Journal of Student Research Volume 11 Issue 4 (2022)

Splitting Hairs: Evaluating the Origin of Human Nakedness

Brianna Fonda[1]

[1]University of Massachusetts - Amherst

ABSTRACT

Humans are the only extant predominantly hairless species in the primate order and are one of a mere handful of mammals with the same trait. Because hairlessness is not the natural condition of mammals and primates, then something in the evolution of *Homo sapiens* would have reduced or eliminated the selection for hair and instead selected for nakedness. This area of research has inspired various competing models that attempt to explain the emergence of hominin hairlessness. The key to evaluating such models, and deducing which evolutionary pressures were at play, lies in determining the timing of hair loss. For instance, if the development of clothing, as some have predicted, was the catalyst for humanity's naked condition, then the chronological data should reflect a later evolution of hairlessness. Here, I examine published molecular and physiological data to evaluate several of these proposed hypotheses. Published genetic, fossil, and experimental data were used to evaluate the fit of each model to determine when hairlessness most likely emerged and which model most likely accurately reflects the evolutionary path of our ancestors. Evidence points to the thermoregulatory hypothesis as the most likely driving force behind the evolution of hairlessness in humans.

Introduction

Hair is a derived trait among mammals that serves many functions and aids in their survival. It serves as both an insulator and as protection against heat and UV radiation from the sun, while also shielding against microbes, parasites, biting insects, and abrasion from the surrounding environment. Hair can be a way to camouflage, which can be beneficial for both predators and prey and may also serve an intraspecies social function that expresses mood based on raising hair in certain bodily regions (Jablonski, 2010).

Despite the benefits of hair, some mammals have evolved to be hairless. Among these are subterranean mammals like naked mole rats, whose hairless appearance is a response to life in the dark where individuals huddle for warmth; cetaceans, who swim for long distances and who benefit from the reduction of drag that hairlessness provides them; large terrestrial mammals with low surface area to body mass ratios that makes losing sufficient heat rather difficult; and, perhaps most curiously, humans (Jablonski, 2010). Even our closest living relative, the chimpanzee, appears to have a substantial amount of body hair compared to modern *Homo sapiens*, suggesting a unique evolutionary pressure acted on our lineage that resulted in humanity's apparent nakedness.

The purpose of this review is to summarize several competing models regarding the evolution of hair loss and to determine which hypothesis or hypotheses accurately reflect the evolutionary history of nakedness in the hominin lineage. First, an overview of the anatomy of hair and its distribution over the body of modern humans will be conducted, followed by a brief summarization of these models and evaluation of the literature regarding the timing of hair loss. These sections will be followed by a discussion that will explore how the data determining when hairlessness occurred intersects with the competing models.

Hair and *Homo sapiens*

Hair is an exclusively mammalian trait that can aid in an animal's survival (Jablonski, 2010). Hair growth begins in a highly vascularized, sac-like organ called the follicle that is located about 3 or 4 millimeters below the skin's surface. In humans, all hair follicles are fused with sebaceous glands, and follicles located in the axillary and pubic regions are also associated with apocrine glands (Harkey, 1993). The secretions of both glands enter the follicle and bathe the hair shaft before it exits onto the skin (Folk and Semken, 1991; Harkey, 1993). The innermost bulb of the follicle is the locus of hair growth and where keratinization, the hardening and solidifying of the hair shaft, occurs (Harkey, 1993).

Hair emerges from the follicle as a shaft of tightly compacted dead cells that contain keratin, which is strung together as long and tightly bound fibers. The cross section of these hair shafts can be a variety of shapes from round and oval shafts to triangular or even kidney-shaped shafts, giving hair their phenotypic texture. There are three distinct parts of a hair shaft that contain three different types of cells. The outermost section of a hair shaft, the cuticle, functions as an anchor for the hair shaft within the follicle and protects the cortex inside the hair shaft; however, the cuticle can become damaged quite easily, resulting in fraying at the ends, commonly known as "split ends". The cortex forms the bulk of the hair shaft and contains pigment granules. These granules form various structures and alignments that determine the color of the hair. The medulla is found within the cortex of thicker hairs and its structure can be quite complex. Beard hairs, for example, can occasionally have double medullas (Harkey, 1993).

Across the human body, many different hair types vary in appearance and distribution. Terminal hairs are quite easy to see as they are long, coarse, and pigmented. They can be found in the parts of the body that are visibly hairy, like the scalp, eyebrows, eyelashes, armpits, pubic area, and on the faces of people who are capable of growing thick facial hair. Vellus hairs, on the other hand, are the very fine, short, non-pigmented hairs that cover most of the body and are found on areas that appear naked, such as on the eyelids, on the forehead, and on the scalp of bald individuals (Harkey, 1993). Vellus hairs can be converted into terminal hairs when androgens are present (Lieberman, 2014). Intermediate hairs are hairs that lie in between terminal and vellus hairs in terms of thickness and pigmentation. These hairs can be found on the arms and legs of adults (Harkey, 1993).

In total two to five million hair follicles exist on the human body, with males and females having the same number of follicles (Kushlan, 1985). While males only appear to have more body hair because of the effect that androgens have on the development of thicker terminal hairs (Randall, 2008), sex can influence the appearance and distribution of hair across the body. Non-sexual hair follicles are not influenced by hormones and do not change following puberty. They produce intermediate hairs that can be found on the arms and legs of both males and females (Harkey, 1993). Ambosexual follicles are found in the axillary and pubic regions, as well as the temporal region of the face. These follicles produce vellus hairs until puberty, when the follicle then begins production of terminal hair except for the temporal region of the face, where follicles will begin producing vellus hairs instead of terminal hairs following puberty (Harkey, 1993). Male sexual follicles are those responsible for producing hair on the chest and abdomen, in the nose and ears, and on the region of the face where facial hair can be grown. Similarly to some ambosexual follicles, male sexual follicles can revert from terminal head hair to vellus hair on the scalp, resulting in a bald appearance (Harkey, 1993). Hirsutism in females, which can have several causes, can result in excess terminal hair growth in patterns like those observed in males (Randall, 2008).

The functionality of our existing terminal hair is not entirely known, though there are some generally accepted hypotheses on the overall functions of hair in regions corresponding with terminal hair growth. Giles (2010) suggests that head hair, especially on females, could be the result of sexual selection. Head hair's ability to be used as social signaling has also been suggested (Kushlan, 1985). Others still have pointed to the potential thermoregulatory advantages of retained hair on the scalp. Having dense hair on this region of our body is highly advantageous in keeping our brains cool as it can form a layer of air between the surface of the scalp and the top of the hair. This layer will remain cool while the hair above absorbs all the heat from the sun. Tightly curled hair is especially efficient in this manner as it increases the space between the scalp and the hair's surface, hence this hair type being the most common in tropical regions (Jablonski, 2010). Eyebrows are likely utilized in communicating mood changes (Rantala, 1999), and facial hair is mostly described as a tool for communication and sexual signaling (Giles, 2010; Kushlan, 1985).

Armpit hair has been suggested to serve in lubricating the arms against the torso during locomotion, though this has been challenged because the absence of these hairs does not hinder the locomotor abilities of children and individuals who shave their armpits (Giles, 2010; Jablonski, 2010). More interestingly, it has been proposed that armpit hair functions to trap pheromones that are useful in reproduction (Jablonski, 2010). Females were found to have increased levels of cortisol, signaling physiological arousal, when exposed to steroidal compounds found in male armpit secretions (Wyart et al., 2007), and those with long menstrual cycles were found to have their cycles shortened. Neonates are also able to recognize the scent of their own mother's underarms and were found to breastfeed more successfully when those smells were present, providing strong evidence that armpit hair is used to trap pheromones (Giles, 2010). Pubic hair has been suggested to serve similar functions to axillary hair. Both lubrication and pheromone trapping have been brought forward as explanations for hair retention in the pubic region, though pheromone trapping is the more popular of the two (Giles, 2010; Jablonski, 2010). Pubic hair may serve to socially signal sexual maturity to others, as well (Giles, 2010).

