13 Body Hair Reduction and Tract Orientation in Man: Hydrodynamics or Thermoregulatory Aerodynamics?

Peter E. Wheeler

SUMMARY

The alleged hydrodynamic advantages of both the sparsity and the alignment of human body hair are frequently cited in favour of the theory that some early hominids lived in water. This hypothesis can be challenged on thermoregulatory grounds alone. It is extremely unlikely that naked-skinned hominids would be energetically viable as aquatic mammals, because of the large surface area to volume ratio resulting from their relatively small size and elongate body form. Alternatively, both the sparsity and the orientation of human body hair can be satisfactorily explained as thermoregulatory adaptations evolved by a large-brained savannah primate to facilitate essential evaporative cooling. In this context, by opposing the direction of natural convection currents rising up the body of a bipedal hominid, the hair tracts may have maximised airflow over the wetter skin surface during the evolutionary period when body hair was being progressively reduced.

INTRODUCTION

There are two ways in which the covering of body hair on modern man differs from that of all other living primates. The first, and most obvious, of these is that, although follicles are still present, the hair emanating from them is so sparse that over most of the body the underlying skin is exposed directly to the environment. The second difference is in the alignment of these hair tracts. This is most easily seen in the covering of body hair, or lanugo, developed by the human foetus during the sixth month and normally shed before birth. On the lower human trunk the hair tracts do not run in parallel down the body, but are inclined diagonally inwards towards the mid-line on both the back and the abdomen (Figure 13.1). However, the extent of this subtle, although significant, realignment should not be overstated.

Both these features were among the key pieces of evidence cited by Hardy (1960) in proposing his aquatic hypothesis of human evolution. In its present form this hypothesis, which has been expanded and elaborated by various authors (Morgan, 1972, 1982, 1987; LaLumiere, 1981; Morris, 1977; Verhaegen, 1985), suggests that between about 4 and 8 million years ago ancestral hominids became adapted to life in the water, before returning to a terrestrial existence. Although most modern adherents of these ideas appear to believe that this period of our

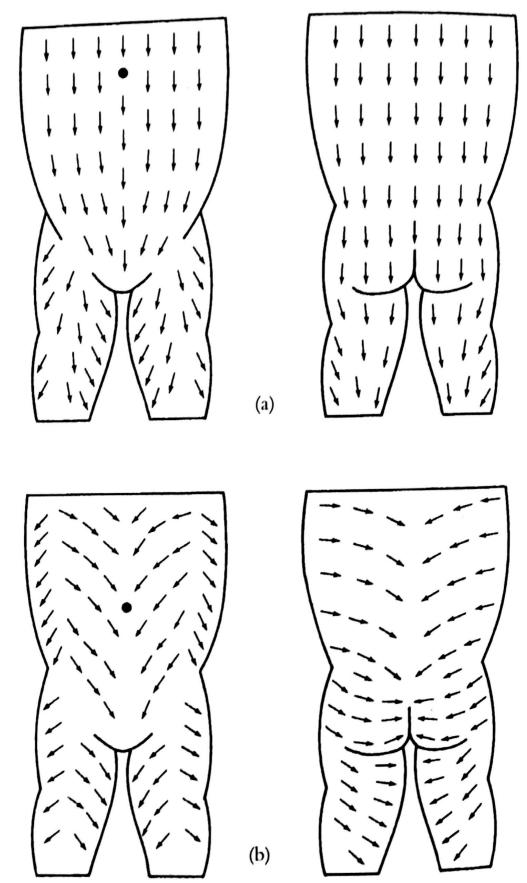


Figure 13.1 Schematic diagrams of the alignment of the major hair tracts on the trunk and limbs of (a) the African apes (Gorilla gorilla shown here) and (b) modern man.

The main difference is that on man these tracts converge diagonally towards the mid-line of the body on both its dorsal and ventral surfaces. (See also Hardy, 1960.)

evolutionary history was spent in marine, rather than freshwater, environments, there appears no general agreement on other aspects of the ecology envisaged for these aquatic apes. For example, if they were swimming and diving in open water they would have been subject to selection pressures very different from those which would have prevailed

if they simply foraged by wading in relatively shallow water.

Within the context of this aquatic hypothesis, both the reduction and the realignment of body hair are interpreted as hydrodynamic adaptations to reduce the drag of the hominid when moving through the water. The loss of functional body hair would have prevented a static boundary layer of fluid from being trapped next to the skin, thereby allowing a freer movement of water over the body surface. The proposal is that, during the transitional period when this reduction was taking place, streamlining was improved by aligning the remaining tracts to follow the path that this flow of water is claimed to have taken over the body (Hardy, 1960). Such a change would only have been selectively advantageous if relatively fast swimming, with the body in a horizontal position, was important to survival. It would have been of no benefit if the hominids spent their time in shallow water with the trunk held upright. However, despite these potential hydrodynamic advantages, there would have been other physical factors in operation which make it extremely unlikely that the human naked skin could have evolved in water.

