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The evolution of sweat glands*

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Abstract. Mammals have two kinds of sweat glands, apocrine and eccrine, which provide for thermal cooling. In this paper we describe the distribution and characteristics of these glands in selected mammals, especially primates, and reject the suggested development of the eccrine gland from the apocrine gland during the Tertiary geological period. The evidence strongly suggests that the two glands, depending on the presence or absence of fur, have equal and similar functions among mammals; apocrine glands are not primitive. However, there is a unique and remarkable thermal eccrine system in humans; we suggest that this system evolved in concert with bipedalism and a smooth hairless skin.

Key words: Evolution – Paleophysiology – Primates – Sweating – Thermoregulation

Water is lost through the skin of all mammals by perspiration but the mechanism is quite varied. In humans for example, there are four perspiration "systems" controlling this water loss: (1) water diffusion directly from capillaries to the environment; (2) body surface sweating from two specialized glands, apocrine and eccrine (thermal sweating); (3) palmar-sole sweating from concentrated eccrine glands; and (4) emotional sweating also produced from localized eccrine (and apocrine) glands in the axilla (armpit) and on the forehead. In this paper we will describe: (i) the four "systems" of perspiration, (ii) the distribution, anatomy, and biochemistry of eccrine and apocrine glands, and (iii) the possible evolution of sweat glands using evodence from comparative mammal physiology, and then attempt to answer the following questions: Are eccrine glands derivatives of apocrine glands. Is apocrine sweat as efficient as eccrine sweat for body temperature control. Is eccrine and apocrine sweat, in theory, equally functional under a heavy coat of hair. Is eccrine sweat a co-evolutionary development with bipedalism and the smooth hairless skin of *Homo sapiens*? Two other physiological phenomena which relate to temperature regulation, mainly panting and the innervation of the sweat glands, are not discussed.

Four systems of human perspiration

Diffusion water. The first system is that of diffusion water which occurs at all times from human skin and from the lungs. Although it varies with atmospheric pressure, this insensible perspiration plays an appreciable role in heat dissipation (Folk 1974).

Thermal sweating. The second system of evaporative cooling depends on distinctive sweat from both apocrine and eccrine glands. One or the other of these types of glands, or both, may have a broad distribution over the body of mammals; they are activated gradually upon exposure to heat. Although both have multiple functions, in this paper we will confine our attention to their thermal function with one exception noted below.

Palmar-sole sweating. The third system depends on the eccrine glands located on the palms or plantar surfaces of mammals which are separately controlled by the nervous system. This system has the function of providing an adhesive surface for grasping and walking; thus some writers refer to the palm and sole surfaces as friction areas.

Emotional sweating. The fourth system is considered by some to be part of the palmar-sole eccrine system, which under appropriate stimuli, are separately activated in the axilla and on the forehead. Kuno (1956) merely asked his subjects to do arithmetic problems to activate this system. Kuno's concept is especially demonstrable by individuals in a cold room who, although being chilled, sweat under the arms and on the forehead, probably because of nervousness.

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Types of human sweat glands

There are three kinds of glands in human skin, sebaceous, apocrine, and eccrine. Sebaceous glands are evenly distributed over the body but are not involved in thermal sweating. They are not present on the palms and soles, although there may be as many as 900/cm^2 on the scalp and face. Sebaceous glands usually are anatomically near an apocrine gland which, in turn, is almost invariably associated with a hair follicle. Because they coat each hair with oil (sebum) as it grows, the sebaceous glands also are called oil glands.

The apocrine gland is distinguished from the eccrine gland by means of its large and spongy appearance, its location deep in the dermis, a duct that leads to the hair follicle associated with the sebaceous gland, and a distinct secretion. Because of this location, the term "epitrichial" (which means "by the hair") has been proposed for apocrine glands. The products of the sebaceous and apocrine glands are mixed as they appear on the surface of the hair follicle.