Hair follicle density can also change depending on the geographic locality of a native population. Dhugga et al. (2014) found a strong relationship between follicle density and skin color, those with darker skin being more likely to have less hair and those with lighter skin having a greater variation in follicle density. Testosterone levels and sexual selection may play a role in this pattern, but the distribution of follicle density globally is still too poorly understood to make any overarching conclusions (Jablonski, 2010).

Explanatory Models for Hairlessness

Human hairlessness is ultimately the result of the shift from longer, thicker, pigmented terminal hair to shorter, finer, non-pigmented vellus hair over most of the body and was not characterized by a decrease in hair follicles (Kamberov et al., 2018). In fact, humans have the same number of follicles as chimpanzees, and both members of Hominini have a decreased follicle density from macaques (Kamberov et al., 2018). This phenomenon may be due to the surface area to body mass ratio of these animals. Macaques have a higher surface area to body mass ratio, and they are readily able to dissipate body heat and use their fur to prevent further heat loss. Chimpanzees, on the other hand, have a lower surface to body mass ratio and have more trouble ridding themselves of excess heat and thus have evolved less dense hair coverage as a result (Schwartz and Rosenblum, 1981). Because humans and chimpanzees have the same number of follicles but a differing appearance, this evolutionary pattern does not serve to entirely explain human hair loss. As such, several hypotheses have been proposed to explain why hair loss has exacerbated further somewhere in the hominin lineage.

Ectoparasite Hypothesis

The ectoparasite hypothesis suggests that human hair loss occurred to combat high levels of ectoparasitic load. Fur can provide a habitable environment for pests like fleas, ticks, and lice, the coverage going so far as to protect their eggs, which could exacerbate an infestation (Dhugga et al., 2014). Some of these parasites are known to carry diseases, especially ticks, which could potentially serve as a massive force of natural selection on hominins (Brown, 2021). There are some problems with this hypothesis, however. Many other animals are also affected by high parasite loads but have not lost their hair, and even with apparent nakedness, ectoparasites still infest humans today in the scalp, underarm, and pubic regions (Allen et al., 2013; Giles, 2010). While this could be a result of an evolutionary cost-benefit analysis whereby the benefits of maintaining hair in these regions outweigh the cost of parasitic infection, an animal becoming naked across most of their body could increase their exposure to mosquitos, biting flies, and other insects that can also be vectors for disease. Though fur may not aid much in protecting an animal from these disease vectors, some form of protection is better than no form of protection (Giles, 2010).

One variation of the ectoparasite hypothesis proposed by Brown (2021) has suggested that ticks, ground-dwelling arachnids that reside around the edges of forested areas, might have been the primary catalyst for hair loss, as they provided a way for the last common ancestor (LCA) between humans and chimpanzees to more easily detect the presence of ticks on the body. The LCA, according to this hypothesis, would have been mainly arboreal and gibbon-like, walking bipedally on the ground when it was not in the trees. Around 5 to 8 million years ago, climatic drying and cooling resulted in forest fragmentation in eastern Africa. This fragmentation increased forest edge habitats and, as a result, tick populations may have bloomed. The LCA would then have been forced to walk between these patches of forest in the search of food and forced to interact with tick populations (Brown, 2021). Tick-borne diseases may have put a significant pressure on LCA populations, favoring less hairy individuals who would better be able to see ticks and rid themselves of these parasites before disease transmission. The loss of hair would have made their offspring unable to cling to them, requiring them to walk bipedally on the ground. This evolutionary scenario would serve as the splitting point between chimpanzees—who would increase grooming habits to combat ticks, allowing them to feed from canopies and travel along the ground utilizing their independently evolved knuckle-walking—and hominins. This evolutionary situation, whereby ticks act as the impetus for hair loss which affected LCA's locomotor repertoire, forcing them to become obligate bipeds, positions the occurrence of hair loss around the same time as the emergence of the hominin clade 5 to 8 million years ago (Brown, 2021).

Another proposed variant ectoparasite hypothesis was suggested by Rantala (1999). He suggests that parasite load increased in hominin populations when they began to live in more permanent settlements. Females with children would have been more likely to stay in these more permanent home bases while males were off hunting (Rantala, 1999). These places were ideal for parasite infestation, resulting in strong selection for less hairy females. This would explain why human females have less terminal hair than their male counterparts, who would not have been exposed to the parasites at their home base to the same degree (Prokop, 2016; Rantala, 1999). When hair loss occurred, hominins living in these settlements developed a layer of subcutaneous fat to protect against the cool, 11° Celsius nighttime temperatures. Clothing and controlled fire use would have also been useful in keeping warm during those cold nights. The permanent settlements described in this evolutionary scenario are proposed to have been first utilized around 1.8 million years ago, implying that hair loss occurred shortly thereafter (Rantala, 1999).

Vestiary Hypothesis

The vestiary hypothesis proposes that hair loss occurred in hominins because of the development and use of clothing. As Kushlan (1985) suggests, the intellectual capacity to use artificial insulation methods like animal skins and fabrics would have served to keep hominins warm at night, allowing them to lose their hair. Utilizing shelter and fire would also have aided them in defending against the cold. This model suggests hair loss occurred around 500,000 years ago in populations of *Homo erectus* (Kushlan, 1985).

Thermoregulatory Hypothesis

One very popular hypothesis regarding hominin hair loss involves the uniquely exaggerated cooling system possessed by humans: eccrine sweating. Increased sweating efficiency would have been the result of hominins utilizing the savanna in the heat of the day. Being active in these hot temperatures would have selected for increased sweating capacity and, thus, hair loss (Dhugga et al., 2014; Lieberman, 2014; Schwartz and Rosenblum, 1981). The ability to walk long distances during the day would have provided a distinct advantage over activity during the cooler early morning and evening hours, when predators are most active. Utilizing these environments could explain why defenseless hominins were able to survive alongside dangerous predators (Lieberman, 2014). Furthermore, the resources hominins found during these long treks, like meat and marrow, would have allowed them to be more competitive on the expanding savannas 3 to 1.8 million years ago (Bramble and Lieberman, 2004; Elias, Menon, Wetzel, and Williams, 2010). Endurance running is also suggested as a behavior that would have been practiced by our ancestors, and the evolution of this unique human ability has been suggested to be the result of the exaggeration of long-distance walking, however, it was improbably the sole cause (Bramble and Lieberman, 2004).

Although a relatively uncommon thermoregulatory strategy, sweating may therefore have played an extremely important role in our evolutionary history. Many animals, like the domestic dog, pant to cool off. Panting is a form of evaporative cooling where water evaporates off the highly vascularized upper respiratory tract. This evaporation transfers energy in the form of heat from the surface of the skin to the atmosphere, which cools the blood below the surface of the respiratory tract, decreasing the core body temperature of the animal (Lieberman, 2014; Wheeler, 1984). Long snouts and protruding tongues in some animals serve as extensions of the respiratory tract that evolved to increase the effectiveness of this cooling method. Animals will also take short, shallow breaths when hot, as this style of breathing facilitates the greatest thermoregulatory advantage. There are some disadvantages with panting, however, as these short shallow breaths can increase CO_2 build up in their lungs. There are also some locomotive behaviors, like galloping, that do not allow an animal to both pant and move at the same time, hence why some ungulates are able to sweat (Lieberman, 2014).