THERMOREGULATORY PROBLEMS OF AQUATIC MAMMALS

If an aquatic mammal is to evolve a naked skin, the hydrodynamic benefits must outweigh the costs that may be incurred. For a higher vertebrate the most significant of these is the higher rate of heat transfer from its body to the surrounding fluid, because of the higher thermal conductivity of water. This presents two major thermoregulatory problems to any aquatic mammal. First, its zone of thermal neutrality that is, the range of environmental temperatures across which it can regulate core temperature just by modulating its conductance - is much narrower in water. This is due to an increase in the lower critical temperature, the temperature below which homeothermy can only be maintained by additional metabolic heat production. Consequently, at all environmental temperatures below this lower critical temperature the energetic costs of life in water will exceed those experienced on land. This difference, which translates directly to a higher food requirement, will continue to increase as environmental temperature falls. Second, since endogenous heat production cannot continue to increase indefinitely, a temperature will be reached below which exposure will

result in death from hypothermia. This lethal limit at which summit metabolism is attained will be considerably lower on land than in the water.

Therefore, a mammal immersed in water must either be able to produce more heat than its terrestrial counterpart, and sustain the additional energetic costs that this involves, or reduce its rate of heat loss. Consequently, a dense coat, together with the insulating boundary layer of fluid that it traps next to the skin, is retained by the majority of aquatic and amphibious mammals. Despite claims to the contrary (Hardy, 1960) these are not just low-temperature species requiring this insulation for the periods they spend out of water. In fact, the only aquatic mammals to have lost most of their body hair are the cetaceans, sirenians, hippopotamuses and a few of the larger pinnipeds (Wheeler, 1985). The reason why the balance of selection pressures is different in these forms, and favours the evolution of a naked skin, is their body mass. Larger animals possess lower thermal conductances (Herreid and Kessel, 1967; Bradley and Deavers, 1980), primarily as a direct consequence of their lower surface area to volume ratios. They are also better able to carry a thick insulating layer of fat or blubber. Although man is better endowed with fat than other primates, its development is extremely limited in comparison with pinnipeds and cetaceans, in which it can comprise up to 50 per cent of total body mass (Kanwisher and Sudnes, 1968; see also Pond, this volume, chapter 12).

Because surface area to volume ratio has such a major influence on the rate of heat loss, all these naked-skinned aquatic mammals display marked specialisations of body shape. Most are extremely fusiform, with a rotund shape and reduced, or even completely lost, external limbs. This adaptation, which minimises the area of skin in contact with the water, has the double advantage of both reducing heat loss and improving the hydrodynamic profile of the animal. However, an associated penalty is that its potential for terrestrial locomotion is usually lost or severely

compromised.

Despite this reduction in size, the appendages of aquatic mammals are still a potential major site of heat loss because of their comparatively high surface area. However, excessive heat loss is usually prevented by regional heterothermy (Scholander and Schevill, 1953; Irving, 1973), a thermoregulatory strategy also employed by many terrestrial higher vertebrates in cold climates (Irving, 1966). This entails bringing the warm arterial blood supply entering a limb into close contact with the cool venous blood draining from it within a vascular network, or rete, located at its base. The resulting counter-current exchange greatly reduces the flow of body heat from the well insulated core into the appendage. This allows the temperature of the extremity to be held well below that of the rest of the body, thereby reducing the temperature

gradient, and consequently the rate of heat flow, between it and the surrounding water. In the case of species inhabiting cold waters, this may entail the limbs operating below 5°C. To enable them to remain functional at these reduced temperatures, alterations of tissue biochemistry are necessary (Irving, Schmidt-Nielsen and Abrahamson, 1957).

Of particular importance are changes in the membrane composition of the excitable cells of the neuromuscular system, which would otherwise experience cold-block and be unable to conduct action potentials (Chatfield, Lyman and Irving, 1953; Miller and Irving, 1963; Miller and Dehlinger, 1969). Despite these modifications their functioning cannot be considered as completely normalised, since the speeds of impulse transmission and muscle contraction will still be somewhat lower than at more normal temperatures. This is not usually too much of a problem, as the appendages of marine mammals are generally rather simple structures used for propulsion and for maintaining directional stability. The considerably more complex human limbs lack vascular retes at their bases, although some limited counter-current heat exchange can take place between the large blood vessels within the arm (Bazett, 1968). Together with a general vasoconstriction of the extremities, this allows the distal portion of the limb to fall to 20-25°C during exposure to low environmental temperatures. Although this has the advantage of conserving energy (Keatinge, 1969), it results in a progressive impairment of the normal manipulative ability and sensitivity of the fingers as their temperature drops below that of the core. Some cold-adapted racial groups are able to retain considerable dexterity of the hand during coldexposure (Eagan, 1966; Steegman, 1975), a response which can be enhanced by previous thermal acclimation (LeBlanc, 1975). However, this is achieved by restoring the hand's warm arterial blood supply to keep its temperature above that of the surrounding water. Therefore, during immersion the circulation can either reduce heat loss from the hand or maintain its manipulative abilities, but not both. This argues strongly against the suggestion (Hardy, 1960) that the dextrous and sensitive human hand evolved as an aquatic adaptation for foraging on the seabed.

