the history of this region that Bantu speakers migrated into this region recently--probably within the past 1,000 years--from parts of West Africa near the equator. The skin-color difference between the Khoisan and Bantu speakers such as the Zulu indicates that the length of time that a group has inhabited a particular region is important in understanding why they have the color they do.

Cultural behaviors have probably also strongly influenced the evolution of skin color in recent human history. This effect can be seen in the indigenous peoples who live on the eastern and western banks of the Red Sea. The tribes on the western side, which speak so-called Nilo-Hamitic languages, are thought to have inhabited this region for as long as 6,000 years. These individuals are distinguished by very darkly pigmented skin and long, thin bodies with long limbs, which are excellent biological adaptations for dissipating heat and intense UV radiation. In contrast, modern agricultural and pastoral groups on the eastern bank of the Red Sea, on the Arabian Peninsula, have lived there for only about 2,000 years. These earliest Arab people, of European origin, have adapted to very similar environmental conditions by almost exclusively cultural means--wearing heavy protective clothing and devising portable shade in the form of tents. (Without such clothing, one would have expected their skin to have begun to darken.) Generally speaking, the more recently a group has migrated into an area, the more extensive its cultural, as opposed to biological, adaptations to the area will be.

Perils of Recent Migrations

DESPITE GREAT IMPROVEMENTS in overall human health in the past century, some diseases have appeared or reemerged in populations that had previously been little affected by them. One of these is skin cancer, especially basal and squamous cell carcinomas, among light-skinned peoples. Another is rickets, brought about by severe vitamin D deficiency, in dark-skinned peoples. Why are we seeing these conditions?

As people move from an area with one pattern of UV radiation to another region, biological and cultural adaptations have not been able to keep pace. The light-skinned people of northern European origin who bask in the sun of Florida or northern Australia increasingly pay the price in the form of premature aging of the skin and skin cancers, not to mention the unknown cost in human life of folate depletion. Conversely, a number of dark-skinned people of southern Asian and African origin now living in the northern U.K., northern Europe or the northeastern U.S. suffer from a lack of UV radiation and vitamin D, an insidious problem that manifests itself in high rates of rickets and other diseases related to vitamin D deficiency.

The ability of skin color to adapt over long periods to the various environments to which humans have moved reflects the importance of skin color to our survival. But its unstable nature also makes it one of the least useful characteristics in determining the evolutionary relations between human groups. Early Western
scientists used skin color improperly to delineate human races, but the beauty of science is that it can and does correct itself. Our current knowledge of the evolution of human skin indicates that variations in skin color, like most of our physical attributes, can be explained by adaptation to the environment through natural selection. We look ahead to the day when the vestiges of old scientific mistakes will be erased and replaced by a better understanding of human origins and diversity. Our variation in skin color should be celebrated as one of the most visible manifestations of our evolution as a species.

MORE TO EXPLORE

The Evolution of Human Skin Coloration.
An abstract of the article is available online at www.idealibrary.com/links/doi/10.1006/jhev.2000.0403

Why Skin Comes in Colors.
The article is also available at www.calacademy.org/calwild/winter2000/html/horizons.html

The Biology of Skin Color: Black and White.
The article is also available at www.discover.com/feb%5f01/featbiology.html

PHOTO (COLOR)
PHOTO (COLOR)

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By Nina G. Jablonski and George Chaplin

NINA G. JABLONSKI and GEORGE CHAPLIN work at the California Academy of Sciences in San Francisco, where Jablonski is Irvine Chair and curator of anthropology and Chaplin is a research associate in the department of anthropology. Jablonski's research centers on the evolutionary adaptations of monkeys, apes and humans. She is particularly interested in how primates have responded to changes overtime in the global environment. Chaplin is a private geographic information systems consultant who specializes in describing and analyzing geographic trends in biodiversity. In 2001 he was awarded the Student of the Year prize by the Association of Geographic Information in London for his master's thesis on the environmental correlates of skin color.

Overview/Skin Color Evolution

• After losing their hair as an adaptation for keeping cool, early hominids gained pigmented skins. Scientists initially thought that such pigmentation arose to protect against skin-cancer-causing ultraviolet [UV] radiation.

• Skin cancers tend to arise after reproductive age, however. An alternative theory suggests that dark skin might have evolved primarily to protect against the breakdown of folate, a nutrient essential for fertility and for fetal development.
Skin that is too dark blocks the sunlight necessary for catalyzing the production of vitamin D, which is crucial for maternal and fetal bones. Accordingly, humans have evolved to be light enough to make sufficient vitamin B yet dark enough to protect their stores of folate.

As a result of recent human migrations, many people now live in areas that receive more or less UV radiation than is appropriate for their skin color.

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**SKIN AND MIGRATION**

THE SKIN OF PEOPLES who have inhabited particular areas for millennia has adapted to allow vitamin D production while protecting folate stores. The skin tones of more recent immigrants will take thousands of years to catch up, putting light-skinned individuals at risk for skin cancer and dark-skinned people in danger of vitamin D deficiency.

<table>
<thead>
<tr>
<th>LONG-TERM RESIDENT</th>
<th>RECENT IMMIGRANT</th>
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<tbody>
<tr>
<td>SOUTHERN AFRICA:</td>
<td></td>
</tr>
<tr>
<td>20-30° S</td>
<td>Khoisan</td>
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<tr>
<td></td>
<td>[Hottentot]</td>
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<tr>
<td>Zulu</td>
<td>arrived about 1,000 years ago</td>
</tr>
<tr>
<td>AUSTRALIA:</td>
<td></td>
</tr>
<tr>
<td>10-35° S</td>
<td>Aborigine</td>
</tr>
<tr>
<td></td>
<td>European - 300 years ago</td>
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<tr>
<td>BANKS OF RED SEA:</td>
<td></td>
</tr>
<tr>
<td>15-30° N</td>
<td>Sudanese</td>
</tr>
<tr>
<td></td>
<td>Arab - 2,000 years ago</td>
</tr>
<tr>
<td>INDIA:</td>
<td></td>
</tr>
<tr>
<td>10-30° N</td>
<td>Bengali</td>
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<td></td>
<td>Tamil - 100 years ago</td>
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WHO MAKES ENOUGH VITAMIN D?

POPULATIONS THAT LIVE in the tropics receive enough ultraviolet [UV] light from the sun to synthesize vitamin D all year long. But those that live at northern or southern latitudes do not. In the temperate zones, people lack sufficient UV light to make vitamin D one month of the year; those nearer the poles do not get enough UV light most months for vitamin D synthesis. The
bottom map shows predicted skin colors for humans based on UV light levels. In the Old World, the skin color of indigenous peoples closely matches predictions. In the New World, however, the skin color of long-term residents is generally lighter than expected—probably because of their recent migration and factors such as diet.