Primates, unlike other mammals, have a greater capacity to sweat. Sweating, like panting, is a form of evaporative cooling where secretions from sebaceous, apocrine, and eccrine glands are evaporated off the skin to cool off an animal's core body temperature. Primates primarily utilize eccrine sweating, especially catarrhines (Best and Kamilar, 2018), while some hooved animals sweat using apocrine glands (Lieberman, 2014). Most mammals are only able to develop eccrine glands on their palms, and sweating from these glands aids in functional gripping (Adelman et al., 1975). Catarrhines, though, have exaggerated the presence of eccrine glands on their body, which is expected given their utilization of hot, open, semi-arid environments. These hotter climates are also associated with increased capillarization of sweat glands (Best and Kamilar, 2018). For example, while chimps and macaques have identical eccrine gland density, chimpanzees have increased capillarization and glycogen content in their eccrine glands which increases their sweating capacity (Best and Kamilar, 2018). Even though other catarrhines have increased sweating capacity compared to other mammals, humans have enhanced their sweating capabilities even further (Kamberov et al., 2018).

Humans do not only sweat to cool off. There are multiple types of human perspiration, and thermal perspiration and evaporative cooling is just one of them. Diffusion of water is a constant form of human perspiration where water escapes from the skin and the lungs. Palmar-sole perspiration is the activation of eccrine glands located on the soles and palms of the feet of mammals. This form of sweating is controlled by the nervous system and is used to grip to surfaces while walking. Emotional sweating could be considered part of this palmar-sole perspiration system because, under appropriate stimuli, these sweat glands can be activated on the axillary region of the body and on the forehead (Folk and Semken, 1991).

Three different types of glands are utilized when humans sweat. Sebaceous glands are present across the entire surface of the body except on the soles and dorsum of the feet and the palms of the hands, though they are found most numerously on the scalp, forehead, cheeks and chin. These glands are located below the surface of the skin and empty directly onto the shaft of hair within the hair follicle, giving hair its oily and unwashed appearance. Sebaceous glands associated with beard follicles, however, open directly onto the surface of the skin (Folk and Semken, 1991; Harkey, 1993). Apocrine glands are often found located near sebaceous glands in regions of the body where apocrine glands are present (Folk and Semken, 1991). These areas include the axilla, the ear canal, the eyelids, and pubic and anal regions (Folk and Semken, 1991; Harkey, 1993). Located deep in the dermis near the base of the follicle, apocrine glands are large and spongy in appearance and have a duct that empties into the hair follicle (Folk and Semken, 1991). Secretions from the apocrine gland combine with sebaceous secretions and coat hairs in an oily mixture (Folk and Semken, 1991; Harkey, 1993). While the secretion itself is odorless, decomposition of the substance by specific species of bacteria produces the smell of body odor (Harkey, 1993). In most species, sebaceous and apocrine glands are the most active sweat glands, but this is not the case for humans (Folk and Semken, 1991). Eccrine glands, which humans possess 2-5 million of, are distributed across the entire body and do not associate directly with hair follicles (Best and Kamilar 2018; Folk and Semken, 1991; Harkey, 1993). These glands, which appear as small, coiled tubules, empty their watery secretions out of pores directly onto the skin (Folk and Semken, 1991; Harkey, 1993; Jablonski, 2010). These glands provide the most thermoregulatory benefits to humans (Best and Kamilar, 2018; Folk and Semken, 1991).

Though catarrhines sweat for thermoregulatory reasons (Best and Kamilar, 2018), making it appear as though hair loss is not required for thermoregulation, nakedness is essential to increase the efficiency of these cooling systems (Wheeler, 1984). The evaporation of sweat directly off the surface of skin, which is highly vascularized in humans, increases the effectiveness of sweating because the underlying blood is cooled directly. To get the same thermoregulatory advantage, a hairy individual would also have to use more water (Jablonski, 2010; Lieberman, 2014). This means that the loss of body hair could have saved hominins from water loss in dry weather conditions. The threshold for heat tolerance is also greater in naked individuals in extreme temperatures. In fact, temperatures where hairlessness would be most advantageous, 29-35°C, are the most typical on the African savanna. In less extreme temperatures, where the environmental temperature does not exceed the temperature of the body, being hairless also allows for cooling by non-evaporative means (Wheeler, 1992).

Other adaptations aid in hominin thermoregulation and may lend support to the thermoregulatory hypothesis. The first regards bipedal locomotion. During the height of the day, when the sun is directly overhead, bipedal posture minimizes the area of the body exposed to intense solar radiation (Dávid-Barrett and Dunbar, 2016; Wheeler, 1984; Wheeler, 1992). It also lifts the torso off the ground where wind temperatures are lower and wind speeds are greater, both of which may aid in the success of evaporative cooling (Wheeler, 1991). Utilizing an upright posture may also explain why head hair was retained, as it could have prevented the head and brain from sunburns and overheating (Wheeler, 1984).

Another hominin adaptation, increased cranial capacity, would have required the evolution of a cooling mechanism for our large brains. It may have even been the ability to cool our brains effectively that allowed it to grow (Jablonski, 2010). Maintaining the body temperature of the brain is extremely important, and it requires the most cooling relative to its size than any other organ. Because of its importance, Cabanac and Caputa (1979) have proposed the presence of a cooling method whereby cooled blood from the face and scalp flows back into the brain through small emissary vessels.

Though the thermoregulatory hypothesis is quite popular, it fails to address several problems. Keeping warm would have been a significant challenge on the savannas at night and other forms of insulation would have been required to make hair loss feasible (Dávid-Barrett and Dunbar, 2016; Wheeler, 1984; Wrangham, 2017). Luckily, humans have evolved a layer of subcutaneous fat that helps to insulate without impeding the function of sweat glands (Wheeler, 1984). Additionally, many hominin fossils have been discovered in the general vicinity of large paleolakes. Because lakes can have climatic effects by absorbing heat during the day and releasing it at night, they may have given hominins just enough heat during the night to obviate the need for artificial insulation or control of fire (Thiery et al., 2015).

There is also the problem of sexual dimorphism. The thermoregulatory hypothesis fails to explain why females have less hair than males. Some believe that endurance running and persistence hunting would have been done primarily by males, indicating that they were the driving selectors for hair loss, but the fact that females have less hair suggests that it was the females driving for the selection of this trait (Giles, 2010). However, because there is no evidence for the division of labor until later in the hominin fossil record (Kuhn and Stiner, 2006), the notion that females could not have been equally involved in the evolution of hairlessness is premature.

Lastly, sweating could have increased the risk of dehydration on the dry savanna (Dávid-Barrett and Dunbar, 2016; Elias et al., 2010). However, a study done by Hora and colleagues (2020) suggests that a *Homo erectus* individual could have run from 5 hours and 32 minutes to 5 hours and 40 minutes without drinking and only lose about 9% of their body mass along the way. This degree of dehydration would not be life threatening. While *H. erectus* might not have been limited by dehydration, the smaller bodied *Homo habilis* would have, suggesting that the ability to run long distances and persistence hunt may not have been possible prior to *H. erectus* (Hora et al., 2020). Because of this, proponents of the thermoregulatory hypothesis argue that substantial hair loss occurred with the emergence of this species roughly 1.85 million years ago (Hammond et al., 2021).

Naked Love Hypothesis

The naked love hypothesis argues that the transition to bipedalism was the first steppingstone in the evolution of hairlessness. Many infant primates will cling to their mother's fur shortly after they are born, so that their mother can navigate through her environment with her infant in proximity. Despite these grasping reflexes still present in human infants' hands and feet, when hominins became bipedal and lost their prehensile feet, their infants would no longer be able to grasp their mothers' fur. While a hominin mother could carry her infant, it is quite tiring, especially when traveling large distances and gathering food. Thus, mothers may have wanted to leave their infants behind, putting them at risk from predators, but if the mother had a strong desire to hold and carry the infant, then she would not leave her infant behind (Giles, 2010).