Even when regional heterothermy is utilised in conjunction with such morphological adaptations as large size, fusiform body shape and thick subcutaneous insulation, it appears that marine mammals still require additional physiological specialisations to cope with the energetic demands of life in the water. The few available data show that pinnipeds and cetaceans possess resting metabolic levels at least twice those characteristic of other eutherian mammals (Kanwisher and Sudnes, 1968; Mount, 1979). In contrast, the more sluggish sirenians have a relatively low metabolic rate associated with a labile core temperature, which is

allowed to fall as water temperature drops below about 22°C (Macdonald, 1984). There is no evidence that the early hominids pursued either strategy, as both the metabolism and core temperature of man are typical of other terrestrial eutherians. However, some coldadapted racial groups do allow their body temperatures to fall slightly, by about 2°C, during periods of cold stress (Hong, 1963; Hammel, 1964).

THE ENERGETICS OF HOMINIDS IN WATER

In view of this conspicuous lack of the specialised thermoregulatory adaptations possessed by aquatic mammals, it is not surprising that death from hypothermia is an all too frequent consequence of prolonged immersion in water (Keatinge, 1969). The energetic reasons for this unfortunate outcome can be clearly seen in Figure 13.2 (a). This shows representative values for the effect of environmental temperature on resting metabolic rate for an adult weighing approximately 70 kg (although there is considerable individual variation). It should be noted that the depicted relationship has been somewhat simplified, as there is no abrupt transition from conductance-modulated to heat-productionmodulated thermoregulation in man (Hardy, Stolwijk and Gagge, 1971), making it difficult to define the lower critical temperature (TLC) with precision. In air, heat production starts to increase at air temperatures lower than about 25°C (Mount, 1979). Since sustainable thermoregulatory metabolism in man is approximately three times basal metabolic rate (BMR) (Swift, 1932), prolonged exposure to temperatures down to about 2°C can be tolerated (Burton and Edholm, 1969). Immersion in water results in an approximate threefold increase in thermal conductance, which raises the TLC to around 33°C (Burton and Bazett, 1936). Assuming that thermogenic capacity in the water is the same as on land, this means that summit metabolism will be attained in water as warm as 25°C. Below this temperature, heat loss will exceed production and there will be a decline in core temperature, resulting in death from cardiac arrest when it reaches about 25°C (Burton and Edholm, 1969). It is generally accepted that most unclothed individuals cannot tolerate long-term exposure to water below about 20°C, although the heat produced by strenuous muscular activity will allow survival for limited periods at even lower temperatures (Keatinge, 1969). When considering human potential as an aquatic mammal, it must be remembered that survival at these water temperatures should not be equated with ecological viability. The situations discussed above all assume that sufficient energy reserves are continually available to fuel the necessary high levels of thermogenesis, and therefore that food supply is never a limiting factor. This is extremely unlikely to be the case, and although it may be theoretically possible to survive in water at 20-25°C,

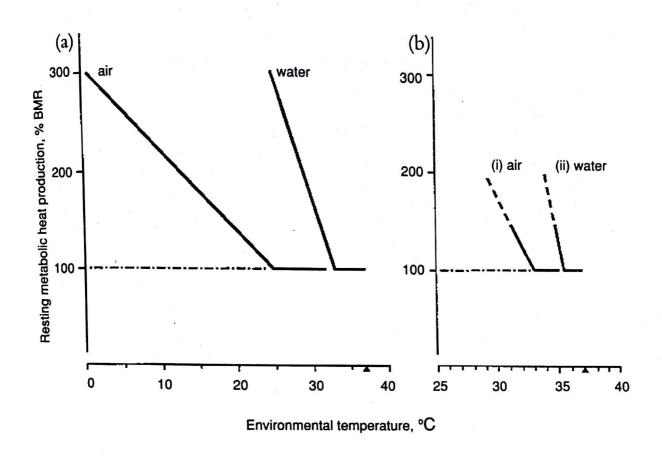


Figure 13.2 The relationship between the resting metabolic heat production (expressed as a percentage of BMR) required to maintain homeothermy and environmental temperature in air and water.