There are a few apocrine glands scattered throughout the body of humans, such as in the pubic and anal regions, but most of them are concentrated in the axilla. Here there is an extensive complex of large apocrine glands together with an equal number of eccrine glands; this aggregation is called the axillary organ and it is found only in humans, gorillas, and chimpanzees. It is little developed in the orangutan and absent in all other primates. Within the axillary organ, the apocrine glands respond to psychic stimuli, while the eccrine glands respond to both thermal signals and stress (Leidal et al. 1982).

Although apocrine glands contribute little to thermal cooling in humans, they are the only effective sweat glands in hoofed animals such as the donkey, cow, horse, and camel (Bullard et al. 1970). In the human fetus, however, at 5 to 5.5 months, apocrine glands are distributed nearly everywhere on the body; after a few weeks most disappear except in the restricted locations. It has been proposed that the ancestorial hominids had apocrine glands widely distributed over the body and that the axillary glands are embryonic rudiments. Apocrine glands are tubular in form; they secrete a milky, viscid, gray or reddish fluid which dries in glistening droplets with a glue-like consistency. When mixed with sebum it is more liquid and forms a lather which serves a cooling function; this lather is seen on the surface of heat-exposed horses. Fat is included in the secretion in the form of fatty acids including baleric, caproic, and caprylic acids. In short, the apocrine glands in human subjects are vestigial except in the armpit; in naked ancestral hominids, probably they were scent glands that secreted in response to stress and to sexual stimulation and today still serve that function.

The eccrine gland is also tubular in form, is smaller than the apocrine gland, and lies in the outer region of the dermis. Humans have two to five million eccrine glands over the body with an average distribution ranging from about 150 to 340/cm^2. All sweat glands are formed before birth and serve the individual for a lifetime. Eccrine glands are most numerous on the palms and soles, then in decreasing order on the head, trunk, and the extremities. They are abundantly distributed between the hairs of the scalp in humans and over the body of the lower primates. Some individuals have more glands than others; also, some have a large number of glands which although apparently normal, are actually functionless.

The composition of sweat from human eccrine glands (thermal glands), always has a lower concentration of sodium and chloride than that found in blood plasma; the chloride content corresponds to a 0.2% or 0.3% solution (about 5 to 100 mEq/l). There is a tendency for the salt concentration in sweat to decrease with human acclimatization to heat. On a hot day in the desert most humans can produce 12 l of eccrine sweat at a rate of 1 l/h; maximal capacities are given as 3.5 l/h (Eichna et al. 1945). Some subjects apparently can produce only 0.5 l/h (Moss 1924). This dilute eccrine solution will clearly be more effective under a heavy coat of hair or fur or on a naked skin than apocrine secretion, because of more rapid evaporation. Kuno (1956) doubts the presence of any fat in eccrine secretions.

To summarize the difference between the two types of glands, the apocrine gland is found deep in the dermis of the skin and is invariably associated with a hair follicle; the eccrine is shallow in the dermis and opens to the surface through its individual pore. The greatest difference between the two glands is in their secretions; a very dilute, watery, and copious fluid is produced by the eccrine glands and a less copious, viscous, and somewhat oily secretion is produced by the apocrine glands.

Apocrine versus eccrine glands

A typical situation and the physical environment

Apocrine glands in humans have been assumed to be the relics of a waning organ system, which was retained only by those mammals that did not develop eccrine glands for the dissipation of heat (Montagna and Parakkal 1974); examples include the donkey and the camel. Both of these are associated with climates that vary diurnally from very hot to very cold; the daytime air temperature may be 40–45° C, bare ground temperature 60–70° C, and the night-time air temperature 10–15° C (Ladell et al. 1944). In such an environment apocrine glands usually dominate as the main source of evaporative cooling. Those species also have a thick coat of hair (65 mm in the camel and 20 mm in the donkey). An apocrine dominated system is not surprising as these glands are always associated with hair and especially with heavy fur coats of this sort (Robertshaw 1985).