Skin-to-skin contact is extremely important and pleasurable for both mother and child. When there is full-naked skin-to-skin contact present during breastfeeding, there is less infant movement and crying, while the mother reports a higher amount of love, likely reflected by the greater release of oxytocin (UvnäsMoberg et al. 2020). Because this is so important, Giles (2010) proposes that the increased skin-to-skin contact experienced by less hairy mothers would have strengthened their connection to their infants and thus increased their desire to carry the infant. This form of selection is referred to as maternal selection, where the mother aids in an infant's survival over another because it is more pleasant to care for (Giles, 2010).

Further expansion of this hypothesis could also imply a sexual selection against hairiness. According to Giles (2004), adult sexuality is often first developed in the mother-infant relationship. Here they learn cuddling, caressing, and skin-to-skin contact. Perhaps having less hair makes the body more sexually attractive because of this increased pleasure developed through the naked relationship between mother and child, which would explain why females have less hair than males and why sexual intercourse between humans lasts much longer than it does in our closest living relatives, chimpanzees and bonobos (Giles, 2010).

Because the loss of the prehensile hallux is the catalyst for the loss of body hair according to this hypothesis, it is expected that the loss of hair would line up with the loss of this trait. This would suggest an early emergence of hairlessness in hominin evolutionary history, around the origins of *Australopithecus* over 4 million years ago (Lieberman, 2014).

Aquatic Ape Hypothesis

The aquatic ape hypothesis provides another possible explanation for the evolution of hair loss. Although it has not received much support, it has been suggested that around 5 to 8 million years ago (Verhaegen, 1985), our ancestors were living on the coast of East Africa and spent a lot of time in the water, evolving traits such as hair loss to aid them in this environment (Hardy, 1960).

While proponents may point to the three species of *Schistosoma* that parasitize humans as evidence of an ancient aquatic lifestyle, as they do not affect other great apes and depend on our species entering water to be transmitted (Ashford, 2000), there are several problems with the aquatic ape hypothesis. Perhaps most seriously, hairlessness evolved in cetaceans to reduce drag when traveling long distances in the water (Jablonski, 2010; Giles, 2010). Modern humans, who can do little more than paddle through the water, would not have seen a great advantage in losing their hair. It also doesn't explain why hominins retained these aquatic traits, such as hairlessness, following their exit from the water. Additionally, aquatic predators, like crocodiles, would have made living in this environment extremely difficult, if not impossible (Giles, 2010).

Melanin-Competition Hypothesis

Melanin, the protein responsible for skin and hair color polymorphic variation, is also useful in protecting the skin against high levels of ultraviolet (UV) radiation from the sun. This has resulted in the evolution of darker skin color in populations experiencing high levels of UV radiation, like those in sub-Saharan Africa, than in areas of the world with less UV radiation. It has also been found to reduce the function of hair follicles and the size and growth of hair. One study by Dhugga et al. (2014) found a strong relationship between follicle density and skin color, with darker skinned individuals tending to have lower follicle density. Short hair length also significantly correlated with darker skin. The authors of this study have posited that because terminal hairs do not always provide effective protection against UV radiation, melanin production increased in hominins. This increase in melanin competed with the growth of hair, reducing their size and thus explaining the difference in hair follicle density distribution across the world. Individuals with lighter skin were also found to have a greater variation in hairiness than those with dark skin. If the suggestions made by these authors are correct, then hair loss would correspond with the emergence of dark skin in the hominin lineage (Dhugga et al., 2014).

Sexual and Cultural Selection Hypotheses

Charles Darwin hypothesized that hair loss was the result of sexually selective pressures (Darwin, 1871). He did not believe hairlessness had any direct advantage to hominins, which, he argued, meant that natural selection was not the driver behind the emergence of this trait. Rather, males would have become more attractive to females with less hair and would only select less hairy mates, ultimately leading to universal hair loss, with stronger selection against hairy females. This would explain why human females appear to have less hair than human males (Darwin, 1871). This hypothesis does not explain why this beauty standard would be universal across the species (which it is not and almost certainly has never been), nor does it suggest a timeline by which hair loss occurred, making it difficult to analyze for the purposes of this review.

Another hypothesis suggesting a cultural selection for hair loss was presented by Harris (2006). She suggests that hair loss is quite novel in the hominin lineage, with Neanderthals possessing a thick coat, along with other adaptations allowing them to keep warm in the European and Asian landscapes during the Ice Age. Over time, when humans began to conceptualize themselves as people and Neanderthals as animalistic, they became determined to distance themselves from the likeness of Neanderthals by ridding themselves of body hair. As a result, any infants born were subject to parental selection and any hairy infants born were abandoned or killed. Sexual selection likely also played a role as males and females would have preferred less hairy mates. This would have resulted in the emergence of hairlessness very recently, perhaps as late as the emergence of *Homo sapiens* roughly 200,000 years ago, though not much earlier (Harris, 2006).

Evaluating the Timing of Hair Loss

There are several ways to go about determining which hypotheses are most likely to accurately reflect the evolution of hair loss. While looking at the strength of the supporting evidence for some might be helpful, it may not work as an effective evaluation tool for all of them because some hypotheses suggest active evolutionary pressures that might not show up in the archaeological record. A more efficient way to evaluate these hypotheses involves examining the evidence pertaining to the timing of hair loss. Determining when the trait emerged could allow us to discount hypotheses that don't predict nakedness occurring during the timeframe suggested by evidence. Several lines of evidence allow predictions on the timing of hair loss: molecular evidence from lice and the MC1R locus and anatomical and physiological evidence from the fossil record.

Molecular Evidence from Lice

Parasites can be important tools for investigating a given organism's evolutionary history, and the parasite proxy approach uses this line of evidence to make inferences about the history of a given host. Human lice, then, can give us insights into our past. It is important to keep in mind, however, that calibrating the molecular clock for such analysis is challenging because fossil evidence of parasites like lice is lacking (Perry, 2014).

Lice are small, wingless insects that infect birds and mammals, with each host having its own specific species (Weiss, 2009). Humans are parasitized by two different species of lice belonging to two different genera: *Pediculus humanus*, the head and body louse and *Pthirus pubis*, the crab or pubic louse (Allen et al., 2013; Reed, Smith, Hammond, Rogers, and Clayton, 2004). Head lice live on the scalp and feed frequently (Allen et al., 2013). Though rare, scratching a bite could lead to infection from typical skin bacteria (Meinking, 1999). Body lice, on the other hand, can be vectors of diseases including trench fever, typhus, and relapsing fever. Transmission of these diseases occur when lice feces are rubbed into an open wound, usually by the host scratching at a bite. Unlike head lice, body lice primarily live on clothing and only move to the skin once or twice a day to feed (Allen et al., 2013; Boutellis et al., 2014). Pubic lice live primarily in pubic hair as they prefer the widely spaced hairs present in this region. These hairs are easier for the lice to grasp, which allows them to easily flatten themselves against the skin (Allen et al., 2013). Because lice do not spend any portion of their lice cycle off the host (Allen et al., 2013), transmission typically occurs during moments of close bodily contact and high levels of infestation can occur in crowded environments, especially if the hygiene in these environments is low (Boutellis, Abi-Rached, and Raoult, 2014).

The evolution of human-parasitizing lice gives interesting clues about the evolutionary past of the African great apes and of hominins. Clothing, often viewed as a sign of sophistication and intelligence, is the driving evolutionary force behind the loss of hair in the vestiary hypothesis (Kushlan, 1985). Because body lice primarily live on clothing, it is safe to assume that their emergence signals clothing use in hominins. Using genetic analysis on the divergence times of head and body lice, Toups et al. (2011) determined this to have occurred 83-170 thousand years ago.