(a) In a nude adult human subject weighing approximately 70 kg. The depicted lower critical temperatures (T_{LC}) of 25 and 33°C, in air and water respectively, are typical literature values (Burton and Bazett, 1936; Mount, 1979), although the actual temperatures reported do vary, between both studies and individual subjects. If environmental temperature falls below that at which maximum metabolic heat production, approximately three times BMR in adult humans, is attained, then core temperature will fall, eventually resulting in death from hypothermia.

(b) (i) In babies weighing approximately 3 kg in air (Hey and O'Connell, 1970). At this age maximum resting heat production (solid line) is only about 1.5 times BMR, although during activity this can increase to almost twice

BMR (broken line).

(ii) The predicted relationship for an infant of similar size immersed in water. This was calculated by assuming that the relation between the thermal conductances of the body surounded by air and water, which will be largely determined by the physical characteristics of these fluids, is the same as that observed in adults (Figure 13.2 (a)).

the hominid's energy budget will find it increasingly difficult to cope with the additional demands placed upon it as temperature falls below 33°C.

As previously stated, there are significant individual differences in the rate of heat loss during immersion, and in general those endowed with thicker deposits of subcutaneous fat display the greatest tolerances (Pugh and Edholm, 1955; Keatinge, 1960; Irving, 1973). It could be argued that any hypothetical aquatic ancestor may have possessed more insulating fat than modern humans. However, set against any advantage gained in this way will have been the problem of his higher surface area to volume ratio, resulting from a smaller body size. The earliest known hominids appear to have been not much larger than the chimpanzee Pan troglodytes (Johanson and White, 1979), probably weighing about 35 kg. The recent discovery of a partial postcranial skeleton of Homo habilis (Johanson et al., 1987) indicates that human body mass has increased significantly, to its present adult mean of about 60 kg, only during the last 1.8 million years. It is also extremely unlikely that any appreciable reduction in thermal conductance was achieved by the evolution of a more rotund body shape. The fossil record clearly indicates that the Australopithecines, and even the earliest recognised member of the genus Homo (Johanson et al.), retained long-limbed proportions similar to the anthropoid apes. Although the hind limbs of these forms are somewhat shorter than modern man's, this potential advantage is offset by their relatively longer arms. Consequently, the relative distance between the hand and core was even greater than in Homo sapiens, which would have made the maintenance of normal manipulative functioning of the fingers in water even more difficult.

So far only the effect of immersion on adult hominids has been considered. The problem of survival in water will be even greater for the smaller juveniles, and in particular for new-born babies. The adherents of the Aquatic Ape Theory clearly believe that some of this early period of life was also spent in the water, suggesting that a new-born baby's extensive subcutaneous fat deposits evolved as an aid to buoyancy (Morgan, 1982, 1987). Even with this fat, the lower critical temperature of a ten-day-old baby, weighing approximately 2.5 kg, is as high as 33°C in air (Hey and O'Connell, 1970), and in water this would increase still further to around 35.5°C (Figure 13.2 (b)). Like most new-born mammals, the thermogenic capacity of human babies is significantly less than that of adults (Hey, 1974; Hill and Rahimtulla, 1965). The summit metabolism of a resting ten-day-old is approximately 1.5 times BMR, and even during periods of muscular activity this only increases to about twice BMR (Hey, 1974). Consequently, such infants would be unable to maintain homeothermy in water as warm as 34°C, only 3°C below their core temperature. Therefore, it is difficult to envisage how babies could have survived in the have survived in the sea, as even in the tropics there are very few coastal areas where surface temperatures exceed 24°C throughout the year. In contrast, an additional advantage of life on land is that some extra heat can be provided when necessary by the parent holding the infant against the body. It is difficult to see how this could be accomplished in water, without drowning the offspring.

In the extremely unlikely event that the early hominids did evolve the adaptations necessary to prevent excessive heat loss in water, further thermoregulatory problems would still have had to be surmounted. The proponents of the Aquatic Ape Theory generally accept that the later stages of human evolution, which are reasonably well documented in the fossil record, probably took place on the African savannah. In fact they go as far as to suggest that some of the features acquired during the proposed aquatic interlude would have been preadaptive for this next evolutionary step. However, the extremely efficient insulation that the early hominids must have developed would have made this transition very difficult. The low thermal conductances of marine mammals such as pinnipeds and cetaceans make metabolic heat dissipation out of the water difficult, and they readily develop hyperthermia at relatively low air temperatures (Whittow, 1976). Even a relatively small amphibious mammal like the beaver will experience hyperthermia above temperatures as low as 20°C (Steen and Steen, 1965). Because of the fundamental incompatibility between the thermoregulatory adaptations required for life in the water and hot terrestrial environments, it is difficult to imagine a more potentially hostile environment for a hypothetical short-limbed hominid, well endowed with thick subcutaneous fat, to colonise than the savannahs of equatorial Africa. The hippopotamus (Hippopotamus amphibius), which does exploit the grasslands in the vicinity of river and lakes throughout much of this region, usually leaves the water only at night, when the lower ambient temperatures and the absence of direct solar radiation greatly reduce the risk of overheating. The sensory specialisations of primates, with their high reliance on vision, would seem to militate heavily against a similar nocturnal foraging strategy.

