The Naked Truth

Recent findings lay bare the origins of human hairlessness—and hint that naked skin was a key factor in the emergence of other human traits

BY NINA G. JABLONSKI

mong primates, humans are unique in having nearly naked skin. Every other member of our extended family has a dense covering of fur—from the short, black pelage of the howler monkey to the flowing copper coat of the orangutan—as do most other mammals. Yes, we humans have hair on our heads and elsewhere, but compared with our relatives, even the hairiest person is basically bare.

How did we come to be so denuded? Scholars have pondered this question for centuries. Finding answers has been difficult, however: most of the hallmark transitions in human evolutionsuch as the emergence of upright walking-are recorded directly in the fossils of our predecessors, but none of the known remains preserves impressions of human skin. In recent years, though, researchers have realized that the fossil record does contain indirect hints about our transformation from hirsute to hairless. Thanks to these clues and insights gleaned over the past decade from genomics and physiology, I and others have pieced together a compelling account of why and when humans shed their fur. In addition to explaining a very peculiar quirk of our appearance, the scenario suggests that naked skin itself played a crucial role in the evolution of other characteristic human traits, including our large brain and dependence on language.

Hairy Situations

To understand why our ancestors lost their body hair, we must first consider why other species have coats in the first place. Hair is a type of body covering that is unique to mammals. Indeed, it is a defining characteristic of the class: all mammals possess at least some hair, and most of them have it in abundance. It provides insulation and protection against abrasion, moisture, damaging rays of sunlight, and potentially harmful parasites and microbes. It also works as camouflage to confuse predators, and its distinctive patterns allow members of the same species to recognize one another. Furthermore, mammals can use their fur in social displays to indicate aggression or agitation: when a dog "raises its hackles" by involuntarily elevating the hairs on its neck and back, it is sending a clear signal to challengers to stay away.

Yet even though fur serves these many important purposes, a number of mammal lineages have evolved hair that is so sparse and fine as to serve no function. Many of these creatures live underground or dwell exclusively in the water.

KEY CONCEPTS

- Humans are the only primate species that has mostly naked skin.
- Loss of fur was an adaptation to changing environmental conditions that forced our ancestors to travel longer distances for food and water.
- Analyses of fossils and genes hint at when this transformation occurred.
- The evolution of hairlessness helped to set the stage for the emergence of large brains and symbolic thought.

-The Editors

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[BENEFITS OF HAIRLESSNESS]

Naked human skin is better at ridding the body of excess heat than is fur-covered skin. Mammals possess three types of glands for the purpose: apocrine, eccrine and sebaceous. In most mammals the outermost layer of the skin, known as the epidermis, contains an abundance of apocrine glands. These glands cluster around hair follicles and coat the fur in a lather of oily sweat. Evaporation of this sweat, which cools the animal by drawing heat away from the skin, occurs at the surface of the fur. But the more the animal perspires, the less effectively it eliminates heat because the fur becomes matted, hampering evaporation. In the human epidermis, in contrast, eccrine glands predominate. These glands reside close to the skin surface and discharge thin, watery sweat through tiny pores. In addition to evaporating directly from the skin surface, this eccrine sweat vaporizes more readily than apocrine sweat, thus permitting improved cooling.

In subterranean mammals, such as the naked mole rat, hairlessness evolved as a response to living in large underground colonies, where the benefits of hair are superfluous because the animals cannot see one another in the dark and because their social structure is such that they simply huddle together for warmth. In marine mammals that never venture ashore, such as whales, naked skin facilitates long-distance swimming and diving by reducing drag on the skin's surface. To compensate for the lack of external insulation, these animals have blubber under the skin. In contrast, semiaquatic mammals-otters, for example-have dense, waterproof fur that traps air to provide positive buoyancy, thus decreasing the effort needed to float. This fur also protects their skin on land.

The largest terrestrial mammals-namely, elephants, rhinoceroses and hippopotamuses-also evolved naked skin because they are at constant risk of overheating. The larger an animal is, the less surface area it has relative to overall body mass and the harder it is for the creature to rid its body of excess heat. (On the flip side, mice and other small animals, which have a high surfaceto-volume ratio, often struggle to retain sufficient heat.) During the Pleistocene epoch, which spans the time between two million and 10,000 years ago, the mammoths and other relatives of modern elephants and rhinoceroses were "woolly" because they lived in cold environments, and external insulation helped them conserve body heat and lower their food intake. But all of today's megaherbivores live in sweltering condi-



tions, where a fur coat would be deadly for beasts of such immense proportions.