Lice can also tell us about the emergence of pubic hair. Pubic hair is believed to have developed during or after the emergence of nakedness, evidenced by the fact that both Old World and New World monkeys have fewer hairs in their pubic region than anywhere else on their body (Weiss, 2009). Therefore, specifically examining the history of the pubic louse can provide insight into human nakedness. The most likely scenario regarding the genetic history of *Pediculus* and *Pthirus* includes a duplication event 13 million years ago (Reed, Light, Allen, and Kirchman, 2007). When the *Gorilla* lineage and the *Homo* and *Pan* lineage split, *Pthrirus* became extinct in the latter lineage and *Pediculus* became extinct in the former. *Pediculus* then likely cospeciated with both *Pan* and *Homo* around 6.39-5.6 million years ago (Reed et al., 2007; Reed et al., 2004), which is reflected in their morphological similarity (Perry, 2014). *Pthirus* continued to exclusively parasitize the *Gorilla* lineage until roughly 3.32 million years ago (with a 95% confidence interval from 1.84-5.61 million years ago), when a crossover event occurred into the hominin lineage (Reed et al., 2007). The pubic hair of a modern human, which is coarser and more widely spaced compared to other regions of the body, is similar to the thick, widely spaced hairs of the gorilla, which may have made this host switch easier (Weiss, 2009).

The crossover event between gorillas and hominins implies the two occupied the same environment simultaneously, and how this occurred has also been the subject of some speculation. Allen et al. (2013) believe that the most likely hominin ancestor directly involved with the crossover event was *Australopithecus afarensis,* as they were habitat generalists and foraged on fibrous food. An *A. afarensis* group may have come across an infected gorilla nest and used it instead of building their own. There are problems with this scenario, though. If australopithecines used a nest only once, as is observed in the extant great apes, they would have had little need to reuse any nest, whether it be one made by their own species or otherwise (Allen et al., 2013).

Another possible explanation regarding the host switch could involve mixed-foraging groups between gorillas and *A. afarensis*. This has been observed between chimpanzees and gorillas, so it is arguable that this occurred occasionally between gorillas and hominins. The most interactive individuals within these groups are juveniles, who would not have had pubic hair, assuming that the development of australopithecine pubic hair is similar in modern humans. This means that the juvenile australopithecine would have had to acquire lice from a juvenile gorilla and then quickly transmitted it to an adult host, making this hypothesis unlikely (Allen et al., 2013). However, children can get infestations of pubic lice within their eyebrows, eyelashes, and the edges of their hairlines (Allen et al., 2013), which would potentially make a crossover event in this manner more plausible.

The most likely scenario, at least according to Allen et al. (2013), is that *A. afarensis* was involved in the scavenging of gorilla remains. Butcher marks on bones (McPheron et al., 2010) imply that hominins were involved in scavenging behaviors, at least occasionally (Jablonski, 2010). This behavior could have put them into contact with infested gorilla carcasses and provided an opportunity for the lice, which are extremely sensitive to their environments and are known to readily flee from dying hosts, to begin parasitizing the scavenging hominin. Such desperation on part of the lice would have made a host switch to an incorrect species more plausible (Allen et al., 2013).

Molecular Evidence from MC1R Locus

Melanocortin 1 receptor (MC1R) is a genetic locus responsible for coding for melanin, the protein involved in skin and hair pigmentation. The genetic history of this locus can be very valuable in determining when hair loss occurred in the hominin lineage. Because the melanin in our skin protects against harmful UV rays, the sun-resistant allele must have taken hold following the exposure of our skin to harsh sunlight (Dhugga et al., 2014). This would have occurred when hominins lost their hair because the LCA's skin may have been pale, as it is in many furry mammals, though the skin color of the LCA is still debated.

Though genetic evidence for the evolution of skin color has been hard to come by due to the sheer number of genes involved in coding for properties of the skin, there has been success in determining a lower bound for the MC1R variant found in some modern-day Africans (Jablonski, 2010). Rogers et al. (2004) determined a lower bound of 565,000 and 1.2 million years ago, though the former assumes an infinite African population at the time of the introduction of the mutant MC1R variant. Ultimately, this means dark skin has been present in the hominin lineage for at least 1.2 million years (Rogers, Iltis, and Wooding, 2004).

Anatomical and Physiological Evidence from the Fossil Record

The appearance of various anatomical and physiological changes in extinct hominins can also inform us about the evolution of hairlessness. Because several hypotheses discussed above link hair loss with bipedalism, it would be worthwhile to first discuss the timing and origins of bipedal locomotion. The earliest argued bipedal hominin, *Sahelanthropus tchadensis*, emerged roughly 6.8 to 7.2 million years ago (Best et al., 2019; Lieberman, 2014). Due to the poor condition of the *Sahelanthropus* cranium, the debate on its status as a hominin has been heavily debated. This debate has continued into recent years as analysis on other potential *Sahelanthropus* specimens has begun. Macchiarelli, Bergeret-Medina, Marchi, and Wood (2020) argue against the idea of a bipedal *Sahelanthropus,* and Daver et al. (2022) argue that *Sahelanthropus* was bipedal. Even so, by the time *Ardipithecus ramidus* emerges 4.5 to 4.3 million years ago, bipedal locomotion was well under way. The pelvis of *Ardipithecus* has laterally oriented ilia, which allow the small gluteal muscles to function as hip abductors, but retains the ancestral divergent hallux. The modern foot with an adducted hallux, associated with *Australopithecus afarensis* 3.9 to 3.0 million years ago further signals a commitment to a bipedal lifestyle (Lieberman, 2014).

As mentioned previously, sweating allows humans to vigorously exercise in the heat. It allows us to endurance run in high temperatures better than any other animal, and this ability clearly necessitates the ability to sweat effectively and, thus, implies hairlessness (Lieberman, 2014; Wheeler, 1984; Wheeler, 1992). Several traits in the fossil record can be evaluated in concordance with this trait. Traits associated with energy efficiency in humans, for example, include the Achilles tendon, a long spring-like tendon that attaches on the calcaneus and helps generate forces more economically. While we do not have any complete calcanei from early *Homo* to inform us of the length of the tendon, the attachment site for the Achilles tendon is very chimpanzee-like in the australopithecines, meaning that a long, human-like Achilles must have originated after 3 million years ago (Bramble and Lieberman, 2004). The longitudinal arch can provide aid in increasing energy efficiency by providing powerful plantar flexion during toe-off (Bramble and Lieberman 2004). This structure is observed to be partially present in australopithecines, such as in STW 57, and appears to be more human-like in *H. habilis* (Harcourt-Smith, 2002). Long legs also increase the energy efficiency of locomotion by increasing the optimum speed of walking and ground contact time. This trait first appears with *H. erectus* (Bramble and Lieberman, 2004).

Skeletal strength is also important when endurance running. The expansion of joint surface areas in the lower limb help spread the forces endured during vigorous running evenly over larger areas. *Homo* has relatively large articular surfaces in the femoral heads, knee, sacroiliac joint, and the lumbar centra. The expansion of joint surfaces in the upper body is not observed. Additionally, the iliac pillar is enlarged in *H. erectus*, which is associated with redistributing stresses (Bramble and Lieberman, 2004).

Endurance running requires a substantial ability to stabilize the body. In order to maintain stability with the large torques from the hips, the upper thorax and arms counter-rotate. This is aided by a narrow and elongated waist, which emerges with *Homo erectus*. The decrease in muscle attachments between the head and pectoral girdle in *Homo* also makes counter-rotating much easier. Wide shoulders aid in these counter-balancing movements and allows for the forearms to shrink in order to save energy. These wide shoulders are characteristic of *Homo* (Bramble and Lieberman, 2004). Head stabilization is also made possible by the nuchal ligament in *H. erectus* (Lieberman, 2014).

It is widely accepted that *Homo erectus* is the first hominin to possess modern body proportions, indicating that hominins had the ability to endurance run in a manner on par with anatomically modern humans by this point (Bramble and Lieberman, 2004; Lieberman, 2014). While early *Homo* possessed some anatomical features associated with increased ability to run more efficiently, it is really with *H. erectus* and later *Homo* that endurance running was possible.

