

Human Locomotion and Heat Loss: An Evolutionary Perspective

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ABSTRACT

Humans are unique in many respects including being furless, striding bipeds that excel at walking and running long distances in hot conditions. This review summarizes what we do and do not know about the evolution of these characteristics, and how they are related. Although many details remain poorly known, the first hominins (species more closely related to humans than to chimpanzees) apparently diverged from the chimpanzee lineage because of selection for bipedal walking, probably because it improved their ability to forage efficiently. However, because bipedal hominins are necessarily slow runners, early hominins in open habitats likely benefited from improved abilities to dump heat in order to forage safely during times of peak heat when predators were unable to hunt them. Endurance running capabilities evolved later, probably as adaptations for scavenging and then hunting. If so, then there would have been strong selection for heat-loss mechanisms, especially sweating, to persistence hunt, in which hunters combine endurance running and tracking to drive their prey into hyperthermia. As modern humans dispersed into a wide range of habitats over the last few hundred thousand years, recent selection has helped populations cope better with a broader range of locomotor and thermoregulatory challenges, but all humans remain essentially adapted for long distance locomotion rather than speed, and to dump rather than retain heat. © 2015 American Physiological Society. *Compr Physiol* 5:99-117, 2015.

Introduction

Humans are distinctive compared to other mammals in numerous respects including being habitually bipedal, and the ability to walk and run long distances at relatively fast speeds in hot, arid conditions. The optimal walking speed for an average-sized human is 1.2 m/s, about 20% faster and four times more efficient compared to our closest relatives, chimpanzees, and about 20% faster and approximately as efficient as a pony's optimal walking speed (117, 133, 161). In addition, although maximum running speed in humans is unimpressive, about half that of most equivalent-sized quadrupeds (52), humans are among the few mammals—and the only species of primate—that can repeatedly run very long distances at relatively fast speeds under aerobic capacity. Other cursorial (running adapted) quadrupeds can run long distances at a trot but not a gallop, yet the preferred trotting speed of a pony, approximately 3 m/s, is only half the speed at which a fit human can run a marathon with nearly equal efficiency (63, 133). Finally, most mammals are able to walk or run long distances only in relatively cool conditions, but humans are the sole species of mammal that excels at long distance trekking and running in extremely hot conditions. No horse or dog could possibly run a marathon in 30°C heat (40).

The purpose of this review is to summarize the evidence for the origins of the special nature of human locomotion and heat loss mechanisms, and to make the argument—first elucidated by Carrier (24)—that these systems share a linked evolutionary history. Although some details remain murky,

multiple lines of evidence suggest that there was strong selection on early hominins (species more closely related to humans than to chimpanzees) to stand and walk efficiently, and that the origins of bipedalism was later followed by additional selection for long distance walking and then for endurance running. In turn, it is reasonable to hypothesize that selection for long distance walking and running created a selective advantage for hominins to dump heat effectively in hot, arid conditions. After modern humans evolved and dispersed all over the globe, further selection occurred to help different populations adapt to a wide range of climatic conditions, but all human populations are variants of a basic adaptive pattern for long-term aerobic exertion in hot habitats.

I first summarize the evidence for the evolution of human locomotion and then heat loss, in both cases drawing on the fossil record as well as comparisons between humans and the African great apes. I then evaluate alternative hypotheses for how these two distinctive systems evolved, and the extent to which they are linked. I conclude with a discussion of the contemporary relevance of the evolutionary bases of these adaptations.

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Published online, January 2015 (comprehensivephysiology.com)

DOI: 10.1002/cphy.c140011

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Bipedalism

Fossil evidence discovered over the last few decades indicates that selection for bipedalism may have been the initial spark that set the human lineage on a different evolutionary path from the African great apes. In fact, the presence of adaptations for bipedalism is a major reason for classifying many of these fossils as hominins (a problem of circular logic if bipedalism evolved more than once). Bipedalism, however, is an unusual form of locomotion that has a long, complex evolutionary history involving several stages, each of which was contingent upon previous stages, and likely driven by selective pressures caused by changing climatic conditions. Therefore, before reviewing the evolutionary transformations that led to modern human walking and running, it is useful to begin with a consideration of the phylogenetic and ecological contexts in which hominin bipedalism first evolved.

Evolutionary context

As Figure 1 illustrates, molecular data unambiguously indicate that humans and chimpanzees share a last common ancestor (LCA) that diverged approximately 5 to 8 million years ago (Ma), and that gorillas diverged from the human-chimpanzee clade approximately 8 to 12 Ma. Molecular evidence that humans and chimpanzees are sister taxa was initially a surprise to paleontologists because chimpanzees and gorillas share many similarities in their cranial and postcranial anatomy, with many differences attributable to the effects of size (9, 54, 55, 151). Among their many similarities, chimpanzees and gorillas habitually knuckle walk, a distinctive form of locomotion that involves resting the forelimbs on the dorsal surface of the middle phalanges of a flexed hand. Knuckle walking is commonly interpreted as a way to

locomote quadrupedally while maintaining adaptations for arboreal climbing such as short hind limbs, long upper limbs, and long, curved manual phalanges (for review, see Ref. 46). Given the unique nature of knuckle walking in combination with additional similarities between chimpanzees and gorillas, it was assumed before molecular data indicated otherwise that these species were closely related cousins who shared a common knuckle-walking ancestor, and that the LCA of humans and the African great apes was unlikely to have been a knuckle walker, but instead a generalized quadruped or possibly even some sort of brachiator with an orthograde (upright) trunk (see Ref. 60).

The fact that chimpanzees and humans are more closely related to each other than to gorillas has necessitated a re-evaluation of hominin origins. From a phylogenetic perspective, the most parsimonious scenario is that knuckle walking and other similarities between the African great apes evolved just once in the LCA of chimpanzees, humans, and gorillas, and that the more recent LCA of just humans and chimpanzees was also a knuckle walker that resembled chimpanzees and gorillas in many respects (125). If not, then the many similarities between chimpanzees and gorillas must have evolved independently, which is highly unlikely.

Reconstructing the LCA as a knuckle-walker has important implications for hypotheses about the origins of bipedalism, but this reconstruction is unsubstantiated and is the subject of much debate for three reasons. First, although the LCA of humans and chimpanzees has never been discovered, there are many species of fossil great apes from the Miocene (23–5 Ma), and few of them closely resemble either chimpanzees or gorillas, especially in terms of their locomotor anatomy. Instead, some such as *Proconsul* are generalized quadrupeds, and others such as *Morotopithecus* are orthograde climbers (97, 171). Second, chimpanzees and gorillas knuckle walk in a slightly different manner, leading some scholars to speculate that this mode of locomotion evolved independently in the two species (77). Third, although there is almost no fossil record of chimpanzee and gorilla evolution, paleontologists have discovered a number of putative early hominins, and some scholars have argued that these early members of the human lineage do not resemble chimpanzees or gorillas (4, 181). Although this view cannot be discounted entirely, the balance of evidence suggests that the LCA was a knuckle-walker. Most importantly, interpretations of the earliest hominins as unlike chimpanzees or gorillas are problematic because these fossils actually resemble chimpanzees and gorillas in most aspects for which they are unlike later hominins (91, 186). In addition, while Miocene apes are diverse, most of these species are unlikely to be closely related to the LCA of humans and chimps, which means that their locomotor adaptations do not refute reconstructions of the LCA as similar to the extant African great apes (114). Finally, although adult gorillas do knuckle walk with more vertical forelimbs than chimps, this difference is exactly what one expects in larger bodied animals, which use less crouched postures for reasons of scaling (10). As with many aspects of their

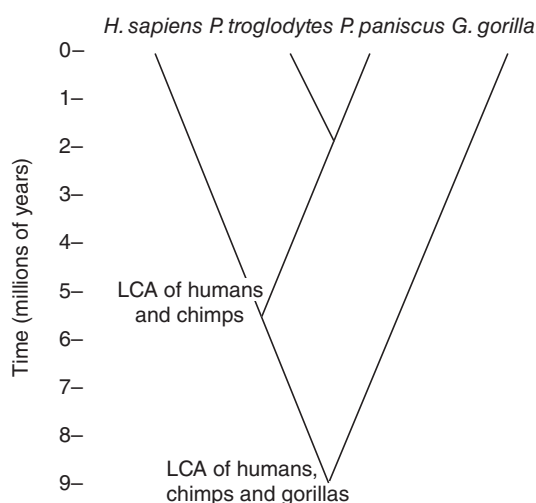


Figure 1 Evolutionary tree showing the relationships among humans, chimpanzees, and gorillas, as well as the Last Common Ancestors (LCA) of humans and chimps, and of humans, chimps, and gorillas. The dates of the divergences are only approximate.

