Review

Ancient adaptations of human skin: why do we retain sebaceous and apocrine glands?

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Introduction

Paleodermatology, from the Greek root "*paleo*" (ancient), is an appropriate term for the study of cutaneous evolution, including the evaluation of physiology, thermoregulation, and structure.[1]

Human evolution has been characterized by a marked decrease in body hair and an increase in the importance of pigment in the naked epidermis as a shield against the harmful effects of solar radiation.[1] Humans are not hairless and, when we use this term with respect to humans, it means the lack of a dense layer of thick fur.[1,2] The number and density of hair follicles are similar to those of our nearest primate relatives; the uniqueness of human skin is that human body hair is miniaturized, very fine, and short, and the skin appears to be naked.[2] In addition, human skin contains a special distribution of sudoriparous eccrine glands which, together with the decrease in body hair, creates a very specific thermoregulatory method that allows us to deal very well with high temperatures, even in situations of strenuous physical activity.[1–3]

These classical and critical features of human skin, such as the hairlessness and large increase in the number of eccrine glands, are not the only adaptations observed. The other characteristics of human skin, however, such as the retention of apocrine and sebaceous glands, are not as obvious or easy to explain.

The critical point: heat regulation

Early mammals were probably small and likely depended on behavioral mechanisms for the control of body temperature, as still observed today in hippopotamuses and elephants, which use the aquatic environment to regulate body heat, or felines, such as lions and leopards, which avoid a large amount of physical activity during the hottest periods of the day.[1,2] As the range of early mammals extended beyond the forests, however, they became exposed to larger amounts of solar radiation. Thus, particularly in the setting of exercise, mammals required new evaporative heat loss mechanisms for the prevention of hyperthermia.[1] The first of these mechanisms probably was panting, as this is widespread in other mammals and in birds. Until species increased in size, this form of evaporative loss was adequate.[2,4] In open environments, large mammals survive by using cool venous blood which drains from the nasal mucosa to reduce the temperature of blood entering the brain through the carotid arteries.[4] Another technique used by many animals is saliva spreading, mostly amongst marsupial species.[4]

Sweating, together with an increase in the number of eccrine sweat glands, is the most effective evaporative heat loss mechanism, and is very useful for keeping the brain cool in tropical and equatorial environments.[1] Other animals, such as horses and cattle, can also use sweating for thermoregulation in a limited way.[3,4]

Heat is exchanged between an organism and its environment by physical processes, such as radiation, conduction, convection, and evaporation.[1–4] The physiologic control of heat exchange depends mainly on postural adjustments which alter the surface area available for heat transfer.[1] Changes in insulation caused by piloerection and variations in cutaneous blood flow are also important to modify the process of heat transfer.[3,4]

Humans possess two to four million eccrine sweat glands, which are distributed over nearly the entire body surface.[3,4] Early in the fifth fetal month, eccrine sweat glands appear in the axillary skin and, a few weeks later, elsewhere on the body.[4] The palms and soles contain the highest concentration of eccrine glands, followed by the scalp and chest.[4,5] A well-acclimatized person can sweat as much as 2.5 L per hour.[5] The secretory activity of the human eccrine sweat glands consists of two major functions: the secretion of an ultrafiltrate of a plasma-like precursor fluid in response to acetylcholine, and the reabsorption of sodium in excess water by the duct, producing hypotonic skin surface sweat.[5,6] Under extreme conditions, when the amount of perspiration reaches several litres a day, the ductal reabsorptive function assumes a vital role in conserving electrolytes.[6–8]

The control system for all of this activity is located at the preoptic hypothalamic area and plays an essential role in regulating body temperature: local heating activates generalized sweating, vasodilatation, and polypnea, whereas local cooling of the preoptic area causes generalized vasoconstriction and shivering.[6–8] This neurologic apparatus exists in many mammals, but is quite sensible in humans and probably evolved together with the skin adaptations already discussed to form one of the most developed heat regulation systems in nature, perfectly able to protect the progressively increasing brain from overheating.

Naked skin in humans

An insulating layer of body hair is important for thermoregulation in most animals.[1,2,9] Naked aquatic animals, such as whales and dolphins, are an important exception because they are characterized by a large size, which provides low thermal conductance.[1–3] Amongst nonaquatic mammals, naked skin appears to be an adaptation which facilitates heat loss in special conditions; for example, naked mole rats and armadillos, and other burrowing animals, spend most of their lives underground.[10]