Discussion

Hairlessness is undoubtedly an oddity among mammals and especially so among primates. The evolutionary pressures responsible for this trait's emergence in our lineage is still unknown, and there has been much speculation as to what those evolutionary pressures might have been. In order to evaluate these hypotheses, investigating external data regarding the timing of hair loss has served to be very helpful. Molecular and morphological data suggest hairlessness most likely occurred between 3.32 and 1.2 million years ago according to genetic evidence from lice and the MC1R locus, with the results of the anatomical and physiological data establishing a date of hair loss somewhere in between the two (Bramble and Lieberman, 2004; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004). Using these dates will allow for the elimination and critical evaluation of various hypotheses that were previously presented.

To begin, Darwin argued that being hairless serves no advantages and would have to be the result of sexual selection, as opposed to natural selection (Darwin, 1871). It is clear, though, that there are certainly advantages to being hairless. Sweating efficiency (Wheeler, 1984) and the ability to see and minimize parasitic infection (Allen et al., 2013; Boutellis et al., 2014; Brown, 2021; Reed et al., 2004) are some of the most obvious advantages, though whether those advantages affect the evolution of hair loss is another matter. Still, Darwin's assertion is probably incorrect.

Two hypotheses predicted hair loss occurring far too late in human evolution to account for the origins of nakedness. The vestiary hypothesis, proposed by Kushlan (1985), predicted that the loss of hair occurred roughly 500,000 years ago. Hominins were already involved in long distance running at this time, meaning they must have had efficient thermoregulatory ability, which necessitated naked skin (Best et al., 2019; Bramble and Lieberman, 2004; Jablonski, 2010; Kamberov et al., 2018; Lieberman, 2014; Wheeler, 1992). Furthermore, even assuming an infinite population size at the time of the mutation of the modern MC1R locus present in some parts of Africa, it would have taken 560,000 years to see the equilibrium of the gene at present (Rogers et al., 2004). Perhaps most problematic, analyzing the divergence of head and body lice leads to an estimate of the development of clothing around 170,000 to 83,000 years ago, much more recent than predicted by Kushlan (1985).

The other model, proposed by Harris (2006), hypothesizing that hair loss was the cause of parental selection against hairy babies, put hair loss occurring after the emergence of *Homo sapiens* roughly 200,000-300,000 years ago (Lieberman, 2014). As with the vestiary hypothesis, this is far too late in hominin's evolutionary history to be supported by the data. Furthermore, as the capacity to investigate the Neanderthal genome has increased, the selection for lighter skin and red hair that has been observed (Lalueza-Fox et al., 2007) suggests that they were under the same pressures for skin variation as modern-day Europeans, meaning they were already hairless.

Several hypotheses fall in line with the dates predicted by the evidence. The aquatic ape hypothesis, though highly popular in academic circles, is one such hypothesis. The aquatic ape hypothesis predicted that hair loss occurred 5 to 8 million years ago during an aquatic stage of hominin evolution (Verhaegen, 1985), and these dates fall in line with the evidence (Bramble and Lieberman, 2004; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004). The upper bounds of the 95% confidence interval of the lice data, which is 5.61 million years, overlap with the aquatic ape hypothesis by 400,000 years (Reed et a. 2007), but, while this may be compelling evidence in favor of this hypothesis, the overwhelming lack of evidence for this aquatic stage and the previously discussed problems it fails to address make the aquatic ape hypothesis implausible.

The naked love hypothesis, which predicted hair loss to occur shortly after the loss of the opposable hallux, as this would have forced hominin mothers to carry their infants (Giles, 2010), is another hypothesis that falls in line with the evidence. The opposable hallux seems to have been lost by *A. afarensis* 3.9-3.0 million years ago (Lieberman, 2014), which is fairly consistent with the lice data (Reed et al., 2007). While the first emergence of this australopithecine is a little older than the average predicted by the phylogeny of lice, it is still within the 95% confidence interval (Perry, 2014). Especially when considering the difficulty of calibrating the molecular clocks used in researching the genetic history of parasites (Perry, 2014), a date falling a little outside the window predicted by Reed et al. (2007) is not unexpected. Rather, the largest problem with this hypothesis is the assumption that skin-to-skin contact is necessarily innate. While it may be feasible that pleasure derived from skin-to-skin contact evolved in hominins to further facilitate the relationship between mother and infants, the idea that this would have existed right at the emergence of hair loss is unsubstantiated. If this hypothesis was accurate, hairlessness occurred because of the benefits that skin-to-skin contact provided, but there would be no reason for hair loss to occur if skin-to-skin contact was not beneficial from the start. There does not appear to be ample evidence to even suggest that this would be the case, though more research could be conducted to establish further understanding of the emergence of the benefits to skin-to-skin contact.

Ectoparasite hypotheses are also compelling responses to the issue of hominin hair loss, though they have pitfalls. Brown (2021) presents a hypothesis that suggests that hairlessness was the result of increased tick infestations with the LCA of modern humans and chimpanzees. While chimpanzee ancestors increased grooming practices, hominins lost their hair. With an estimated emergence from 5 to 8 million years ago (Brown, 2021), it only overlaps with the molecular lice data within its upper limit of 5.61 million years (Reed et al. 2007). This makes it difficult to immediately dismiss and, thus, more discussion of this hypothesis will be beneficial. The grooming practices of chimpanzees is especially interesting when investigating the validity of this hypothesis. Brown (2021) suggests that some populations of LCA increased their grooming practices to combat the increased prevalence of ticks, leading to the divergence of the two lineages. However, data suggest that grooming, especially in catarrhines, is much more socially dependent, and less related to hygienic factors. Time spent grooming is correlated significantly with group size, lending support to this idea (Dunbar, 1991). Gamble, Gowlett, and Dunbar (2018) argue that humans also socially groom one another, though through less conventional means. If this were the case, and it appears that the data lends its support, then the hypothesis proposed by Brown (2021) is unsubstantiated.

Another ectoparasite hypothesis, proposed by Rantala (1999), suggests that hair loss emerged roughly 1.8 million years ago with the habitation of a fixed home base. This falls within the 3.32-1.2-million-year range predicted by the evidence evaluated (Bramble and Lieberman, 2004; Jablonski, 2010; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004), but there is a major flaw with this proposal. Females would have been inhabiting those home bases, according to this hypothesis, and would have been more likely to interact with ectoparasites, increased selection for hairlessness (Rantala, 1999). While parasites may be more likely to spread in a sedentary living space, individuals could encounter most parasites, like lice, outside of a space occupied for a long period of time. Gorillas, for example, are parasitized by lice, despite utilizing single-use nests (Allen et al. 2013). There also is no evidence for this sort of labor division until the Upper Paleolithic, long after the period suggested by this hypothesis (Kuhn and Stiner, 2006). The most compelling evidence for this hypothesis, then, is the existence of the flea, *Pulex irritans*, as a human ectoparasite. This is because fleas, unlike lice, complete their life cycle off the host, requiring them to live near their host. In fact, humans are the only species of catarrhine to be parasitized by fleas (Rantala, 1999). The origin of this flea, however, appears to be in South America roughly 14,000 years ago (Buckland and Sadler, 1989), and more recent data seem to corroborate these earlier findings (Zurita et al., 2019). This means that human fleas started parasitizing hominins long after the emergence of anatomically modern humans, which discounts the ultimate suggestion made by Rantala (1999), whereby increased sedentism in hominins made them more susceptible to ectoparasites. As such, the strength of this hypothesis is diminished.