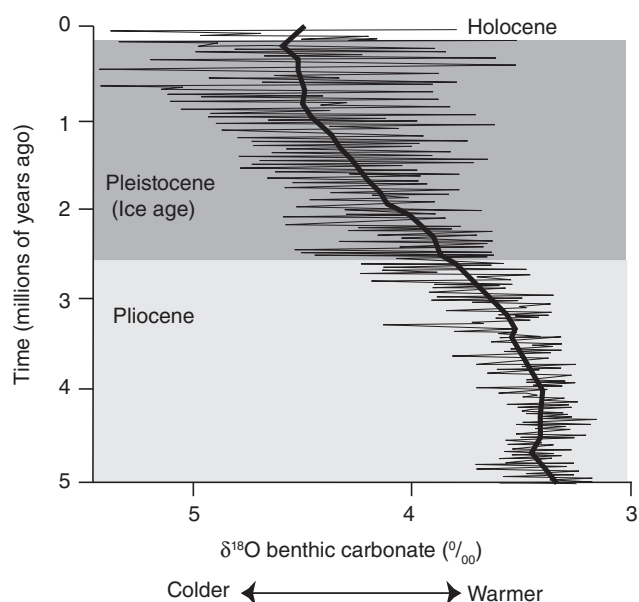


Figure 2 Record of the temperature of the earth's oceans based on $\delta^{18}\text{O}$ from benthic carbonates. Note the general cooling trend over the last 5 million years, but with much variation.

anatomy and diet, locomotor differences between gorillas and chimpanzees are best explained as consequences of size.

Debates over the nature of the LCA remain resolved, but the hypothesis that they were knuckle walkers has far-reaching implications for hypotheses about why and how bipedalism evolved in the rainforest contexts in which the LCA, like extant great apes, almost certainly lived. Africa during this period, the late Miocene, was warmer and wetter than today, but was generally trending (but with many fluctuations) toward becoming cooler and drier as a result of global and regional changes (Fig. 2) (11, 26, 76). Major consequences of these changes were fractionation of the rain forests and the expansion of more open woodland habitats, which appear to be the dominant ecological context in which the earliest hominins have been unearthed (see below). More open habitats must have been a source of stress for primarily frugivorous apes because the patches of fruit on which they relied would have become smaller, more dispersed, and more seasonal. Although there are many proposed explanations for why bipedalism initially evolved (for reviews, see Refs. 46, 60, 91), the two leading hypotheses propose that these stresses favored incipient bipedalism in ways relevant to food acquisition. The first hypothesis is that bipedalism initially evolved as a postural adaptation for more effective upright feeding. Studies by Hunt (68) and by Crompton and colleagues (32, 33, 163) have shown that apes often stand upright when either feeding on the ground or in trees. If hominins with anatomical variations that improved their ability to stand upright had a foraging advantage as fruits became more rare, they might have been at a selective advantage. The second hypothesis, which is not exclusive of the first, is that bipedalism was selected to improve locomotor efficiency as

hominins needed to travel longer distances to find fruit (131). Chimpanzees rely on fruit for more than 75% of their diet, and travel on average only 2 to 3 km per day (119). Yet, the highly flexed limb postures required for knuckle walking are highly inefficient, costing four times more energy per unit body mass per unit distance than humanlike bipedalism (117, 154). If early bipeds were able to reduce their cost of locomotion, they would have reaped substantial energetic benefits if and when they needed to travel longer distances than chimps to forage. Testing this hypothesis, however, requires reliable reconstructions of the locomotor repertoire of not just the LCA but also the first hominins.

Major transitions in hominin bipedalism

Although the first hominins appear to have been bipeds, they probably stood, walked, and ran very differently from modern humans. Instead, hominin bipedalism appears to have evolved via three major stages (summarized in Figs. 3 and 4), each of which contributed in different ways to the suite of locomotor

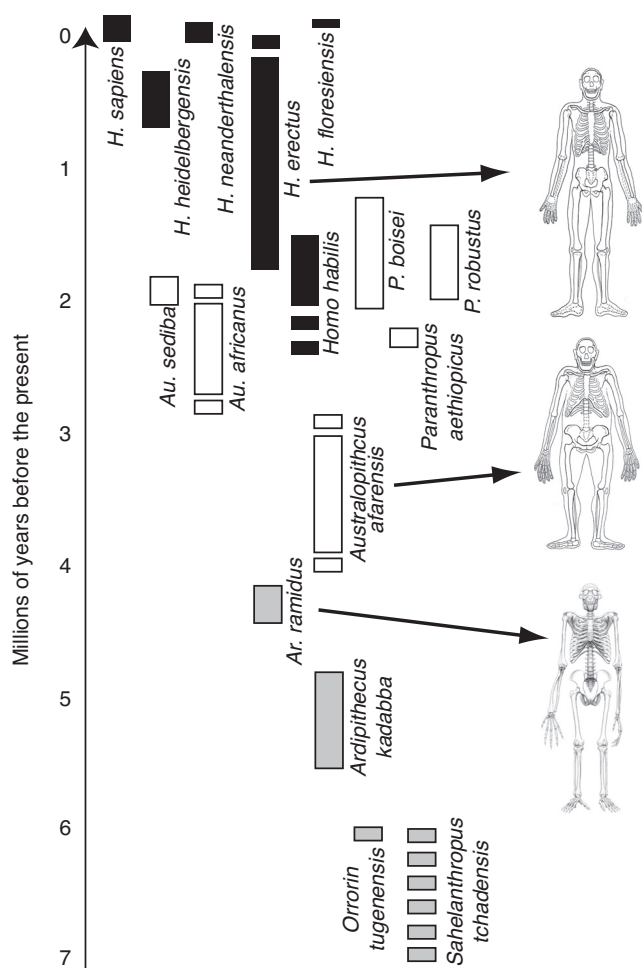


Figure 3 Dates of species of hominins with representative skeletons from each of the major stages of human evolution. Species in the genus *Homo* are in black, species in the genus *Australopithecus* are in white, and early hominin species and genera are in gray.