Are apocrine glands primitive?

The fact that the human fetus temporarily supports apocrine glands led some workers to designate the apocrine system as a primitive organ (Harrison and Montag-

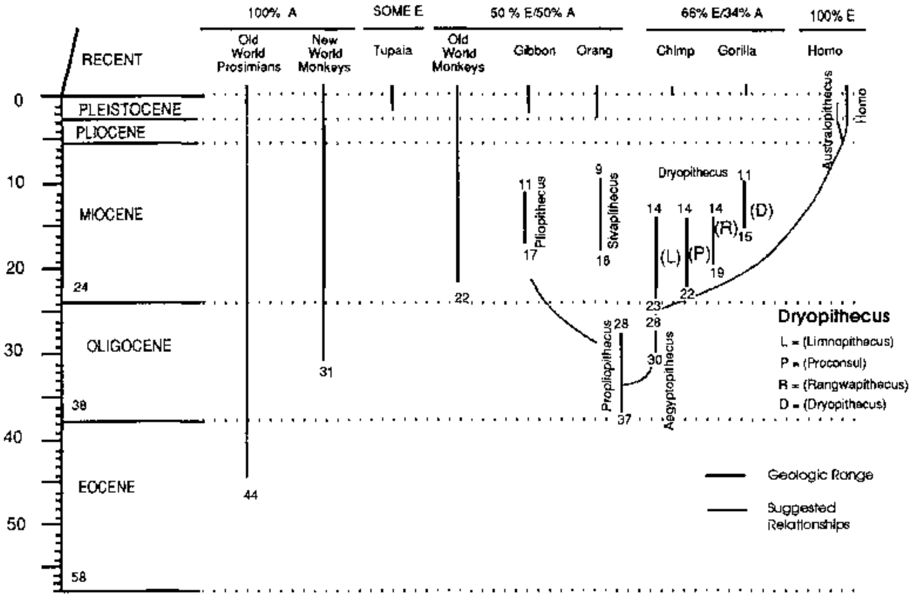

Fig. 1. The chart shows the present-day distribution of apocrine (A) and eccrine (E) sweat glands among the primates along with suggested ancestral relationships. The relative abundance of sweat glands was derived from Kuno (1956), Harrison and Montagna (1969), Montagna and Parakkal (1974), and Whittow (1971). Possible evolutionary relationships were taken from Carroll (1987), Ciochon and Fleagle (1987), Philbeam (1984), and Szaley and Delson (1979). The geological timescale is based upon Van Eysinga (1975) and Woodburne (1987)

na 1969). However, the skin of the most primitive living mammal, the egg-laying duck-billed platypus, has well differentiated apocrine glands associated with its body fur; it also has typical functional eccrine sweat glands. The tree shrew, *Tupaia*, believed by most workers to be the best living representative of early primates, also has nearly as many eccrine glands as apocrine glands in its hairy skin. The condition of the platypus and tree shrew illustrate that the two types of glands in early mammals 65 million years ago probably were separate organs with different functions. We deduce that considering mammals as a whole, both eccrine sweat glands and apocrine glands probably date at least to the Paleocene and were equally specialized at that time. Any eccrine derivation from an apocrine gland would pre-date the Tertiary and hence the whole evolutionary time-scale of primate development. This illustrates the danger of trying to reconstruct the phylogenetic history of any organ system by study of modern species.

The apocrine glands found in human subjects, in histological terms, are classical examples of apocrine glands and show no sign of a degenerative tendency. Although Sato et al. (1987) state that the human apocrine gland is slightly modified to produce more fluid as in the eccrine gland, there apparently has been evolutionary change in the apocrine glands in some taxa. In prosimians (Fig. 1), there is a ratio of one thermal apocrine gland in its hair follicle, associated with 20 hair follicles without any apocrine glands. Eccrine glands are also present in humans, but there is one apocrine gland for each hair follicle, although there are a few apocrine glands that are not associated with hair follicles.