THE THERMOREGULATORY HYPOTHESIS

Although fluid flow may have caused the selection pressure which shaped the direction of the hair tracts on the human body, this could have happened for reasons other than that of streamlining an aquatic ape. Probably the most widely accepted of the numerous hypotheses which have been proposed to account for the functional naked skin of humans (Morris, 1967) is that it evolved to facilitate the dissipation of excess body heat in an animal inhabiting a warm terrestrial environment. The loss of body hair and of the boundary layer of air trapped by it both reduces the

1

overall thermal conductance and allows large amounts of additional heat to be lost by sweating. In fact, the naked skin together with its associated sweat glands provides humans with the most effective mammalian whole-body cooling system known. This requirement does not necessarily imply that the early hominids had a particularly energetic mode of life, since, as previously discussed (Wheeler, 1984), they would have lacked the ability of other savannah mammals to selectively cool the heat-sensitive brain, and would have been therefore unusually sensitive to hyperthermia in this very thermally stressing environment.

Proponents of the Aquatic Ape Theory have challenged the idea that the human naked skin can be satisfactorily explained as a thermoregulatory adaptation. Most of their arguments rely on drawing superficial analogies with other savannah mammals, all of which have retained a covering of body hair. However, these criticisms usually fail to appreciate the full complexity, and interspecific differences, of mammalian thermoregula-tory strategies.

For example, it has been claimed that since a wide variety of mammals sweat, the idea that a naked skin is a prerequisite for this form of cooling is a 'misconception' (Morgan, 1987). However, the possession of active cutaneous sweat glands, which vary markedly in density between species (Robertshaw, 1968; Robertshaw and Taylor, 1969; Mount, 1979), should not necessarily be equated with effective heat dissipation. There are two principal reasons why the presence of dense body hair reduces the efficiency of evaporative cooling. First, it traps a relatively static layer of air next to the body hair, which restricts airflow over the wetted skin surface. Therefore, as sweat evaporates the relative humidity of this boundary layer increases, limiting further fluid loss. Second, some of the secreted fluid evaporates from the fibres of the coat, and consequently it takes most of its latent heat of vaporisation from the surrounding air rather than from the body of the animal. These two factors severely limit the rate at which even copiously sweating mammals can lose heat if they retain dense body hair. For example, ungulates are among the species with the greatest reliance on cutaneous, as opposed to respiratory, evaporative cooling (Mount). These possess an average of 800-1500 sweat glands per cm² (Macfarlane, 1968), which compares favourably with human densities of between approximately 2000 per cm² on the palms and soles of the feet and 100-200 per cm² over most of the rest of the body (Mount). However, at high environmental temperatures the maximum rate of evaporative heat loss from the skin of the cow is only 25 per cent of that from a similar area of human skin under comparable conditions (Bianca, 1965).

Another finding cited as evidence against the thermoregulatory hypothesis (Morgan, 1982, 1987) is that artificial removal of the pelage from a sheep can result in a rise in its temperature when exposed to high