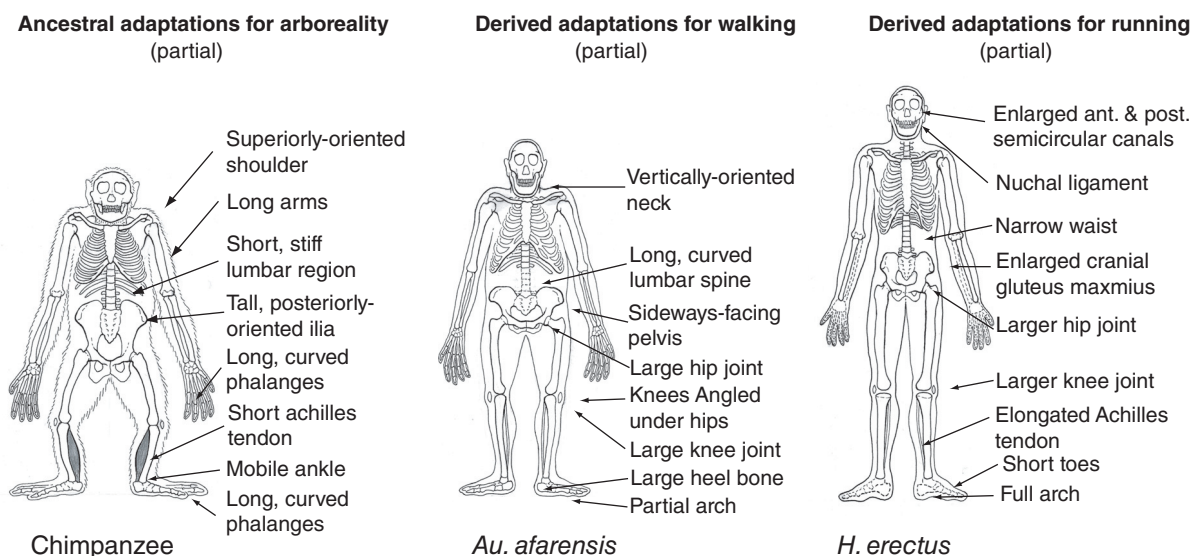


Figure 4 Comparison of major locomotor features in chimpanzees, australopiths, and humans. Highlighted are ancestral features for arboreal locomotion in chimpanzees, derived features for walking in *Australopithecus*, and derived features for running in *Homo*.

adaptations observable in modern humans. To understand human bipedalism therefore requires considering each of these stages, beginning with the earliest known hominins.

Stage 1: Earliest hominins

The oldest proposed hominin species is *Sahelanthropus tchadensis*, whose remains have been found in Chad in sediments dated to between 6.0 and 7.2 Ma (17, 18, 82, 168). The only material described so far for *Sahelanthropus* is a partial cranium, several mandibular fragments, and numerous teeth, but the cranium is almost surely that of a biped because its inferiorly oriented foramen magnum is nearly parallel relative to the long axis of the orbits, indicating a vertical upper neck, hence habitual upright posture (192). A second species from Kenya, *Orrorin tugenensis*, is dated to 6 Ma, and includes a partial femur that has several features typical of later bipedal hominins (4, 113, 126). Finally, two early species assigned to the genus *Ardipithecus* have been found in Ethiopia: *Ar. kadabba* (dated to 5.2–5.8 Ma) and *Ar. ramidus* (dated to 4.3–4.5 Ma) (58, 150, 181, 182). Little is known about *Ar. kadabba*, but among the fossils assigned to *Ar. ramidus* is a partially complete skeleton (nicknamed “Ardi”) that has numerous features indicative of bipedalism. The most important of these is the pelvis, which, although distorted, was short and probably had laterally-oriented ilia, permitting the small gluteal muscles to function as hip abductors (in apes, these muscles function primarily as extensors) (96). The *Ar. ramidus* foot also has several indications of a partially rigid midfoot, and as well as hyperextensible phalanges (95). It has been argued that *Ar. ramidus* has other adaptations for bipedalism such as a long, lordotic lumbar region and an inwardly angled femur, but these features are not preserved in the skeleton and remain

conjectural. *Ar. ramidus* also has numerous chimp-like adaptations for climbing trees such as a very divergent hallux, long and curved phalanges, a slightly inverted subtalar joint, and relatively long arms. A partial foot that is similar to Ardi’s, but dated to 3.4 Ma, suggests that this type of foot persisted for at least a million years (57).

To what extent and how the earliest hominins were bipedal is difficult to reconstruct. Without postcranial evidence, we can establish only that *Sahelanthropus* was a postural biped; in addition, *Ar. ramidus* lived approximately 1.5 million years after the first putative bipedal hominins. If we assume that *Ar. ramidus* was representative of earlier hominin species, then it is not unreasonable to reconstruct the earliest hominins as being a combination of arboreal climbers and bipedal walkers. Analyses of their feet suggest they probably walked like chimps on the lateral margin of the foot (95), but there are not yet enough data to infer reliably whether they had inefficient bent-hip bent-knee gaits or more extended lower limbs during walking. In other words, they may have been occasional or facultative bipeds. Even so, whatever form of bipedalism they practiced was clearly different from their more habitually bipedal descendants who are classified in the genus *Australopithecus*, and who represent the second major stage in hominin locomotor evolution.

Stage 2: Australopiths

The australopiths (the colloquial term for species in the genus *Australopithecus*) comprise a diverse group of hominins that lived in Africa between 4 and 1 Ma (see Fig. 3). Much of the variation among australopith species is craniodental, reflecting adaptations to diverse diets, but recently recovered evidence reveals that these species also varied appreciably in terms of locomotion. The three species for which we have the

best data are *Au. afarensis*, which lived in East Africa from 3.9 to 3.0 Ma; *Au. africanus*, which lived in South Africa from 3 to 2 Ma; and *Au. sediba*, which is found in South African sites dating to 1.8 to 2.0 Ma (for reviews, see Refs. 46 and 89). As summarized in Figure 4, all of these species retain adaptations evident in great apes and earlier hominins for tree climbing including relatively short legs, long arms, and long, curved pedal phalanges; but they also had more modern feet than *Ardipithecus* including an adducted hallux, and a partial longitudinal arch; in addition, they had a long lumbar region with a strong lordosis that positioned the body's center of mass above the hips; a wide pelvis with efficient hip abductors; medially positioned knees; and enlarged lower extremity joints to withstand the higher stresses caused by bipedalism (see Refs. 2, 60, 172). The greatest variation appears to be in the foot and ankle. Whereas the posterior calcaneus (heel bone) in *Au. afarensis* is large and inferiorly flat like a modern human's to stabilize the foot during heel strike, it is small and triangular in cross-sectional shape in *Au. sediba*, which probably walked on a more inverted foot (39). Other features in *Au. sediba* such as its narrow thorax and upwardly-oriented shoulder joint also would have benefited climbing performance (28).

The general picture of the australopiths is that they were habitual and effective walkers and climbers, but that some species such as *Au. sediba* may have been more arboreally adapted than others such as *Au. afarensis* and *Au. africanus*. A group of species termed the "robust" australopiths (some paleontologists group them in a separate genus, *Paranthropus*), which are characterized by craniodental adaptations for chewing very mechanically demanding food, also appear to have been effective, habitual bipeds, but there are hints they might have differed from earlier, more gracile species such as *Au. africanus* and *Au. afarensis* in subtle ways (2, 158, 159). The likely overall diversity among australopiths makes sense given what is known about ongoing climate change in Africa during this period, the Pliocene (5.3–2.8 Ma) (see Fig. 2). As Africa continued to become cooler and drier during the Pliocene, albeit with many swings back and forth, there was considerable variation within and between regions, often because of intense tectonic activity (26, 38, 76, 111). Although fruits must have remained an important part of their diet, the australopiths were probably under intense pressure to exploit non-fruit plant foods, many of them very tough and fibrous, and which required more travel time to acquire in perilous open habitats (for review, see Ref. 90). It, therefore, makes sense that many australopith species were under selection to be efficient at long-distance walking but also to retain arboreal adaptations for access to fruits as well as protection from predators.