These considerations do not apply to hominids, and so our naked skin evolved for a different reason. Most anthropologists believe that bipedality was a critical adaptation in response to the human need to forage on low-density or scattered resources in equatorial environments.[1,10–13] Fossil foot bones from early hominids confirm that bipedality existed four million years ago,[14] and possibly well before this period if we consider the recently described postcranial fossil findings of *Ardipithecus ramidus kadabba* (5.2–5.6 million years ago) and *Sahelanthropus tchadensis* (seven million years ago).[14] Bipedalism was, according to Wheeler,[10–12] a preadaptation to the loss of body hair. This anatomical modification was probably related to climatic changes that transformed a wet environment of forests into dry savannah.[1,2,10–14]

Recent ergonometric evaluations comparing walking energetics and biomechanics for adult chimpanzees and humans have demonstrated that bipedalism is more efficient and reduces the energy cost of walking compared with our ape-like ancestors.[15–17] Human walking is 75% less costly than both quadrupedal and bipedal walking in chimpanzees, and this variation is explained by biomechanical differences in anatomy and gait, with the decreased cost of human walking attributable to our more extended hip and longer hindlimb.[15] An evaluation of the cost of locomotion (COL), measured as the mass-specific rate of oxygen consumption (mL O_2/kg/m), reveals that COL is four times greater in chimpanzees with quadrupedal locomotion than in human walking (0.19 vs. 0.05).[15] Analyses of these features in early fossil hominids, coupled with analyses of bipedal walking in chimpanzees, have indicated that bipedalism in early ape-like hominids may indeed have been less costly than quadrupedal "knucklewalking" that is typical of all apes except humans.[15,17]

Another important point to consider is that a body shape capable of reducing sun exposure would be very advantageous. An animal with a bipedal posture possesses the ideal body form, as the major axis of the body has been rotated from a horizontal to a vertical position.[1–3] In addition, in a bipedal position, a greater proportion of the body surface is higher above the ground; this position helps to increase the rate of heat loss by both evaporation and forced convection.[1,5,6] In many ways, it is possible to consider bipedality itself as a thermoregulatory adaptation to life in hot environments.[1] The functionally naked skin of humans, with its wide distribution of eccrine sweat glands, provides the necessary cooling defense against hyperthermia.[1] Although most savannah animals possess cutaneous sweat glands, the thermoregulatory effectiveness of these glands is reduced by pelage, which restricts air flow over the skin surface.[1,3]

Pagel and Bodmer[18] have proposed that humans possibly also evolved hairlessness to reduce parasite loads, especially ectoparasites that may carry diseases. Fleas and ticks affect animals directly by biting and causing local irritation, and indirectly by carrying a variety of infectious diseases. Primates devote substantial amounts of time to grooming, increasingly so as the group size increases, mostly to remove ectoparasites.[18] Early humans probably lived in close quarters as hunter–gatherer social groups in which rates of ectoparasite transmission were high.[19] This initial naturally selected evolution towards a decreased amount of body hair may then have been reinforced by other cultural adaptations unique to humans, such as the use of clothes. It is possible that sexual selection acted as a positive selective pressure towards hairlessness as reduced ectoparasite loads became a desirable trait in the mate. The common use of depilatory agents nowadays testifies to the continuing attraction of hairlessness, especially in human females.

The paradox of the apocrine glands

Apocrine sweat glands are important for most mammals, including primates. The only two mammals capable of sustained running are horses and humans.[20] Copious sweat is produced in horses by the apocrine glands and in humans by the eccrine glands. Humans have one of the lowest density of apocrine glands amongst all primate species; the localization of these glands to restricted hairy regions, and the fact that they do not appear to be stimulated by heat exposure, make it difficult to determine their exact function.[1]

The apocrine sweat glands of sheep and goats respond to heat exposure in an unusual manner in that sweating appears to consist of a relatively large synchronized series of moisture discharge onto the surface of the skin. The quantity of sweat is small and not very effective in dissipating heat. Thus, by comparison with the sweating capability of humans, this type of sweat gland appears to be somewhat "primitive."[3] The anatomical structure of apocrine glands, directly connected to the hair structure, and the fact that secretion is mostly associated with the release of smell, probably readapted apocrine glands to functions related to territorial marking or to part of an alarm reaction, whereby danger was communicated to others in the group, leaving eccrine glands with the function of heat control.[3,20] Cultural evolution in hominids and the development of language, as well as the use of clothes, reduced the importance of apocrine glands in their original function.