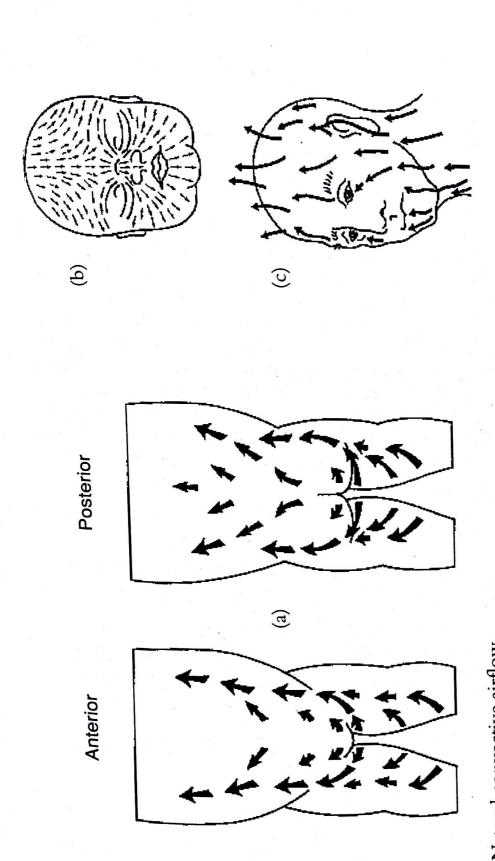
levels of direct solar radiation (Parer, 1963; Macfarlane, 1976). This entirely predictable outcome occurs because the layer of air normally trapped by the coat acts as a barrier not only to the loss of metabolic heat but also to the uptake of energy from the environment. However, this observation has little direct relevance to the evolution of the human naked skin, for two main reasons. First, the pattern of evaporative cooling in man is very different from that of sheep. The latter possess relatively fewer and less active cutaneous sweat glands, relying instead mainly on evaporation from the respiratory tract - by panting - to dissipate excess heat at high environmental temperatures (Macfarlane, 1968; Johnson, 1976). Consequently, the shorn animal has to endure a considerably elevated external heat load, while only slightly increasing its potential for evaporative cooling. It is a critical assumption of the thermoregulatory hypothesis that the loss of body hair by hominids occurred only in association with the development of an elaborate sweatgland system. Second, the sheep, like all savannah mammals other than man, is a quadruped. As previously discussed (Wheeler, 1984), bipedalism was probably the essential preadaptation required to allow the evolution of a naked skin by mammals the size of hominids in environments where they are exposed to high radiant heat loads. The reason is that a quadruped exposes more than twice the surface area to the sun at high elevations, when the intensity of its incident radiation is greatest, than does a similarly proportioned biped. This confers on the biped the double benefit of reducing both its total heat load and the area of its skin presented perpendicularly to the most intense fluxes, where it is at greatest risk of thermal and ultraviolet-B damage. It is even possible that these thermoregulatory advantages were important selection pressures favouring the original adoption by hominids of bipedalism as a mode of terrestrial locomotion. Morgan (1987) has suggested that shade-seeking during the most thermally stressing period of each day would remove the need for such a postural adaptation. Although hominids probably could have survived by adopting such a strategy, those individuals which did would have been at a competitive disadvantage to any not needing to restrict their diurnal activity in this way. As these animals were probably exploiting scattered or clumped food resources (Lovejoy, 1981) this difference would have been particularly significant because, in such species, foraging success is principally determined by the available search time.

In summary, this thermoregulatory hypothesis asserts that the full benefit of cutaneous evaporative cooling can only be realised by a naked-skinned mammal, and that such hair loss will probably be a net advantage only to a species possessing both well developed sweat glands and a bipedal posture. Since no other savannah mammal possessed this unique

combination of features, it is only to be expected that they have all retained a shielding covering of body hair.

This thermoregulatory hypothesis not only satisfactorily accounts for the evolution of man's functionally naked skin, but it can also provide a plausible, although somewhat speculative explanation for the pattern of the residual hair tracts. Throughout the transitional period when the coat was being progressively reduced, it will have been advantageous if the remaining hair was orientated to minimise the amount of direct solar radiation reaching the skin, while maximising the air flow over it. Fortunately, there is no conflict between the solutions to these problems. To optimise the interception of incident energy with the minimum amount of hair, this should lie tangentially to the incoming rays. Therefore, the alignment of the hair tracts on humans is ideal to shield the skin from the sun at high elevations, when its fluxes are strongest. However, it should be noted that in this respect the human hair tract pattern offers little, if any, advantage over that of the living anthropoid apes. Although hair tract direction can have little influence on forced convective airflow over the skin because of the continually changing orientation of the body to the prevailing wind, the situation with regard to the air currents produced by natural convection, which predominates at windspeeds below 0.2m per second (Kerslake, 1972), is very different.

This process, in which air warmed by contact with the skin expands and rises, has been studied in modern humans. The flow of this convective boundary layer is laminar as it rises up alongside the lower limbs, but becomes turbulent as its velocity increases over the upper body (Lewis et al., 1969; Clarke and Toy, 1975). Natural convection will be particularly strong in open equatorial environments, since both the body and ground surfaces are being heated by direct solar radiation. These currents can be utilised to promote the evaporation of sweat if the remaining body hair is orientated to encourage them to flow down to the skin surface, rather than deflect them across the surface of the coat. To achieve this it will be advantageous if the hair lies in direct opposition to the path taken by the natural convection currents rising up the body. Model experiments (Figure 13.3 (a)) indicate that the observed pattern of hair tracts on the human body is close to the optimum arrangement. Convergence of the currents flowing up the insides of the legs creates a region of higher pressure in the region of the crutch. As this column of air divides and passes over the lower abdomen and back, it spreads sideways from the mid-line of the body, displacing the relatively lowerpressure air which has risen directly up the outer surfaces of the legs, and runs counter to the hair tracts on the trunk. The orientation of the hair tracts on the shoulders and upper chest and back will have had little thermoregulatory significance, since over these surfaces the rising air currents are more turbulent and become detached from the body.