Stage 3: *Homo*

The third and last major stage in hominin locomotor evolution occurred in the Genus *Homo* (see Figs. 3 and 4). Substantial variation has led to much confusion over the taxonomy of early *Homo*, but most experts recognize at least two major

species: *H. habilis* and *H. erectus*. Limited postcranial remains attributed to *H. habilis*, which may be as old as 2.3 Ma and persisted until 1.4 Ma, suggest that body size and proportions in this species were similar to *Australopithecus*, but an isolated partial foot (OH 8) that might be from *H. habilis* has numerous derived features including a definitive longitudinal arch (59). *H. erectus*, in contrast, is much more like modern humans in terms of its postcranial anatomy. Although body size varies enormously in the species (body mass estimates range from 40–70 kg), they had relatively long limbs (118), relatively large joints in the lower extremity and spine (72, 135, 139), basin-shaped pelvis with relatively large gluteal muscles (92), and narrow waists. Footprints that were likely made by *H. erectus* are extremely modern, indicating a full arch with short toes, and a long striding gait (8, 41). In addition, many adaptations for arboreal locomotion that were present among australopiths are absent in *H. erectus*. Although *H. erectus* postcrania differ in some respects from those of modern humans, most notably in having more flared ilia, their overall locomotor anatomy is similar enough to infer that they walked and ran like living humans (Fig. 4).

There are several alternative hypotheses to explain the shift to modern locomotor anatomy that occurred across the transition from *Australopithecus* to *Homo*. One hypothesis is that australopith bipedalism was partially apelike with an inefficient bent-hip bent-knee gait that was necessitated by retained adaptations for arboreal locomotion, and that the transition to *Homo* was driven by selection to improve walking efficiency (147, 160). A corollary of this hypothesis is that selection for long-distance walking efficiency came at the expense of adaptations for arboreality such as short legs, and long, curved toes. This view, however, has been challenged by several lines of evidence including the orientations of trabeculae in fossil distal tibia of *Au. africanus*, which indicate that this species loaded its ankles, hence its knees, in extended postures unlike those used by chimps (6). In addition, footprints dated to 3.6 Ma from Laetoli, Tanzania that were likely made by *Au. afarensis* are consistent with modern striding gaits (33, 121). Finally, some other features characteristic of australopiths such as long toes and long femoral necks would not have compromised walking performance (132), and there is no evidence that selection for improved walking performance would have selected against upper limb features that are useful for climbing but which have little to no effect on walking such as long forearms, curved manual phalanges, and superiorly oriented shoulder joints.

A second hypothesis regarding the locomotor differences between *Australopithecus* and *Homo* is that this transition was partially driven by selection for endurance running (15). In terms of skeletal anatomy, several lines of evidence support this hypothesis. Most importantly, species in the genus *Homo*, especially beginning with *H. erectus* but also including *H. sapiens*, have numerous features that would have improved performance in running but not walking. Since the predominantly mass-spring gait mechanics of running differ markedly from the primarily pendular mechanics of walking, a large

proportion of these features include potential adaptations for storing and releasing elastic energy such as a long Achilles tendon (inferred indirectly from the small apelike insertion on the posterior calcaneus in *Australopithecus*), and evidence for a close-packed calcaneo-cuboid joint, which helps the longitudinal arch function as a spring (2, 84). Many additional novel features in the genus *Homo* may be adaptations for stabilization during running, which is a more serious challenge than during walking. These features include relatively larger anterior and posterior semicircular canals than in apes and australopiths, which help the head sense and adjust to the rapid pitching forces generated by running (56); narrow waists and shoulders that are largely decoupled from the head, and which allow the torso to rotate independently of the pelvis and head; a nuchal ligament, which helps passively stabilize the head during running (90); and an expanded cranial portion of the gluteus maximus to counter high pitching forces on the trunk (92). Another set of derived skeletal features relevant to running performance may be adaptations to cope with the higher internal and external forces generated by running. These features including relatively larger joint surface areas in the lower extremities and lower spine (72, 135); short toes, which decrease moments around the metatarsophalangeal joints (132); and a shorter femoral neck (94).

Below we will consider why selection might have favored adaptations for long-distance running in *Homo*, but there is reason to speculate that climbing performance must have been compromised by some of these features, notably low shoulders that have fewer muscular connections to the upper spine and head, relatively shorter forearms, shorter and straighter toes, and relatively longer legs (2). Selection for endurance running may therefore explain why humans are the only primate that is poorly adapted for arboreal locomotion. That said, not all derived features in *Homo* are adaptations for running; some of them would also have benefited walking, and some might be related to other functional tasks such as throwing or tool-making (127).

Altogether, each of the three major transitions in hominin locomotion (facultative bipedalism and climbing in early hominins, habitual walking and facultative climbing in australopiths, and walking and running in the genus *Homo*) was contingent on previous events, was driven by climatic change, and involved trade-offs. It is worth reiterating that selection for bipedalism was probably spurred by fragmentation of rain forest habitats and might not have been advantageous had the LCA not been relatively inefficient (a hypothesis that is dependent on how one reconstructs the LCA). Whatever its initial benefits, habitual bipedalism resulted in a loss of stability and speed among early hominins. Selection for more dedicated long distance walking in *Australopithecus* took place in the context of increasing cooling and drying of Africa over the Pliocene (26, 111). Such conditions would have favored hominins better able to walk long distances to forage for widely dispersed foods in increasingly open, arid, and hot habitats. Although the australopiths retained many adaptations for arboreal locomotion, selection for more efficient

walking possibly came at the expense of some performance abilities in the trees. Finally, running was probably selected for as open grassland habitats continued to expand as the Ice Age began between 3 and 2 Ma (see Fig. 2). Expansion of these habitats favored the evolution of many herbivores, in turn leading to selection for a variety of carnivores, of which *Homo* appears to be just one example (166). Since bipedal hominins are necessarily slow (two legs can generate half the power of four legs), endurance running may have been an adaptation to enable bipedal hominins to hunt herbivores in a novel way known as persistence hunting, which also requires adaptations for dumping heat. However, before evaluating hypotheses for how selection may have favored the transitions described above, it is first necessary to review the derived thermoregulatory features that enable active humans to keep cool, and how and when these adaptations might have evolved.

Heat Exchange

Compared to most mammals, humans have an impressive ability to keep cool during strenuous physical activity in hot conditions. In fact, as argued below, these capabilities may have played an important role in hominin evolution, first helping slow, unsteady bipeds forage over long distances when predators were less likely to hunt them, and then helping hominins become diurnal predators themselves. Before evaluating these hypotheses, it is useful to first review the evolution of four derived sets of adaptations for preventing hyperthermia in humans: an increased ability to sweat; an external nose; enhanced ability to cool the brain; and an elongated, upright body.

Sweating

One of the most distinctive aspects of human anatomy and physiology is an increased capacity to cool through sweating. Sweating cools via evaporative heat loss when secreted water (sweat) vaporizes on the surface of the skin. Since it requires 580 calories (2426 J) to transfer 1 g of water at 35°C to water vapor at the same temperature, this phase transition transfers considerable energy in the form of heat from the organism to the atmosphere, thus cooling the body surface where the phase shift occurs.

Although sweating is an extremely effective method of cooling, it is a specialized form of heat exchange that derives from other forms of evapotranspiration, notably panting. Consequently, before discussing the origins and evolution of sweating, it is useful to first consider panting, which is the primary mechanism of cooling in all non-human mammals. Panting occurs from the evaporation of water in the upper respiratory tract, primarily in the oral cavity, the oropharynx, and the upper portion of the trachea. Since the respiratory epithelium of the pharynx is highly vascularized, evapotranspiration during panting efficiently cools blood, hence core body temperature. Panting is extremely efficient and effective, but

has several constraints. First, panting exchanges body heat only on the surface of the respiratory tract, whose area is limited even in animals that expand respiratory surface area with nasal turbinates, elongated snouts, or protruded tongues. Second, since panting primarily occurs in the dead space of the respiratory tract during shallow breaths, panting efficiency is elevated primarily by increasing the frequency of respiration while decreasing tidal volume (129, 146). However, rapid, shallow breaths cause CO₂ buildup in the lungs, risking alkalosis and requiring the alternation of panting breaths that ventilate only dead space with deep, inspiratory breaths. This alternation, moreover, is prevented in galloping quadrupeds in which fore-aft tilting of the body causes the viscera to oscillate forcefully in phase with stride frequency, inhibiting diaphragmatic contractions between strides (14). As a result, most quadrupeds cannot gallop for long distances in hot conditions because they cannot pant while galloping, and thus rapidly overheat (162).