By examining the thermoregulatory significance of apocrine and eccrine glands in many mammals, it is apparent that two patterns of evolution have occurred. In furred animals, the apocrine glands have taken over the role of temperature regulation as animals have increased in size and the need for an additional mode of evaporation has developed because of the size-related constraints on panting as a heat loss mechanism.[3,20] The evolution of thermoregulatory sweating in humans and anthropoid primates shows a different mechanism. The disappearance of hair from the face and body has been accompanied by the spread of eccrine glands and a decrease in apocrine glands.[4–6] The loss of panting in humans may be related to the development of speech, as panting and a highly developed speech mechanism would be incompatible because of the necessary reduction in the nasal passages to accommodate a larger brain.[3–6]

Nevertheless, we still need to explain why apocrine glands remain in humans despite the fact that they apparently lost their physiologic importance a long time ago. In the long evolutionary history of humans, powerful selection factors would have operated on hunter–gatherers who relied on sustained endurance running to hunt medium-sized mobile game.[20] On a hot savannah plain, success would have attended those hunters best able to defer dehydration and resist the extreme thermoregulatory challenge. Adaptation to contain the loss of sweat drops from the body surface would have been crucial. An unstable sweat drop that falls to the ground is a sweat drop wasted in a tropical environment, as it will have contributed little to the evaporative cooling of the skin surface and its loss will hasten dehydration. The retention of sweat on the skin surface will be encouraged by anything that lowers the surface tension of the sweat, so that it forms a sheet rather than drops. The oily secretion from apocrine glands is likely to have emulsifying properties and probably fulfills a surfactant role and discourages drop formation.[20,21]

Why do we still have sebaceous glands?

In humans, sebaceous glands are found over much of the body surface. They have an uncertain role, but the fact that they are under complex hormonal control argues against their vestigial nature.[4,20–23] They are usually associated with hair follicles and are particularly well developed in certain areas, such as the scalp, face, and, to a lesser extent, the upper back and chest.[22,23] It may be noted that, in a naked human, these are areas which are most exposed to the weather and rain.[23] It is interesting to emphasize that the progressive size reduction of the hair in humans was not followed by a corresponding decrease in the size of sebaceous glands, which are very large and responsive to hormonal stimuli, as observed in many diseases, such as acne, hidradenitis suppurativa, and Fox–Fordyce disease.

The sebum from sebaceous glands also contributes to surfactant action in a similar manner to apocrine gland secretion. Below 30 °C, the fluid consistency of the sebum changes and suddenly assumes either a solid or highly viscous character; however, at and above 30 °C, sebum acts as a potential emulsifier of sweat because its surface tension decreases to about 25 dyn/cm.[3,20,21] Thus sebum seems to have at least three thermoregulatory roles. The first is to coat the straight hair of northern populations and create a water-repellent pelage.[3,20,21] Southern populations have nonmatting helical scalp hair which serves the double function of reflecting sunlight whilst at the same time allowing the "breeze-over-body," generated by running, to penetrate the hair and cool the sweaty scalp. Second, at higher temperatures, sebum acts as a surfactant for eccrine secretions.[3,20,21] Third, at lower temperatures, in its viscous form, sebaceous secretion acts as a local repellent of rain on exposed skin.[3,21] It may be postulated, therefore, that the outcome of secretory interactions is for an externally generated fluid, rain, to be projected off the skin in cool wet conditions, whereas, in hot conditions, the internally generated fluid, eccrine sweat, is encouraged to spread in a film across the skin and to be retained on the surface.[21] There is a rapid emulsification of skin lipid and sweat, but the process is much slower for skin lipid and distilled water.[4,20] Emulsification also occurs much more quickly at a temperature of 33 °C than at lower temperatures.[21]

This represents a very efficient temperature-dependent switch in function on the part of the sebum, and was probably selected in our ancestors as a "second-line adaptation" when hairlessness and the large increase in the amount of eccrine glands were in the process of being established or already established.

Conclusions

Human skin adaptations, including the retention of sebaceous and apocrine glands, are the result of ancient physical modifications to climatic and environmental changes over the last four to seven million years, mostly restricted to the tropical savannah in Africa. These skin adaptations probably coevolved together with bipedality and other physical changes, such as those described on the teeth, skulls, and joints of the lower limbs, which can be easily observed in fossils.[2,14]

Most human skin adaptations are related to the critical importance of dealing with heat loss and the need to avoid hyperthermia during physical activity.[1,2] Naked skin and a massive increase in the amount of eccrine glands over the body surface were the two most critical modifications, but the retention of both apocrine and sebaceous glands was also important in this process, probably because of the surfactant properties of their secretions, which help sweat to spread in a film across the skin and to be retained on the surface.[20] This sweat film is a very effective evaporative heat loss mechanism based on convection, and its effectiveness is largely increased by the presence of sebum on the surface of the epidermis.

Other secondary effects, such as the reduction of infestations by ectoparasites and sexual selection, probably helped to maintain these new characteristics in later hominids of the human lineage.[18] Although the skin and other soft tissues are not fossilized, as are bones and teeth which can be studied directly, cutaneous adaptations can be inferred from the study of other mammalian features and by the observation of the physical modifications that occurred in the hominid lineage. That is the aim of paleodermatology, a multidisciplinary subject that encompasses dermatology, anthropology, physiology, and orthopedics, amongst others.[1]

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