Are apocrine glands efficient?

The composition of the sweat from the apocrine gland and the volume of water produced is very different from that of the eccrine gland. In spite of a much lower production of water, the apocrine gland is still effective as a cooling organ. For example, in one study the highest sweating rates were as follows: 0.6 mg/cm^2 per min from donkey; 0.4 mg/cm^2 per min from camel; 0.25 mg/cm^2 per min from cattle (Whittow 1971). In another study the water used from these glands to dissipate heat, when corrected for diffusion water loss, was as follows: the percent of body weight/day devoted to evaporative cooling was 1% in the camel, 4.5% in the donkey, and 7% for the human eccrine glands (Yousef and Dill 1969). There was obvious water conservation on the part of the camel and the donkey, but this cannot be attributed solely to the presence of apocrine glands. These sweat glands work exquisitely in concert with the protective fur insulation, as will be discussed in a later section. Furthermore, the camel and the donkey can both preserve their plasma volume in the heat, which is not the case with humans (Yousef et al. 1970).

Apocrine and eccrine sweating in lower primates

There have been few studies of sweating in lower primates possibly because of the erroneous idea that they do not sweat. As late as 1981, Schwartz and Rosenblum stated that there is "an absence of effective thermal sweating in most monkeys and apes." This error devel-

Table 1. The body locations for sweating in some lower primates with examples of typical sweating values, combining the apocrine and eccrine contributions (Gisolfi et al. 1982)

Species	Location
Stump-tailed macaque	General body surface
Japanese monkey	General body surface
Baboon	General body surface
Squirrel monkey	Only palms and soles
Rhesus macaque	Chest 0.04 (mg/cm^2 per min) Leg 0.05 (mg/cm^2 per min)
Patas monkey	Chest 0.38 (mg/cm^2 per min) Leg 0.28 (mg/cm^2 per min)

oped because some species were studied after being maintained under constant conditions in animal rooms (22° C). It was learned that they must be heat acclimated in order to be able to produce copious sweat (Gisolfi et al. 1985). Furthermore, the monkey which sweats most profusely, the patas, has only recently been studied (Gisolfi et al. 1982). All old world monkeys that have been studied have in their fur both apocrine and eccrine glands (Fig. 1). Examples of the amounts of sweating are given in Table 1; the sweating of the patas monkey is two to six times higher than in the rhesus, and the patas eccrine glands are larger than those of the rhesus (Sato et al. 1990).

Apocrine versus eccrine sweating rates

It is now relevant to compare the maximum sweating rates (in g/m^2 per h) of apocrine compared with eccrine glands of four different species. For apocrine glands these are: sheep 32, horse 100, cow 150, antelope 30 120 (6 species). For eccrine glands, from five human exercise laboratories, these are: 366, 500, 540, 573, and 884 (Folk 1974, p 247). Some of this sweating took place under a heavy coat of wool or hair and a question that should be asked is: how efficient is this process?

Many desert animals have heavy insulating fur, as do many higher primates. When desert animals are in strong sunlight their fur insulation will cut down on environmental heat gain. This was easily demonstrated in an experiment by Schmidt-Nielson (1964); when the fur was removed from two camels which were then reexposed to heat on the desert, they evaporated 50% more water than they did prior to shearing in order to maintain a regulated body temperature (3 l/day per 100 kg body weight compared with 2 l/day per 100 kg). The principle of the use of clothing as a heat barrier was also shown with human subjects; Adolph showed that men wearing light khaki clothing in sunlight had 55% less heat gain than nude men (Folk 1974).