Human hairlessness is not an evolutionary adaptation to living underground or in the water—the popular embrace of the so-called aquatic ape hypothesis notwithstanding [*see box on opposite page*]. Neither is it the result of large body size. But our bare skin is related to staying cool, as our superior sweating abilities suggest.

[THE AUTHOR]



Nina G. Jablonski is head of the anthropology department at Pennsylvania State University. Her research focuses on the natural history of human skin, the origin of bipedalism, the evolution and biogeography of Old World monkeys, and the paleoecology of mammals that lived during the past two million years. She has conducted fieldwork in China, Kenya and Nepal. This is her second article for Scientific American. The first, co-authored with George Chaplin and published in October 2002, described the evolution of human skin color.

Sweating It Out

Keeping cool is a big problem for many mammals, not just the giant ones, especially when they live in hot places and generate abundant heat from prolonged walking or running. These animals must carefully regulate their core body temperature because their tissues and organs, specifically the brain, can become damaged by overheating.

Mammals employ a variety of tactics to avoid burning up: dogs pant, many cat species are most active during the cooler evening hours, and many antelopes can off-load heat from the blood in their arteries to blood in small veins that has been cooled by breathing through the nose. But for primates, including humans, sweating is the primary strategy. Sweating cools the body through the production of liquid on the skin's surface that then evaporates, drawing heat energy away from the skin in the process. This wholebody cooling mechanism operates according to the same principle as an evaporative cooler (also known as a swamp cooler), and it is highly effective in preventing the dangerous overheat-



ing of the brain, as well as of other body parts.

Not all sweat is the same, however. Mammalian skin contains three types of glands—sebaceous, apocrine and eccrine—that together produce sweat. In most species, sebaceous and apocrine glands are the dominant sweat glands and are located near the base of hair follicles. Their secretions combine to coat hairs with an oily, sometimes foamy, mixture (think of the lather a racehorse generates when it runs). This type of sweat helps to cool the animal. But its ability to dissipate heat is limited. G. Edgar Folk, Jr., of the University of Iowa and his colleagues showed nearly two decades ago that the effectiveness of cooling diminishes as an animal's coat becomes wet and matted with this thick, oily sweat. The loss of efficiency arises because evaporation occurs at the surface of the fur, not at the surface of the skin itself, thus impeding the transfer of heat. Under conditions of duress, heat transfer is inefficient, requiring that the animal drink large amounts of water, which may not be readily available. Fur-covered mammals forced to exercise energetically or for prolonged periods in the heat of day will collapse from heat exhaustion.

Humans, in addition to lacking fur, possess an extraordinary number of eccrine glands-between two million and five million-that can produce up to 12 liters of thin, watery sweat a day. Eccrine glands do not cluster near hair follicles; instead they reside relatively close to the surface of the skin and discharge sweat through tiny pores. This combination of naked skin and watery sweat that sits directly atop it rather than collecting in the fur allows humans to eliminate excess heat very efficiently. In fact, according to a 2007 paper in Sports Medicine by Daniel E. Lieberman of Harvard University and Dennis M. Bramble of the University of Utah, our cooling system is so superior that in a marathon on a hot day, a human could outcompete a horse.

Showing Some Skin

Because humans are the only primates that lack coats and have an abundance of eccrine glands, something must have happened since our hominid lineage diverged from the line leading to our closest living relative, the chimpanzee, that favored the emergence of naked, sweaty skin.

[ALTERNATIVE IDEAS]

Why the Aquatic Ape Theory Doesn't Hold Water

A mong the many theories that attempt to explain the evolution of naked skin in humans, the aquatic ape theory (AAT)—which posits that humans went through an aquatic phase in their evolution—has attracted the most popular attention and support. First enunciated by English zoologist Sir Alister Hardy in a popular scientific article in 1960, the AAT later found a champion in writer Elaine Morgan, who continues to promote the theory in her lectures and writings. The problem is, the theory is demonstrably wrong.

The AAT holds that around five million to seven million years ago tectonic upheavals in the Rift Valley of East Africa cut early human ancestors off from their preferred tropical forest environments. As a result, they had to adapt to a semiaquatic life in marshes, along coasts and in floodplains, where they lived for about a million years. Evidence of this aquatic phase, Morgan argues, comes from several anatomical features humans share with aquatic and semiaquatic mammals but not with savanna mammals. These traits include our bare skin, a reduced number of apocrine glands, and fat deposits directly under the skin.