(a) The 1:5 scale model represents a hypothetical bipedal hominid, weighing 35 kg and standing 1.25 m high, proportioned approximately intermediate between reconstructions of Australopithecus afarensis and the chimpanzee Pan troglodytes. Both the model and the supporting horizontal surface were painted black and radiantly heated from above, using visual and infra-red wavelengths. Small holes in the baseboard allowed the introduction of smoke from below to visualise, and photographically record, the resulting airflow. Although there was a slight amount of (b) Hair tracts on the head of a human foetus (after Hardy, 1960). The alignments of those on an adult are similar. wandering, the arrows show the routes usually taken by the rising convection currents. Figure 13.3 Natural convective airflow.

(c) Natural convective airflow over the human head, as visualised by Schlieren photography (after Lewis et al., 1969).

However, there appears to be an extremely good correspondence between the pattern of hair tracts and the natural convection currents, as visualised by Schlieren photography of living subjects (Lewis et al., 1969), over the head (Figure 13.3 (c)).

CONCLUSION

Therefore, an aquatic period in our past is not needed to explain either the sparsity or the arrangement of hair on the human body. In fact, the energetic costs of a naked skin for a mammal of the shape and size of hominids argue strongly against such an aquatic mode of life. If the changes in the orientation of the hair tracts on the lower human body do have any functional significance, then one plausible explanation for them would be in terms of a thermoregulatory adaptation, enhancing cutaneous evaporation in the period before functional hair was completely lost, without the need to invoke any water currents running in the opposite direction. If correct, this interpretation is particularly interesting, because the pattern is clearly that of air currents over a biped rather than a quadruped. This means that body hair must still have been sufficiently dense to exert an effect on the airflow over the skin after the evolution of bipedality, which is consistent with the proposal (Wheeler, 1984, 1985) that an upright posture was an essential preadaptation for the acquisition of a naked skin.

REFERENCES

Bazett, H.C., 1968, The regulation of body temperatures. In Physiology of Heat Regulation and the Science of Clothing, ed. L.H. Newburgh (New York: Hafner).

Bianca, W., 1965, Cattle in a hot environment. Journal of Dairy Research, 32, 291-345.

Bradley, S.R. and Deavers, D.R., 1980, A re-examination of the relationship between thermal conductance and body weight in mammals. Comparative Biochemistry and Physiology, **65A**, 465–76.

Burton, A.C. and Bazett, H.C., 1936, A study of the average temperature of the tissues, the exchanges of heat and vasomotor response in man by means of a bath calorimeter.

American Journal of Physiology, 117, 36.

Burton, A.C. and Edholm, O.G., 1969, Man in a Cold Environment (New York and London: Hafner).

Chatfield, P.O., Lyman, C.P. and Irving, L., 1953, Temperature adaptations of nerves in leg of gull. American Journal of Physiology, 172, 639-44.

Clark, R.P. and Toy, N., 1975, Natural convection around the human head. Journal of Physiology, London, 244, 283-93.

Eagan, C.J., 1966, Effects of cold on circulation in fingers of Eskimos and whites. International Journal of Biometeorology, 10, 293–304.

Hammell, H.T., 1964, Terrestrial animals in cold: recent studies of primitive man. In Adaptation to the Environment, ed. D.B. Dill (American Physiological Society), 413-34.

Hardy, A., 1960, Was man more aquatic in the past? New Scientist, 7, 642-54.

Hardy, J.D., Stolwijk, J.A.J. and Gagge, A.P., 1971, Man. In Comparative Physiology of Thermoregulation and H. M. Dress). Thermoregulation, vol. II: Mammals, ed. G.C. Whittow (New York: Academic Press),

Herreid, C.F. and Kessel, B., 1967, Thermal conductance in birds and mammals. Comparative Biochemistry and Physiology, 21, 405–14.

Hey, E.N., 1974, Physiological control over body temperature. In Heat Loss from Animals and Man: Assessment and Control, ed. J.L. Monteith and L.E. Mount (London: Butterworth), 77-95.

Hey, E.N. and O'Connell, B., 1970, Oxygen consumption and heat balance in the cot-

nursed baby. Archives of Disease in Childhood, 45, 335-43.

Hill, J.R. and Rahimtulla, K.A., 1965, Heat balance and the metabolic rate of new-born babies in relation to environmental temperature. Journal of Physiology, London, 180,

Hong, S.K., 1963, Comparisons of diving and non-diving women of Korea. Federation

Proceedings, 22, 831-3.

Irving, L., 1966, Adaptations to cold. Scientific American, 214, 94-101.

Irving, L., 1973, Aquatic mammals. In Comparative Physiology of Thermoregulation, vol. III: Special aspects of thermoregulation, ed. G.C. Whittow (New York: Academic Press),

Irving, L., Schmidt-Nielsen, K. and Abrahamson, N.S., 1957, Melting points of animal

fat in cold climates. Physiological Zoology, 30, 93-105.

Johanson, D.C. and White, T.D., 1979, A systematic assessment of early African hominids. Science, 203, 321-30.