How efficient is sweating underneath this insulation? The principles would be he same whether they were apocrine secretions or eccrine secretions. The most efficient evaporative cooling occurs at the skin surface; water vapor is then transferred through the fur to the atmosphere. The skin surface will be cool and the highly vascular skin will bring heat from the core of the body to the site of evaporation. Meanwhile, the dry fur insulates the body against inward environment heat flow. However, if the fur is wet from sweating, then maximum evaporation occurs at the surface of the fur at some distance from the skin. Now heat from the blood vessels is impeded in its transfer to the site of evaporation. Thus, much more body water must be used for cooling. Such a situation is easily seen when a horse "lathers up" from apocrine sweat (a condition seen even in winter as horses labor through deep snow drifts). The moral is that there would be an advantage under exercise conditions to an *absence* of fur insulation when the conditions are the heat of the desert. The first situation (i.e., a desirable evaporation *at* the skin) is more apt to occur when camels and donkeys remain quiet on the desert. We see from the above that there is a penalty to pay when they must exercise vigorously in strong sunlight (i.e., the fur is wet down). In our studies of cold weather physiology we often use the expression "a tropical man in arctic clothing" to describe the situation when a heavily dressed person must exercise in the cold (Folk 1974). The reverse situation exists on the desert as "the tropical camel must exercise in arctic fur."

There is, however, some behavioral protection under these circumstances, which is related to the length of fur; camels and donkeys in the desert have thick fur and are apt to plod slowly while in sunlight; horses and zebras in the tropics have shorter fur and are apt to exercise more vigorously. However, in humans there is a mechanism that favors exercise and sweating under a heavy coat of insulation; Shkolnik et al. (1980) showed an important bellows or chimney effect to explain the enhancement of convection beneath the robes of Arab natives. This mechanism also applies in part to the loose fur of sled dogs that run in the cold.

Reduction in insulation as an aid to sweat glands

Analysis of the relations between apocrine glands and heavy insulation must also include the night-time environment; here the donkey and camel are exercising under the heat sink of the night sky. In a model that is based upon loose clothing on human subjects (and it applies to the 6 cm of hair on a camel), Belding et al. (1947) showed that in an environment cool enough to cause water vapor to condense, evaporation would not be fully effective and there would be inefficiency of sweating. An example will suffice: the work for 2 h of a human subject was 163 kcal/kg per h under cool circumstances with heavy insulation; the sweating rate was 235 g/h. However, this sweat was only 65% effective (compared to work in the heat), even though the final mean skin temperature was 32.8° C. In this experiment the initial rectal temperature was 37.0° and the final was 37.4° C. This inefficiency can be partially counteracted by the lowering of insulation due to the air movement. This was substantiated when total clothing insulation in one experiment was reduced from a resting value of 2.5 Clo to 1.25 Clo when subjects ran at 6 miles/h. To check upon the accuracy of this experiment we built a physical model in the form of a heated cylinder with dimensions approximating those of a human arm. This cylinder could be driven back and forth to simulate the movements of a limb. Four layers of insulation, analogous to thick camel hair in a cool environment, were loosely attached to the cylinder. When the cylinder was still, the insulation value was 1.7 Clo; when it was moving at the frequency of limb movement when walking at 3.5 miles/h, the insulation was 0.9 Clo, a 47% reduction in insulation due to the movement. Thus we see that thick fur has an advantage as a heat barrier in strong sunlight and also there are compensatory mechanisms which come to the fore when this insulation must be tolerated during exercise.

In more detail, Cena and Monteith (1975) and Clark et al. (1973) describe a method for measuring energy fluxes, thermal resistances, and conductivities of animal coats and human clothing to complement calorimetric studies of energy balance. Gebremedhin (1985) has carried the analysis further; this model for animal coats assesses not only the appropriate environmental variables but also six basic structural properties of the fur layer. The model shows a prediction accuracy of better than 10% of measured values. A totally different approach was used to study just the lower primates by Schwartz and Rosenblum (1981); they counted the hairs per unit area of 23 primate species. Increasingly massive primates were found to have systematically fewer hairs per equal unit of body surface, an adaptation to overcome thermal constraints imposed by the decreasing ratios of surface area to volume in progressively massive primates (see also following section).