The AAT is untenable for three major reasons. First, aguatic mammals themselves differ considerably in the degree to which they exhibit Morgan's aquatic traits. Thus, there is no simple connection between, say, the amount of hair an animal has and the environment in which it lives. Second, the fossil record shows that watery habitats were thick with hungry crocodiles and aggressive hippopotamuses. Our small, defenseless ancestors would not have stood a chance in an encounter with such creatures. Third, the AAT is overly complex. It holds that our forebears shifted from a terrestrial way of life to a semiaquatic one and then returned to living on terra firma full-time. As John H. Langdon of the University of Indianapolis has argued, a more straightforward interpretation of the fossil record is that humans always lived on land, where the driving force behind the evolution of naked skin was climate change that favored savanna grasslands over woodlands. And from a scientific perspective, the simplest explanation is usually the correct one. N.J.

[WHEN NAKEDNESS EVOLVED] ANCESTORS ON THE MOVE

Although the fossil record does not preserve any direct evidence of ancient human skin, scientists can estimate when nakedness evolved based on other fossil clues. Protohumans such as the australopithecines (left) probably led relatively sedentary lives, as today's apes do, because they lived in or near wooded environments rich in plant foods and freshwater. But as woodlands shrank and grasslands expanded, later ancestors, such as Homo ergaster (right), had to travel ever farther in search of sustenanceincluding meat. This species, which arose by 1.6 million years ago, was probably the first to possess naked skin and eccrine sweat, which would have offset the body heat generated by such elevated activity levels.

► Australopithecus afarensis, represented here by the 3.2-millionyear-old Lucy fossil, was apelike in having short legs that were not well suited to traveling long distances.



Perhaps not surprisingly, the transformation seems to have begun with climate change.

By using fossils of animals and plants to reconstruct ancient ecological conditions, scientists have determined that starting around three million years ago the earth entered into a phase of global cooling that had a drying effect in East and Central Africa, where human ancestors lived. With this decline in regular rainfall, the wooded environments favored by early hominids gave way to open savanna grasslands, and the foods that our ancestors the australopithecines subsisted on-fruits, leaves, tubers and seeds-became scarcer, more patchily distributed and subject to seasonal availability, as did permanent sources of freshwater. In response to this dwindling of resources, our forebears would have had to abandon their relatively leisurely foraging habits for a much more consistently active way of life just to stay hydrated and obtain enough calories, traveling ever longer distances in search of water and edible plant foods.

It is around this time that hominids also began incorporating meat into their diet, as revealed by the appearance of stone tools and butchered animal bones in the archaeological record around 2.6 million years ago. Animal foods are considerably richer in calories than are plant foods, but they are rarer on the landscape. Carnivorous animals therefore need to range farther and wider

BEATING THE HEAT

Naked skin is not the only adaptation humans evolved to maintain a healthy body temperature in the sweltering tropics where our ancestors lived. They also developed longer limbs, increasing their surface-to-volume ratio, which in turn facilitated the loss of excess heat. That trend seems to be continuing even today. The best evidence of this sustained adaptation comes from populations in East Africa, such as the Dinka of southern Sudan. It is surely no coincidence that these people, who live in one of the hottest places on earth, also have extremely long limbs.

Why do modern humans exhibit such a wide range of limb proportions? As our forebears migrated out of tropical Africa into cooler parts of the world, the selection pressures changed, allowing for a variety of body shapes to evolve. than their herbivorous counterparts to procure a sufficient amount of food. Prey animals are also moving targets, save for the occasional carcass, which means predators must expend that much more energy to obtain their meal. In the case of human hunters and scavengers, natural selection morphed the apelike proportions of the australopithecines, who still spent some time in the trees, into a long-legged body built for sustained striding and running. (This modern form also no doubt helped our ancestors avoid becoming dinner themselves when out in the open.)

But these elevated activity levels came at a price: a greatly increased risk of overheating. Beginning in the 1980s, Peter Wheeler of Liverpool John Moores University in England published a series of papers in which he simulated how hot ancestral humans would have become out on the savanna. Wheeler's work, together with research my colleagues and I published in 1994, shows that the increase in walking and running, during which muscle activity builds up heat internally, would have required that hominids both enhance their eccrine sweating ability and lose their body hair to avoid overheating.