Given the limitations of panting, it is hardly surprising that natural selection has favored alternate means of heat exchange through evapotranspiration on the skin's surface. A few mammals such as rodents and kangaroos apply saliva to their skin (36), but the most efficient strategy is to sweat, which takes advantage of large surface areas. Heat exchange through sweating has only evolved in a few mammals because it requires at least three factors, all of which are derived in humans: the ability to sweat enough but not too much water on the skin's surface, air convection at the skin's surface, and effective conduction of blood below the skin's surface.

Eccrine glands

Sweating in which evapotranspiration occurs on the body surface is not unique to humans, but humans have a specially elaborated system of cutaneous sweat glands that differs in several important respects from other mammals, including those that also sweat. To understand these differences it is necessary to distinguish between apocrine and eccrine glands (Fig. 5). Apocrine glands consist of a large, spongy-shaped secretory duct that is located deep within the dermis, combined with a long, more tubular excretory duct that leads to a hair follicle, often in conjunction with a sebaceous gland (leading to the alternate term *epitrichial gland*, which means "by the hair"). Apocrine glands are controlled by sympathetic adrenergic nerves, and secrete in association with sebaceous glands a viscous fluid that includes lipids, proteins, and steroids. In contrast, eccrine glands are smaller than apocrine glands, lie only in the outer portion of the dermis, and consist of a coiled secretory tube and a relatively straight excretory duct that extends to the skin's surface. The excretory duct of eccrine glands is formed by a double layer of epithelial cells that are capable of resorbing some of the constituents of sweat, especially salt, thereby allowing eccrine sweat to average about 99 percent water. Unlike apocrine glands, eccrine glands are not directly associated with hair follicles, and they are innervated by sympathetic cholinergic nerves.

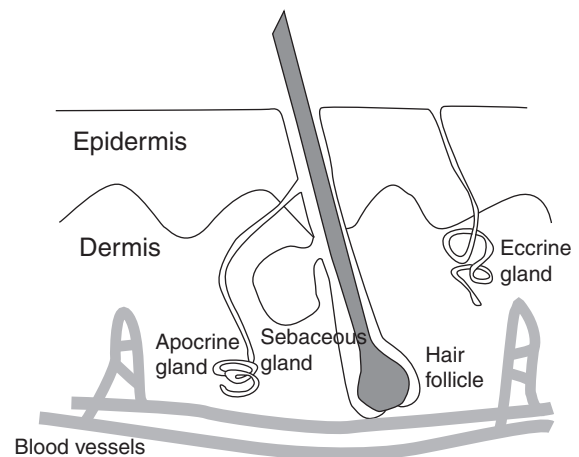


Figure 5 Schematic of differences between eccrine and apocrine glands (see text for details)

Humans, like most mammals, have both apocrine and eccrine glands, but differ in the relative distribution and number of these gland types. Almost all mammals have apocrine glands in certain regions of the skin in association with hair follicles but develop eccrine glands solely in the palms of the hands and soles of the feet to increase frictional gripping capabilities (1). Although apocrine glands probably evolved to produce odorants for olfactory and pheromonal communication, several groups of mammals evolved the ability to use apocrine glands for cooling by evapotranspiration. The best-studied mammals are tropical ungulates such as cows, sheep, camels, goats, and horses, which are known to sweat when thermally stressed (19, 145, 183, 190). Not all ungulates, however, use apocrine glands for thermoregulation, a capacity which appears to correlate with short fur (see below) and body size; smaller, furrer mammals rely almost entirely on panting, while larger, short-haired animals have higher densities of sweat glands to dump more heat (130). One interesting exception to these trends is the Bedouin black goat, whose black fur absorbs radiant heat, posing a special thermoregulatory challenge that may have triggered selection for copious sweat production by a relatively small number of apocrine glands (13, 70). Marsupials such as kangaroos also use apocrine sweat for cooling, but only during vigorous physical activity (37).

The evolution of cutaneous glands in primates followed a very different path. Like most small-bodied mammals, strepsirrhine primates (lemurs, lorises, and galagos) and New World Monkeys (platyrrhines) have mostly apocrine glands over the general body surface and lose evaporative heat only by panting (65). Although reliable data from most primate species are not available, enough evidence exists to indicate that Old World Monkeys (catarrhines) uniquely evolved an elaborated system of eccrine glands, comprising approximately 50 percent of subcutaneous glands (53, 61, 71, 80, 104, 105, 141, 183). Data on gland distribution from apes are also limited, but several studies report that gibbons and orangutans

resemble Old World Monkeys, and that approximately two-thirds of the cutaneous glands in chimpanzees and gorillas are eccrine (43,48,105). Assuming these data are correct, the fact that human cutaneous glands are nearly 100% eccrine indicates that humans are most appropriately viewed as the extreme of a trend among monkeys and apes. To what extent the high density of human eccrine glands results from more eccrine glands relative to other primates as well as from fewer apocrine glands is poorly established but both factors may be important. Eccrine gland density in chimps is reported to be 50% of that in humans (105). In addition, although human embryos develop apocrine gland placodes throughout the skin, these incipient glands atrophy and disappear everywhere except the axillary and pubic regions (12,142), where apocrine glands still perform ancient communicative functions.

Although eccrine glands are likely denser and more numerous in humans than in other primates, including apes, their evaporative function is nonetheless similar. Several studies have demonstrated that non-human primates sweat in response to heat and/or exercise stress (71,98,157) and that acclimatization to thermal stress increases this response in monkeys and apes as in humans (65,141,157). These studies did not separate the relative contributions of apocrine and eccrine secretions to sweat, but the limited evidence available suggests that total sweat rates in non-human primates are much lower than in humans. Hiley (65) reported maximum secretion rates of 97 and 80 g/m²/h in baboons and chimpanzees, respectively, similar to heat-induced apocrine secretion rates reported in ungulates (32–150 g/m²/h), and far below the maximum values recorded in humans, which vary between 366 to 884 g/m²/h (47). It is therefore unlikely that non-human primates can match maximum sweating rates in humans, which typically exceed 1 L/h (48). It also unknown how effective non-human primate sweating is in terms of heat exchange.