Bipedal evolution

What was the evolutionary pathway from four-footed furry mammals thermally protected by apocrine glands to a bipedal naked mammal protected by eccrine glands? The approach must be speculative (Ciochon and Fleagle 1987). Because bipedal progression is very common among reptiles, birds, and many mammals (e.g., the arctic hare and the kangaroo rat), none of which have eccrine glands (except possibly on the feet), it is clear that there is no direct relationship between the bipedal position and eccrine glands. However, there is obviously a special advantage to bipedalism since it occurs in a striking variety of unrelated forms. Humans are unique as the only living bipedal mammal with both a naked skin and a totally eccrine-dependent cooling system.

When did the presumed ancestors of present-day humans become bipedal? There is an excellent set of approximately 3 500 000-year-old footprints at Laetoli, Tanzania, which indicate that an upright pre-human biped was present (Fleagle 1988) at that time. The lightly built creature who produced these tracks now is referred to as *Australopithecus afarensis*. Although these animals could walk bipedally, the skeleton of *A. afarensis* (and that of closely related *A. africanus*) "was intermediate between those of living apes and humans, suggesting that these early hominids were both arboreal climbers and terrestrial bipeds" (Fleagle 1988, p 418). Both species lived in an open environment and were vulnerable to predators such as the large cats, but their way of life must have been successful since they remained largely unchanged for almost two million years (Fleagle 1988). During the latter part of their reign, they were joined by a larger and stronger bipedal species, *A. robustus* (Fig. 2). This species and a somewhat later but still larger species, *A. boisei*, were more "bipedal and less aboreal than *A. afarensis*" (Fleagle 1988, p. 426). Another genus, *Homo habilis*, then appeared in east Africa and lived alongside *A. boisei*. *H. habilis* had a distinctly human-like foot and is interpreted as primarily bipedal. It did retain relatively large hands and maintained some suspensory attributes. Totally erect posture apparently occurred still later with *Homo erectus* and became refined in *H. sapiens*.

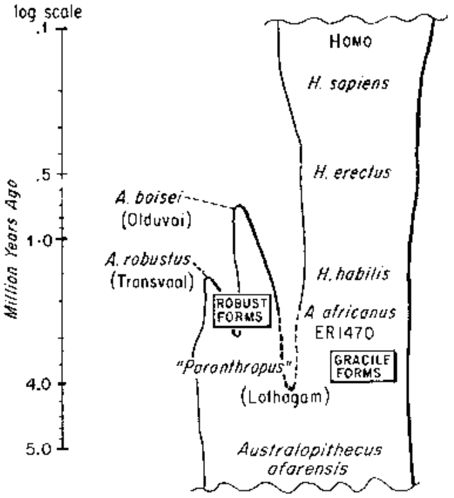

Fig. 2. This model of late Pliocene/Quaternary human relationships, one of a number that have been proposed, would allow the robust australopiths to maintain a heavy fur coat and permit the gracile forms to have reduced body hair. Alternatively, both could have been involved in fur reduction (diagram modified from Grahame Clark)

The next question is why this transition to bipedalism occurred. Apparently these early ancestors of man, including some of their predecessors, began to venture from forested to more savanna/parkland situations. In more open country, bipedal animals have an advantage in that an individual can stand up to search for predators, navigate visually, move rapidly over open expanses, reach higher for forage, and carry and use implements, weapons, or food. Along with living in a savanna habitat, the ancestors of *H. sapiens* apparently changed their feeding habits and behaviour so that they added hunting and scavenging to supplement the vegetarian aspect of their diet.

Life on a savanna required covering long distances rapidly, and necessitated an advanced system for thermal cooling. For this kind of life the most copious water-producing gland possible would be advantageous. We have shown in an earlier section that the eccrine gland serves this function well. One need only see the remarkable films of the stone-age men of the Kalahari running for hours after a wounded giraffe (two full days of chase) in order to understand the value of the copious secretion of the eccrine gland to such a life-style.