When did this metamorphosis occur? Although the human fossil record does not preserve skin, researchers do have a rough idea of when our forebears began engaging in modern patterns of movement. Studies conducted indeHomo ergaster was the first hominid to possess long, striding legs, seen here in the 1.6-million-year-old Turkana Boy skeleton. Such elongated limbs facilitated sustained walking and running.



pendently by Lieberman and Christopher Ruff of Johns Hopkins University have shown that by about 1.6 million years ago an early member of our genus called *Homo ergaster* had evolved essentially modern body proportions, which would have permitted prolonged walking and running. Moreover, details of the joint surfaces of the ankle, knee and hip make clear that these hominids actually exerted themselves in this way. Thus, according to the fossil evidence, the transition to naked skin and an eccrine-based sweating system must have been well under way by 1.6 million years ago to offset the greater heat loads that accompanied our predecessors' newly strenuous way of life.

Another clue to when hominids evolved naked skin has come from investigations into the genetics of skin color. In an ingenious study published in 2004, Alan R. Rogers of the University of Utah and his colleagues examined sequences of the human *MC1R* gene, which is among the genes responsible for producing skin pigmentation. The team showed that a specific gene variant always found in Africans with dark pigmentation originated as many as 1.2 million years ago. Early human ancestors are believed to have had pinkish skin covered with black fur, much as chimpanzees do, so the evolution of permanently dark skin was presumably a requisite evolutionary follow-up to the loss of our sun-shieldGoing furless was not merely a means to an end; it had profound consequences for subsequent phases of human evolution. ing body hair. Rogers's estimate thus provides a minimum age for the dawn of nakedness.

Skin Deep

Less certain than why and when we became naked is how hominids evolved bare flesh. The genetic evidence for the evolution of nakedness has been difficult to locate because many genes contribute to the appearance and function of our skin. Nevertheless, hints have emerged from large-scale comparisons of the sequences of DNA "code letters," or nucleotides, in the entire genomes of different organisms. Comparison of the human and chimp genomes reveals that one of the most significant differences between chimp DNA and our own lies in the genes that code for proteins that control properties of the skin. The human versions of some of those genes encode proteins that help to make our skin particularly waterproof and scuff-resistant-critical properties, given the absence of protective fur. This finding implies that the advent of those gene variants contributed to the origin of nakedness by mitigating its consequences.

The outstanding barrier capabilities of our skin arise from the structure and makeup of its outermost layer, the stratum corneum (SC) of the epidermis. The SC has what has been described as a bricks-and-mortar composition. In this arrangement, multiple layers of flattened



SOCIAL SIGNALING is an important function of fur—from raised hackles indicating aggression to coat patterns that help members of the same species to recognize one another. We humans compensate for our lack of fur by decorating our bodies with tattoos, jewelry and other adornments. We also have complex facial expressions, as well as the ability to convey our emotions through language.



dead cells called corneocytes, which contain the protein keratin and other substances, are the bricks; ultrathin layers of lipids surrounding each of the corneocytes make up the mortar.

Most of the genes that direct the development of the SC are ancient, and their sequences are highly conserved among vertebrates. That the genes undergirding the human SC are so distinctive signifies, therefore, that the advent of those genes was important to survival. These genes encode the production of a unique combination of proteins that occur only in the epidermis, including novel types of keratin and involucrin. A number of laboratories are currently attempting to unravel the precise mechanisms responsible for regulating the manufacture of these proteins.

Other researchers are looking at the evolution of keratins in body hair, with the aim of determining the mechanisms responsible for the sparseness and fineness of body hair on the surface of human skin. To that end, Roland Moll of Philipps University in Marburg, Germany, and his colleagues have shown that the keratins present in human body hair are extremely fragile, which is why these hairs break so easily compared with those of other animals. This finding, detailed in a paper Moll published in 2008, suggests that human hair keratins were not as important to survival as the hair keratins of other primates were over the course of evolution and thus became weak.

Another question geneticists are eager to answer is how human skin came to contain such an abundance of eccrine glands. Almost certainly this accumulation occurred through changes in the genes that determine the fate of epidermal stem cells, which are unspecialized, in the em-

OF LICE AND MEN

In recent years researchers have looked to lice for clues to why humans lost their body hair. In 2003 Mark Pagel of the University of Reading in England and Walter **Bodmer of John Radcliffe Hospital** in Oxford proposed that humans shed their fur to rid their bodies of disease-spreading lice and other fur-dwelling parasites and to advertise the health of their skin. Other investigators have studied head and body lice for insight into how long after becoming bareskinned our ancestors began to cover up with clothing.