Fur loss

One critical factor that influences the effectiveness of evapo-transpiration for heat exchange is hair, especially dense hair, colloquially known as fur. Almost all mammals have fur, which has multiple functions that include protection (e.g., from bites and thorns), visual communication, camouflage, reflecting radiant heat, and acting as an insulator by limiting thermal conduction (heat transfer from the body surface to the outside) and convection (the movement of air relative to the body surface). However, the thickness and density of fur results in two trade-offs for sweating animals. First, evapo-transpiration cools the body only if the phase transition from water to vapor occurs along the skin's surface, where it can cool underlying blood. Fur thus hinders effective cooling by moving the location of most evaporation away from the skin's surface. Second, fur inhibits or reduces air convection at the skin's surface, limiting the rate of evaporation where it has the highest cooling potential. As one would predict, mammals that use sweat to cool tend to have short, sparse fur (128). In

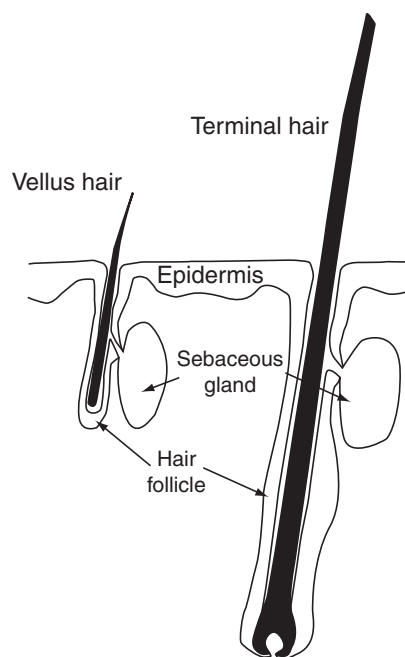


Figure 6 Schematic of differences between vellus and terminal hair (see text for details).

one famous experiment, Schmidt-Nielsen (144) found that shearing a camel (fed *ad libitum* water) doubled its rate of water loss after being shorn.

Humans are typically described as mostly hairless, but a more accurate description is that they are mostly furless. The average human has approximately 2 to 5 million hairs on the body surface, with a density of 500 to 1000 follicles/cm² in a neonate and 55 to 800 follicles/cm² in adults with much variation depending on body region, sex, hair color, and other factors (170). However, with the exception of the scalp, axilla, and pubic regions, almost all hair follicles in humans produce vellus rather than terminal hair (Fig. 6). Vellus hairs, which are extremely fine and less than 2 mm long, grow from shallow follicles that are not connected to sebaceous glands (99). During ontogeny, vellus hair follicles are converted by androgens (primarily dihydrotestosterone) to terminal follicles, which are deeper, larger and connected to sebaceous glands. Terminal hair is thus thicker, longer, and more pigmented. It is, therefore, incorrect to state that humans are hairless. Further, it is possible that the density of vellus hair follicles in humans follows predictions of scaling. As noted by Schwartz and Rosenblum (149), terminal hair density in primates scales with negative allometry relative to body surface area, with larger bodied primates such as chimps and gorillas having sparser terminal hair than gibbons or macaques. To test whether humans fit this trend will require comparative data on scaling of hair follicle density rather than just terminal hair density.

Despite much speculation over why and when humans were selected to be generally furless, the most popular hypotheses focus on thermoregulation because a transition

from terminal to vellus hair removes the insulation that fur normally provides and thus markedly increases air convection near the skin, allowing more heat exchange (3). One hypothesis is that selection on early hominins in more open habitats was made possible by the fact that large-bodied apes such as chimpanzees already have relatively sparse hair and thus lacked sufficient pelage for reflecting exogenous heat or protecting the skin from harmful UV radiation (148). Under such conditions, improved sweating efficiency led to selection for further fur loss as well as higher melanin content. A related hypothesis is that once hominins became bipedal, their bodies (except the tops of their heads) were exposed to significantly less solar radiation, decreasing the benefit of fur for reflecting radiation while simultaneously increasing the benefit of fur loss to increase the rate and efficiency of evaporative cooling by sweating (176-179). Another hypothesis is that selection for either trekking or long distance running promoted selection for fur loss because of the elevated need to dump endogenous heat production caused by running and walking (15, 136). These and other hypotheses are difficult to evaluate, however, in large part because we do not yet know when hominins transitioned from having predominantly vellus rather than terminal hair, and when eccrine gland distribution was elaborated.

Subcutaneous heat convection

Sweating exchanges heat only if evapotranspiration is able to cool blood near the skin's surface and then circulate the blood to the core, replacing it with more hot blood to be cooled. Consequently, another variable that affects efficient heat exchange from evapotranspiration is the extensiveness and control of blood circulation in the dermal layer of the skin. According to Montagna (Ref. 104: p. 16) "In no other animal is skin so abundantly vascularized, not even in the great apes." Published evidence to support this statement, however, is descriptive rather than quantitative (5) highlighting the need for detailed studies of differences in dermal vascularization between humans and non-human primates.

Nasal cooling

Most heat exchange occurs through evapotranspiration, but another set of derived adaptations for heat exchange in humans is in the nose, even though these adaptations are not regulated by reflexes and account for a smaller percentage of cooling. Like most terrestrial vertebrates, humans use the respiratory epithelium in the internal portion of the nose to warm or cool inspired air to approximately 37°C, and to add moisture to attain approximately 75% to 80% humidity by the time it reaches the lungs; about one-third of this heat and moisture is then recaptured during expiration in temperate conditions (30). One important difference between humans and other mammals, however, is the ratio of the surface area of nasal epithelium in the internal nose, where heat and moisture exchange occur, relative to the volume of airflow (which is

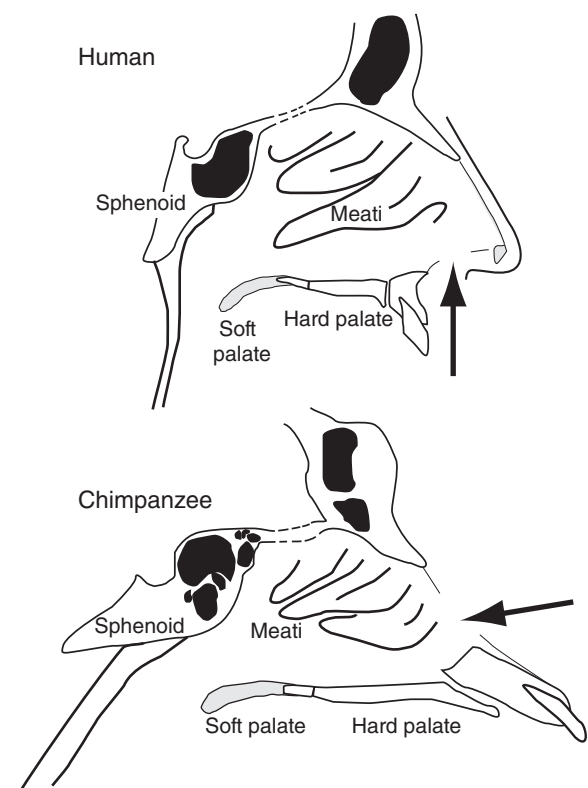


Figure 7 Midsagittal comparison of the external and internal nasal cavities in humans and chimpanzees. Note the lack of a rostrum in humans, combined with the presence of an external nasal cavity, which alters the orientation of flow through the nostrils, producing more turbulent flow.

proportional to body mass). Although many primates including chimpanzees have a generally shorter snout (rostrum) than other mammals, the genus *Homo* lacks a snout altogether (see Fig. 7). As a result, non-human primates have significantly smaller nasal epithelial surface areas relative to body mass than most mammals, reflecting the generally warm, humid environments in which they live (90). This ratio, however, is considerably more extreme in humans, whose short, retracted midface results in a nasal epithelium surface area one-tenth the expected value for a mammal of the same body mass, as shown in Figure 8 (90). Because of a relatively short neck, humans also have a similarly small tracheal surface area relative to body mass. Since the genus *Homo* appears to have evolved in hot, arid habitats (26), it is unlikely that midfacial shortening evolved in humans as a thermoregulatory adaptation. Instead, the small surface area/volume ratio of the nasal epithelium must have imposed special challenges by limiting the ability to exchange heat and moisture. As one might expect, humans appear to have evolved several related adaptations for heat exchange to cope with these constraints.