The melanin-competition hypothesis is also concordant with the data (Bramble and Lieberman, 2004; Dhugga et al., 2014; Jablonski, 2010; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004). While it appears to be sound, the idea that melanation of the skin emerged before hair loss began to occur is questionable, but it is not entirely implausible as great apes have decreased follicle density compared to smaller primates (Schwartz and Rosenblum, 1981) and may have less UV protection. More research into the effectiveness of chimpanzee hair at blocking UV radiation may shed light onto the sequence of skin melanation and hair loss proposed by this hypothesis. However, even though the melanin-competition hypothesis may not turn out to be the initial catalyst for hair loss, it would be premature to entirely dismiss the effect of melanin concentration on the reduced ability of follicles to produce terminal hair (Dhugga et al., 2014). Perhaps it is the case that another hypothesis explains the initial catalyst for hair loss, but that increased melanin concentration helped the process along.

This leaves the thermoregulatory hypothesis, which predicted hairlessness emerging roughly 1.85 million years ago with *Homo erectus*, as the most likely explanation for hominin hair loss (Hammond et al., 2021; Jablonski, 2010; Lieberman, 2014). This falls neatly within the dates suggested by evidence previously evaluated (Bramble and Lieberman, 2004; Jablonski, 2010; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004). It narrowly falls in the 95% confidence interval of the lice data which puts the lower limit at 1.84 million years (Reed et al., 2007), though it is much more easily associated with the physiological and MC1R dates (Bramble and Lieberman, 2004; Lieberman, 2014; Rogers et al., 2004). The strength of the thermoregulatory hypothesis is bolstered by the other thermoregulatory advantages that hominins have adapted as discussed previously in the section dedicated to summarizing this hypothesis (Bramble and Lieberman, 2004; Jablonski, 2010; Lieberman, 2014). *Homo erectus* clearly has physiological features that make activities associated with endurance running much easier than it would be for australopithecines, or even for earlier *Homo* (Bramble and Lieberman, 2004; Lieberman, 2014). As such sweating efficiency must have improved between the two, and because hairlessness is associated with increased sweating efficiency (Wheeler, 1984), it is likely that this is when the trait first appeared.

Conclusion

While many questions that pertain to human hairlessness remain unanswered, anatomical and physiological data from the fossil record and molecular evidence from lice and the MC1R locus indicate that hair loss occurred between roughly 3.32 million years ago and 1.2 million years ago (Bramble and Lieberman, 2004; Jablonski, 2010; Lieberman, 2014; Reed et al., 2007; Rogers et al., 2004). While some hypotheses can be dismissed due to lack of evidence or the need for further research, investigating some questions may shed light onto the evolution of this trait. The melanin-competition hypothesis could provide evidence for hominin hair loss, but it could also clear up our understanding of global hair distribution. Regardless, based on current knowledge, the analysis conducted in this review indicates that the thermoregulatory hypothesis provides the best explanation for the evolution of hairlessness. However, other selective pressures may have reinforced the selection of hair loss.

Acknowledgements

I thank Dr. Brigitte Holt for guidance and mentorship throughout the research process and composition of this paper.

References

Adelman, S., Taylor, C., & Heglund, N. (1975). Sweating on paws and palms: What is its function? *American Journal of Physiology-Legacy Content*, *229*(5), 1400–1402. https://doi.org/10.1152/ajplegacy.1975.229.5.1400

Allen, J., Worman, C., Light, J., & Reed, D. (2013). Parasitic Lice Help to Fill in the Gaps of Early Hominid History. In J. Brinkworth & K. Pechenkina (Eds.), *Primates, Pathogens, and Evolution*. New York, NY: Springer New York. Retrieved from http://link.springer.com/10.1007/978-1-4614-7181-3

Ashford, R.W. (2000). Parasites as indicators of human biology and evolution. *Journal of Medical Microbiology*, *49*(9), 771–772. https://doi.org/10.1099/0022-1317-49-9-771

Best, A., & Kamilar, J. M. (2018). The evolution of eccrine sweat glands in human and nonhuman primates. *Journal of Human Evolution*, *117*, 33–43. https://doi.org/10.1016/j.jhevol.2017.12.003

Best, A., Lieberman, D. E., & Kamilar, J. M. (2019). Diversity and evolution of human eccrine sweat gland density. *Journal of Thermal Biology*, *84*, 331–338. https://doi.org/10.1016/j.jtherbio.2019.07.024

Boutellis, A., Abi-Rached, L., & Raoult, D. (2014). The origin and distribution of human lice in the world. *Infection, Genetics and Evolution*, *23*, 209–217. https://doi.org/10.1016/j.meegid.2014.01.017

Bramble, D. M., & Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature*, *432*(7015), 345–352. https://doi.org/10.1038/nature03052

Brown, J. G. (2021). Ticks, hair loss, and non-clinging babies: A novel tick-based hypothesis for the evolutionary divergence of humans and chimpanzees. *Life*, *11*(5), 435. https://doi.org/10.3390/life11050435

Buckland, P. C., & Sadler, J. P. (1989). A Biogeography of the Human Flea, Pulex irritans L. (Siphonaptera: Pulicidae). *Journal of Biogeography*, *16*(2), 115–120. https://doi.org/10.2307/2845085

Cabanac, M., & Caputa, M. (1979). Natural selective cooling of the human brain: Evidence of its occurrence and magnitude. *The Journal of Physiology*, *286*(1), 255–264. https://doi.org/10.1113/jphysiol.1979.sp012617

Darwin, C. (1871). *The descent of man, and Selection in relation to sex, Vol 1.* London: John Murray. https://doi.org/10.1037/12293-000

Daver, G., Guy, F., Mackaye, H. T., Likius, A., Boisserie, J.-R., Moussa, A., … Clarisse, N. D. (2022). Postcranial evidence of late Miocene hominin bipedalism in Chad. Nature. https://doi.org/10.1038/s41586-022-04901-z

Dávid-Barrett, T., & Dunbar, R. I. M. (2016). Bipedality and hair loss in human evolution revisited: The impact of altitude and activity scheduling. *Journal of Human Evolution*, *94*, 72–82. https://doi.org/10.1016/j.jhevol.2016.02.006

Dhugga, A., Henneberg, M., & Kumaratilake, J. (2014). Variation of human hairiness: A possible adaptation to solar radiation and melanin. *Anthropological Review*, *77*(2), 219–232. https://doi.org/10.2478/anre-2014-0017

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, *57*(3), 121–131. https://doi.org/10.1159/000156574

Elias, P. M., Menon, G., Wetzel, B. K., & Williams, J. J. W. (2010). Barrier requirements as the evolutionary "driver" of epidermal pigmentation in humans. *American Journal of Human Biology*, *22*(4), 526–537. https://doi.org/10.1002/ajhb.21043

Folk, G. E., & Semken, A. (1991). The evolution of sweat glands. *International Journal of Biometeorology*, *35*(3), 180–186. https://doi.org/10.1007/BF01049065

Gamble, C., Gowlett, J., & Dunbar, R. (2018). *Thinking big: How the evolution of social life shaped the human mind*. London: Thames and Hudson Ltd. (Original work published 2014)

Giles, J. (2004). *The nature of sexual desire*. Westport, Conn: Praeger.