Although body lice feed on blood, they live on clothing. Thus, the origin of body lice provides a minimum estimate for the dawn of hominid garb. By comparing gene sequences of organisms, investigators can learn roughly when the species arose. Such analyses in lice indicate that whereas head lice have plagued humans from the start, body lice evolved much later. The timing of their appearance hints that humans went naked for more than a million years before getting dressed. bryo. Early in development, groups of epidermal stem cells in specific locations interact with cells of the underlying dermis, and genetically driven chemical signals within these niches direct the differentiation of the stem cells into hair follicles, eccrine glands, apocrine glands, sebaceous glands or plain epidermis. Many research groups are now investigating how epidermal stem cell niches are established and maintained, and this work should clarify what directs the fate of embryonic epidermal cells and how more of these cells become eccrine sweat glands in humans.

Not Entirely Nude

However it was that we became naked apes, evolution did leave a few body parts covered. Any explanation of why humans lost their fur therefore must also account for why we retain it in some places. Hair in the armpits and groin probably serves both to propagate pheromones (chemicals that serve to elicit a behavioral response from other individuals) and to help keep these areas lubricated during locomotion. As for hair on the head, it was most likely retained to help shield against excess heat on the top of the head. That notion may sound paradoxical, but having dense hair on the head creates a barrier layer of air between the sweating scalp and the hot surface of the hair. Thus, on a hot, sunny day the hair absorbs the heat while the barrier layer of air remains cooler, allowing sweat on the scalp to evaporate into that layer of air. Tightly curled hair provides the optimum head covering in this regard, because it increases the thickness of the space between the surface of the hair and the scalp, allowing air to blow through. Much remains to be discovered about the evolution of



human head hair, but it is possible that tightly curled hair was the original condition in modern humans and that other hair types evolved as humans dispersed out of tropical Africa.

With regard to our body hair, the question is why it is so variable. There are many populations whose members have hardly any body hair at all and some populations of hirsute folks. Those with the least body hair tend to live in the tropics, whereas those with the most tend to live outside the tropics. Yet the hair on these nontropical people provides no warmth to speak of. These differences in hairiness clearly stem to some extent from testosterone, because males in all populations have more body hair than females do. A number of theories aimed at explaining this imbalance attribute it to sexual selection. For example, one posits that females prefer males with fuller beards and thicker body hair because these traits occur in tandem with virility and strength. Another proposes that males have evolved a preference for females with more juvenile features. These are interesting hypotheses, but no one has actually tested them in a modern human population; thus, we do not know, for instance, whether hairy men are in fact more vigorous or fecund than their sleeker counterparts. In the absence of any empirical evidence, it is still anybody's guess why human body hair varies the way it does.

Naked Ambitions

Going furless was not merely a means to an end; it had profound consequences for subsequent phases of human evolution. The loss of most of our body hair and the gain of the ability to dissipate excess body heat through eccrine sweating helped to make possible the dramatic enlargement of our most temperature-sensitive organ, the brain. Whereas the australopithecines had a brain that was, on average, 400 cubic centimeters—roughly the size of a chimp's brain—*H*. *ergaster* had a brain twice that large. And within a million years the human brain swelled another 400 cubic centimeters, reaching its modern size. No doubt other factors influenced the expansion of our gray matter—the adoption of a sufficiently caloric diet to fuel this energetically demanding tissue, for example. But shedding our body hair was surely a critical step in becoming brainy.

Our hairlessness also had social repercussions. Although we can technically raise and lower our hackles when the small muscles at the base of our hair follicles contract and relax, our body hairs are so thin and wispy that we do not put on much of a show compared with the displays of our cats and dogs or of our chimpanzee cousins. Neither do we have the built-in advertising-or camouflage-offered by zebra stripes, leopard spots, and the like. Indeed, one might even speculate that universal human traits such as social blushing and complex facial expressions evolved to compensate for our lost ability to communicate through our fur. Likewise, body paint, cosmetics, tattoos and other types of skin decoration are found in various combinations in all cultures, because they convey group membership, status and other vital social information formerly encoded by fur. We also employ body postures and gestures to broadcast our emotional states and intentions. And we use language to speak our mind in detail. Viewed this way, naked skin did not just cool us downit made us human.

MORE TO EXPLORE

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