The first set of adaptations is to increase turbulence. In most mammals, airflow through the internal nose is primarily laminar, which has the advantage of generating less resistance but also creates a velocity gradient in which flow rates

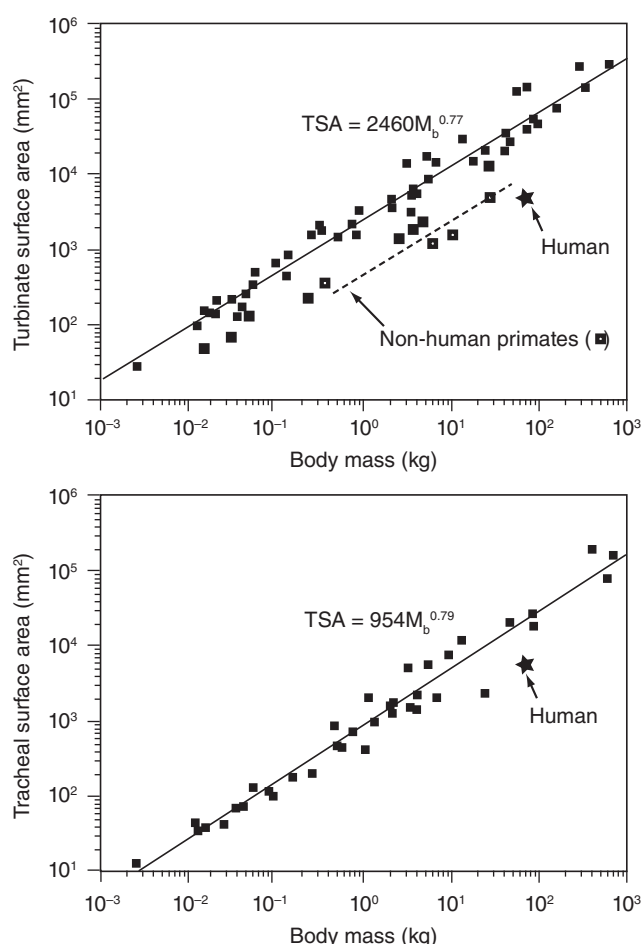


Figure 8 Scaling of surface area of the turbinates (top) and trachea (bottom) relative to body mass in a wide range of mammals. Humans fall significantly below the line (Data courtesy of T Owerkowitz, summarized in Ref. 90).

approach zero along the wall of the nose, forming an inert boundary zone estimated to be 0.25 mm in humans (56). Since this boundary is enough to reduce the respiratory epithelium's capacity for heat and moisture exchange, it is not surprising that the genus *Homo* evolved several features to increase turbulent flow in the nasal cavity, thus eliminating any laminar boundary and causing more air to flow across the epithelial surface. The most distinctive nasal feature that enhances turbulence is the external nose, unique to humans, in which a series of cartilages create a vestibular space that is mostly devoid of epithelium, but which orients the nares (nostrils) nearly 90° relative to the airway of the internal nose, increasing turbulence (29, 143). A related set of features that increase turbulence are several pairs of valve-like constrictions, 30 to 40 mm² in area, formed by the nostrils and between the external and internal nasal chambers. These valves function as Venturi throats (nozzles) that generate turbulence when air transitions from low velocity and high pressure in the external nasal cavity to high pressure and low velocity in the internal nose (169). There are also indications that the human

nose generates more turbulent airflow during exhalation, thus helping to conserve water, because of two additional derived features: the right angle formed between the nasopharynx and the internal nose, and the aperture created by the internal choanae (posterior nasal apertures) and the inner nose. The extent to which these features increase turbulence is untested.

Another important thermoregulatory adaptation in humans is obligate oral breathing during vigorous exercise. As described by the Hagen-Poiseuille equation, resistance in a tube increases in proportion to volumetric flow rate, and inversely to the tube's radius to the power of 4 during laminar flow and to the power of 5 during turbulent flow (70). Increases in flow rate and turbulence thus become a significant constraint during vigorous exercise when breathing rates more than double to 40 breaths/min and tidal volume can triple to 1.5 L/breath (31). Although exercising humans decrease air-flow resistance in the nasal cavity by increasing nostril diameter and expanding the nasal cavity through vasoconstriction of the respiratory mucosa (109, 138), resistance rapidly becomes too great for the lungs to overcome, requiring humans to switch to either oral breathing or combined oronasal breathing during vigorous exercise (107, 175). Intriguingly, humans are the only mammal species that switches to obligate oral or oronasal breathing during vigorous activity (103) raising the possibility it is an adaptation for dumping heat endurance running, but at the expense of greater rates of water loss (15).

Unlike sweating and fur loss, nasal adaptations can be partially traced in the fossil record, as shown in Figure 9. The most important line of evidence is eversion of the lateral margins of the nasal (piriform) aperture, which first appear in early *Homo* fossils ascribed to *H. habilis* and *H. erectus* that are dated to about 2 million years ago (51). This outward orientation of the piriform margins, unique to *Homo*, indicates that the nasal cartilages did not lie flat in the same plane as the rest of the midface, as in apes such as chimpanzees, but instead formed a protruding external nasal vestibule. Another line of evidence for enhanced nasal turbulence is the nasal sill (also shown in Fig. 9), a discontinuity between the nasal aperture and the inner nasal chamber that is absent in the African great apes, but first appears in some species of *Australopithecus* such as *Au. afarensis*, and is particularly pronounced in *Homo* (75). More recent selection for nasal shape related to turbulence is evident among modern humans populations that originated in Africa but then adapted to diverse environmental conditions over the last few hundred thousand years. Many studies have documented that modern human populations which have long been living in more arid climates (cold or hot) have significantly taller nasal apertures that are relatively more narrow and that have higher epithelial surface area to nasal volume ratios (23, 50, 67, 185, 189).

Brain cooling

A major thermoregulatory challenge for all animals is to maintain a stable temperature in the brain, and it is commonly argued that human brain cells can only briefly tolerate

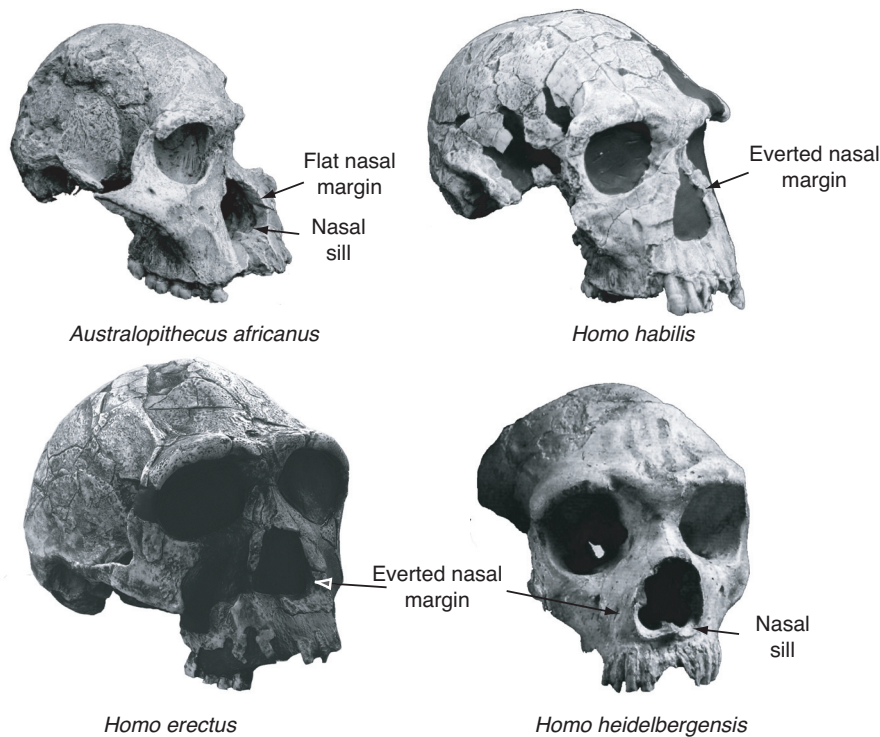


Figure 9 Comparison of the face in four hominin species showing variation in the nasal sills and margins. Top left, *Australopithecus africanus*; Top right, *Homo habilis*; Bottom left, early African *Homo erectus*; Bottom right, *Homo heidelbergensis*. In all species of *Homo*, the lateral margin of the nasal aperture is everted, indicating the presence of an external nose.