Giles, J. (2010). Naked love: The evolution of human hairlessness. *Biological Theory*, *5*(4), 326–336. https://doi.org/10.1162/BIOT_a_00062

Hammond, A. S., Mavuso, S. S., Biernat, M., Braun, D. R., Jinnah, Z., Kuo, S., … Palcu, D. V. (2021). New hominin remains and revised context from the earliest Homo erectus locality in East Turkana, Kenya. *Nature Communications*, *12*(1), 1939. https://doi.org/10.1038/s41467-021-22208-x

Harcourt-Smith, W. (2002). Form and Function in the Hominoid Tarsal Skeleton (Doctor of Philosophy, University College London). University College London. Retrieved from https://discovery.ucl.ac.uk/id/eprint/1383046

Hardy, A. (1960). Was Man More Aquatic in the Past? The New Scientist, 7(174). Retrieved from https://books.google.com/books?id=qUi12M-fpMsC&printsec=frontcover#v=onepage&q&f=false

Harkey, M. R. (1993). Anatomy and physiology of hair. *Forensic Science International*, *63*(1–3), 9–18. https://doi.org/10.1016/0379-0738(93)90255-9

Harris, J. R. (2006). Parental selection: A third selection process in the evolution of human hairlessness and skin color. *Medical Hypotheses*, *66*(6), 1053–1059. https://doi.org/10.1016/j.mehy.2006.01.027

Hora, M., Pontzer, H., Wall-Scheffler, C. M., & Sládek, V. (2020). Dehydration and persistence hunting in Homo erectus. *Journal of Human Evolution*, *138*, 102682. https://doi.org/10.1016/j.jhevol.2019.102682

Jablonski, N. G. (2010). The naked truth. *Scientific American*, *302*(2), 42–49. Retrieved from https://www.jstor.org/stable/26001896

Kamberov, Y. G., Guhan, S. M., DeMarchis, A., Jiang, J., Wright, S. S., Morgan, B. A., … Lieberman, D. E. (2018). Comparative evidence for the independent evolution of hair and sweat gland traits in primates. *Journal of Human Evolution*, *125*, 99–105. https://doi.org/10.1016/j.jhevol.2018.10.008

Kuhn, S. L., & Stiner, M. C. (2006). What's a mother to do? The division of labor among neandertals and modern humans in eurasia. Current Anthropology, 47(6), 953–981. https://doi.org/10.1086/507197

Kushlan, J. A. (1985). The vestiary hypothesis of human hair reduction. *Journal of Human Evolution*, *14*(1), 29–32. https://doi.org/10.1016/S0047-2484(85)80092-0

Lalueza-Fox, C., Ro¨mpler, H., Caramelli, D., Sta¨ubert, C., Catalano, G., Hughes, D., … Hofreiter, M. (2007). A melanocortin 1 receptor allele suggests varying pigmentation among Neanderthals. Science, 318(5855), 1453–1455. https://doi.org/10.1126/science.1147417

Lieberman, D. E. (2014). Human locomotion and heat loss: An evolutionary perspective. In R. Terjung (Ed.), *Comprehensive Physiology* (1st ed., pp. 99–117). Wiley. https://doi.org/10.1002/cphy.c140011

Macchiarelli, R., Bergeret-Medina, A., Marchi, D., & Wood, B. (2020). Nature and relationships of Sahelanthropus tchadensis. Journal of Human Evolution, 149, 102898. https://doi.org/10.1016/j.jhevol.2020.102898

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., … Béarat, H. A. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*(7308), 857–860. https://doi.org/10.1038/nature09248

Meinking, T. L. (1999). Infestations. *Current Problems in Dermatology*, *11*(3), 73–118. https://doi.org/10.1016/S1040-0486(99)90005-4

Miller, S. L., & Maner, J. K. (2010). Scent of a Woman: Men's Testosterone Responses to Olfactory Ovulation Cues. *Psychological Science*, *21*(2), 276–283. https://doi.org/10.1177/0956797609357733

Perry, G. H. (2014). Parasites and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *23*(6), 218–228. https://doi.org/10.1002/evan.21427

Prokop, P. (2016). Male preference for female pubic hair: An evolutionary view. *Anthropologischer Anzeiger*, *73*(2), 169–175. https://doi.org/10.1127/anthranz/2016/0583

Randall, V. A. (2008). Androgens and hair growth. Dermatologic Therapy, 21(5), 314–328. https://doi.org/10.1111/j.1529-8019.2008.00214.x

Rantala, M. J. (1999). Human nakedness: Adaptation against ectoparasites? *International Journal for Parasitology*, *29*(12), 1987–1989. https://doi.org/10.1016/S0020-7519(99)00133-2

Reed, D. L., Light, J. E., Allen, J. M., & Kirchman, J. J. (2007). Pair of lice lost or parasites regained: The evolutionary history of anthropoid primate lice. *BMC Biology*, *5*(1), 7. https://doi.org/10.1186/1741-7007-5-7

Reed, D. L., Smith, V. S., Hammond, S. L., Rogers, A. R., & Clayton, D. H. (2004). Genetic analysis of lice supports direct contact between modern and archaic humans. *PLoS Biology*, *2*(11), e340. https://doi.org/10.1371/journal.pbio.0020340

Rogers, A. R., Iltis, D., & Wooding, S. (2004). Genetic variation at the mc1r locus and the time since loss of human body hair. *Current Anthropology*, *45*(1), 105–108. https://doi.org/10.1086/381006

Rosinger, A. Y. (2020). Biobehavioral variation in human water needs: How adaptations, early life environments, and the life course affect body water homeostasis. *American Journal of Human Biology*, *32*(1). https://doi.org/10.1002/ajhb.23338

Schwartz, G. G., & Rosenblum, L. A. (1981). Allometry of primate hair density and the evolution of human hairlessness. *American Journal of Physical Anthropology*, *55*(1), 9–12. https://doi.org/10.1002/ajpa.1330550103

Thiery, W., Davin, E. L., Panitz, H.-J., Demuzere, M., Lhermitte, S., & van Lipzig, N. (2015). The impact of the african great lakes on the regional climate. *Journal of Climate*, *28*(10), 4061–4085. https://doi.org/10.1175/JCLI-D-14-00565.1

Toups, M. A., Kitchen, A., Light, J. E., & Reed, D. L. (2011). Origin of clothing lice indicates early clothing use by anatomically modern humans in africa. *Molecular Biology and Evolution*, *28*(1), 29–32. https://doi.org/10.1093/molbev/msq234

Uvnäs-Moberg, K., Ekström-Bergström, A., Buckley, S., Massarotti, C., Pajalic, Z., Luegmair, K., … Dencker, A. (2020). Maternal plasma levels of oxytocin during breastfeeding—A systematic review. PLOS ONE, 15(8), e0235806. https://doi.org/10.1371/journal.pone.0235806

Verhaegen, M. J. B. (1985). The aquatic ape theory: Evidence and a possible scenario. Medical Hypotheses, 16(1), 17–32. https://doi.org/10.1016/0306-9877(85)90036-2

Weiss, R. A. (2009). Apes, lice and prehistory. *Journal of Biology*, *8*(2), 20. https://doi.org/10.1186/jbiol114

Wheeler, P. E. (1984). The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution*, *13*(1), 91–98. https://doi.org/10.1016/S0047-2484(84)80079-2

Wheeler, P. E. (1991). The thermoregulatory advantages of hominid bipedalism in open equatorial environments: The contribution of increased convective heat loss and cutaneous evaporative cooling. *Journal of Human Evolution*, *21*(2), 107–115. https://doi.org/10.1016/0047-2484(91)90002-D

Wheeler, P. E. (1992). The influence of the loss of functional body hair on the water budgets of early hominids. *Journal of Human Evolution*, *23*(5), 379–388. https://doi.org/10.1016/0047-2484(92)90086-O

Wrangham, R. (2017). Control of fire in the paleolithic: Evaluating the cooking hypothesis. *Current Anthropology*, *58*(S16), S303–S313. https://doi.org/10.1086/692113

Wyart, C., Webster, W. W., Chen, J. H., Wilson, S. R., McClary, A., Khan, R. M., & Sobel, N. (2007). Smelling a Single Component of Male Sweat Alters Levels of Cortisol in Women. *Journal of Neuroscience*, *27*(6), 1261–1265. https://doi.org/10.1523/JNEUROSCI.4430-06.2007

Zurita, A., Callejón, R., García-sánchez, Á. M., Urdapilleta, M., Lareschi, M., & Cutillas, C. (2019). Origin, evolution, phylogeny and taxonomy of Pulex irritans. Medical and Veterinary Entomology, 33(2), 296–311. https://doi.org/10.1111/mve.12365