Johanson, D.C., Masao, F.T., Eck, G.G., White, T.D., Walter, R.C., Kimbel, W.H., Asfaw, B., Manega, P., Ndessokia, P. and Suwa, G., 1987, New partial skeleton of Homo habilis from Olduvai Gorge, Tanzania. Nature, 327, 205-9.

Johnson, K.G., 1976, Evaporative temperature regulation in sheep. In Progress in Animal Biometeorology, vol. I, part I, ed. H.D. Johnson (Amsterdam: Swets & Zeitlinger), 140-7.

Kanwisher, J. and Sudnes, G., 1968, Physiology of a small cetacean. Hvalradets Skrifter, 48, 45.

Keatinge, W.R., 1960, The effects of subcutaneaous fat and of previous exposure to cold on the body temperature, peripheral blood flow and metabolic rate of men in cold water. Journal of Physiology, London, 153, 166-78.

Keatinge, W.R., 1969, Survival in Cold Water (Oxford: Blackwell).

Kerslake, D., 1972, The Stress of Hot Environments (Cambridge: Cambridge University Press).

LaLumiere, L.P., 1981, The evolution of human bipedalism. Philosophical Transactions of the Royal Society of London, Series B, 292, 103-7.

LeBlanc, J., 1975, Man in the Cold (Springfield, Illinois: Charles C. Thomas).

Lewis, H.E., Foster, A.R., Mullan, B.J., Cox, R.N. and Clark, R.P., 1969, Aerodynamics of the human microenvironment. Lancet, i, 1273-7.

Lovejoy, C.O., 1981, The origin of man. Science, 211, 341-50.

Macdonald, D. (ed.), 1984, The Encyclopaedia of Mammals: I (London: Allen & Unwin). Macfarlane, W.V., 1968, Adaptation of ruminants to tropics and deserts. In Adaptation of

Domestic Animals, ed. E.S.E. Hafez (Philadelphia: Lea & Febinger), 164-82.

Macfarlane, W.V., 1976, Adaptation to climatic zones and the ecophysiology of ruminants. In Progress in Animal Biometeorology, vol. I, part I, ed. H.D. Johnson (Amsterdam: Swets & Zeitlinger), 425-33.

Miller, L.K. and Dehlinger, P.J., 1969, Neuromuscular function in cold. Comparative

Biochemistry and Physiology, 28, 915–21.

Miller, L.K. and Irving, L., 1963, Sensitivity of rat nerve to cold. American Journal of Physiology, 204, 359-62.

Morgan, E., 1972, The Descent of Woman (London: Souvenir Press). Morgan, E., 1982, The Descent of Woman (London: Press).

Morgan, E., 1984, The aquatic hypothesis. New Scientist, 1405, 11-13.

Morgan, E., 1987, Lucy's child. New Scientist, 1540, 13-15.

Morris, D., 1967, The Naked Ape (London: Cape).

Morris, D., 1977, Manwatching (London: Cape).

Mount, L.N., 1979, Adaptation to Thermal Environment (London: Edward Arnold).

Parer, J.T., 1963, Wool length and radiant heating effects in sheep. Journal of Agricultural Science, Cambridge, 60, 141-4.

Pugh, L.G.C. and Edholm, O.G., 1955, The physiology of Channel swimmers. Lancet, ii, 761-8.

Robertshaw, D., 1968, The pattern and control of sweating in the sheep and the goat. *Journal of Physiology, London*, **198**, 531–9.

Robertshaw, D. and Taylor, C.R., 1969, A comparison of sweat gland activity in eight species of East African bovids. *Journal of Physiology, London*, 203, 135–43.

Scholander, P.F. and Schevill, W.E., 1953, Counter-current vascular heat exchange in the fins of whales. *Journal of Applied Physiology*, **8**, 279–82.

Steegman, A.T., 1975, Human adaptation to cold. In *Physiological Anthropology*, ed. A. Damon (London: Oxford University Press), 130–66.

Steen, I. and Steen, J.B., 1965, Thermoregulatory importance of the beaver's tail. Comparative Biochemistry and Physiology, 15, 267-70.

Swift, R.W., 1932, The effects of low environmental temperatures upon metabolism. 2: The influence of shivering, subcutaneous fat and skin temperature on heat production. *Journal of Nutrition*, **5**, 227–49.

Verhaegen, M., 1985, The aquatic ape theory: evidence and a possible scenario. *Medical Hypotheses*, 16, 17–32.

Wheeler, P.E., 1984, The evolution of bipedality and loss of functional body hair in hominids. *Journal of Human Evolution*, 13, 91–8.

Wheeler, P.E., 1985, The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. *Journal of Human Evolution*, 14, 23–8.

Whittow, G.C., 1976, Temperature regulation in marine mammals. In *Progress in Animal Biometerorology*, vol. I, part I, ed. H.D. Johnson (Amsterdam: Swets & Zeitlinger), 88–94.