Hairless skin

At this point it is pertinent to question the extent of insulation on the ancestors of humans. A reasonable clue can be sought with the great apes that share ancestry with *H. sapiens*. It is notable that the chimpanzee, the gorilla, and the baboon carry heavy fur coats. They function well as raincoats and two of these species tolerate a 6-month period of rainfall with dry skin. Dense fur also protects the animals from thorns and brush. As noted earlier, bipedalism became effective with the transition from a forested to a drier savanna habitat. It also is clear that there are advantages to surface evaporation from a wet naked skin with exercise in a hot environment; thick hair with apocrine sweat protects against heat but only until vigorous exercise is initiated; at this time the entire coat becomes wet and maximum evaporation is transferred from the skin to the coat/air interface. Nakedness is more advantageous with activity if it can be shielded by garments to protect against solar radiation.

The loss of body hair is easily linked to loss of apocrine glands but acquiring widely distributed eccrine sweat glands is not. Many now "hairless" mammals (e.g., elephants, rhinos, domestic pigs, and mole-rats), which presumably lost their body hair during the evolutionary process, do not use thermal sweat glands in cooling; none of these, however, move rapidly for extended periods of time. What then was the pathway for hair loss and eccrine sweat development as the primary cooling device in the human family? There was probably no single cause; but perhaps the trend was started by initiation of a small bias toward hairlessness in a primate in which eccrine glands were already widespread (Fig. 1).

As noted earlier, one adaptive reward is related to volume/surface ratios because heat loss is strongly controlled by this factor (Schwartz and Rosenblum 1981). Large primates must dispel vast quantities of core-generated heat through a comparatively tiny shell. Since monkeys and apes, if heat acclimatized, are perfectly capable of sweating, then hair loss (and therefore the loss of associated apocrine glands) could easily be combined with an increase in eccrine sweating. The only alternative of *H. sapiens* to reducing a high radiant heat intake by reflective means was to ensure efficient heat loss by evaporative cooling. Natural selection would permit a further reduction of a remnant coat to its present vestigial condition, except in areas involved with display.

The evolution of eccrine glands

The probable factors in temperature regulation in the *Australopitheus-Homo* complex are displayed in the generalized chart of primate evolution (Fig. 1). All prosimians, monkeys, and apes have thermal apocrine glands associated with hair; all also have eccrine glands, at least on the friction surfaces of the hands, feet, and tail; the great apes have them distributed over the body. Thus, the building material was present in great apes to provide a generous supply of eccrine glands to the ancestors of *Homo*. Montagne and Parakkal (1974) stated: "probably the evolution of sweat glands has not followed a single path from a common origin but may have gone along parallel or convergent paths." The path for the chimpanzee and the gorilla has resulted in a distribution of over 60% eccrine glands; that for monkeys, the gibbon, and orangutan involves a 50/50 distribution. If these apes evolved into hairless animals, their skin would contain only eccrine glands because the linked apocrine component would be lost; there are no thermal apocrine glands which are not associated with hair follicles. By this evolutionary sleight of hand a thermally modern hominid with a smooth, relatively hairless skin supplied only with eccrine glands would be achieved. In other words, hominids evolved to the point of losing body hair, and synchronously lost thermal apocrine glands; thermal eccrine glands were then "favored". Another question that remains is why eccrine glands are present, although generally functionless without acclimation, in old world "simians"; possibly there was another "savanna" genus with naked skin earlier in the Tertiary.

Conclusion

From the evidence of comparative mammalian physiology, we suggest that the very common apocrine sweat gland is not primitive but is both specialized and efficient as a cooling organ in an animal with a heavy fur coat and relatively slow movement. The remarkable thermal eccrine sweating system of humans probably evolved in concert with bipedalism, a smooth hairless skin, and adaptation to open country by the ancestors of *H. sapiens*.

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