temperatures above 41°C (e.g., Refs. 21 and 45). Some tropical ungulates and carnivores evolved a carotid rete, in which cooled venous blood from the nasal cavity exchanges heat with carotid blood through a counter-current flowing anastomotic network, but retes never evolved in primates. Further, maintaining thermal homeostasis in the brain is a special problem in humans for two reasons. First, humans must cool relatively more brain tissue than any other terrestrial mammal because our brains are approximately five times larger than expected for a mammal of the same body mass (101). Second, humans are the only primate that regularly engages in prolonged vigorous activity in hot conditions. Are humans adapted to cooling the brain simply by cooling the core through sweating, or did hominins evolve additional mechanisms for neural cooling, and what role did these adaptations play in human brain evolution?

One uniquely human adaptation may be enhanced heat exchange in the head. According to several studies, the scalp has one of the highest densities of eccrine glands in the body (21,80), and it has been proposed that blood cooled by sweating in the scalp actually flows backward into the brain through tiny emissary veins, thus acting as a specialized, regional cooling system (20,45,191). This hypothesis, however, is controversial, and has yet to be supported by *in vivo* data. Another untested hypothesis is that humans have an expanded cavernous sinus compared to other primates (22). Such expansion would also be advantageous because it functions as a

counter-current exchange system in which cooled blood from the superficial cortical and ophthalmic veins passes around hotter arterial blood arising from the core. A final hypothesis is that the expanded thickness of spongy bone (diplöe) in the cranial vault of *Homo* acts as a thermal insulator keeping the brain cool (90).

Further research is needed to test if humans evolved special mechanisms for brain cooling and, if so, when they evolved. Falk (45) has shown that the frequency of emissary veins more than doubled in genus *Homo* compared to *Australopithecus*. If reverse flow occurs in these veins, then it is possible this cooling mechanism underwent selection as humans became more active runners or trekkers (see below). An alternative or additional hypothesis is that the evolution of these cooling mechanisms released constraints on the evolution of larger brains in active hominins (44).

Posture and body shape

A final category of features relevant to how hominins coped with heat stress is posture and variations in body shape. The most influential hypothesis, proposed by Wheeler, is that upright posture and locomotion was an adaptation to reduce exogenous heat gain from solar radiation (176). When the sun is at its zenith, a bipedal human exposes only 7% of its surface area to maximal radiation, approximately one-third the maximally exposed surface area of a similar-sized quadruped

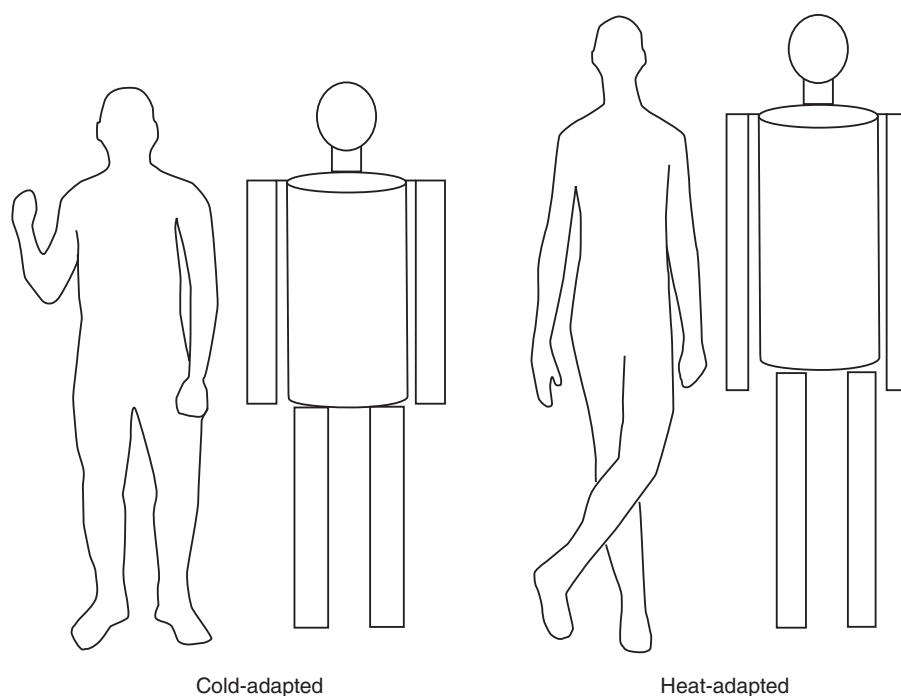


Figure 10 Schematic of Bergmann and Allen's rules, comparing cold- versus hot-adapted body forms (modified, with permission, from Ref. 134). The cold-adapted body form has a much lower ratio of surface area to volume.

(177, 179). Wheeler also argued that bipedalism is adaptive for sweating by elevating the torso, forelimbs and head higher above the ground surface where wind speed is greater and temperatures are lower (178). Wheeler's model clearly predicts that furless, sweating hominins would have had a thermoregulatory advantage if they were upright bipeds, but it is unclear if early hominins were furless, how much radiation they were exposed to, and to what extent they were active at midday, when most animals in open habitats seek shade. It is therefore unclear whether bipedal posture evolved to facilitate heat exchange among the first hominins, or whether sweating and fur loss evolved later in human evolution, perhaps in the genus *Homo*.

Related factors that influence heat exchange are body size and limb length (see Fig. 10), both of which affect surface area to volume ratios because the volume of an object such as a sphere scales to its radius to the power of three ($4/3\pi r^3$) but the surface area scales to its radius to the power of two ($4\pi r^2$). As classically formulated, Bergmann's rule states that within homeothermic species, populations in colder regions will be larger than those in warmer regions in order to retain heat by minimizing surface area to volume ratios. Because extremities such as limbs, tails and ears have high surface area to volume ratios, a related ecogeographical trend is Allen's rule, that populations in colder regions have relatively shorter extremities than populations in warmer regions. Although Bergmann's rule has been shown to apply to many birds and mammals (103), it is only partly relevant to hominins because bipedal body shape is better approximated as a cylinder in

which the surface area to volume ratio remains constant independent of height as long as the radius is constant (134). Among human populations, the correlation between latitude and hip width is approximately 0.90, independent of variation in stature (134), but body mass correlates with latitude only for extreme comparisons (49). These findings help explain why species in the genus *Homo* such as early African *H. erectus* that lived in open, hot habitats have relatively narrow pelves, whereas archaic *Homo* species such as Neanderthals that lived in Ice Age Eurasia have relatively wide pelves (2). Allen's rule has also been shown to explain much ecogeographical human variation, with populations from relatively warmer climates having longer limbs relative to body mass than those from colder habitats (164). Since most variation in upper and lower extremity length is caused by variation in humerus or femur length relative to body mass, the ratio of the radius to humerus (brachial index) and the tibia to femur (crural index) are strongly correlated with latitude in both extant and fossil human populations (165).

Evolutionary scenarios linking locomotion and heat loss

Although the first hominins were probably either occasional or habitual bipeds, special human abilities to walk and run long distances evolved subsequently over the course of several major transitions, with more efficient walking probably being selected for in some species of *Australopithecus* and

endurance running then evolving in *Homo* possibly along with additional improved walking capabilities. As summarized above, we do not know when hominins developed the ability to cool effectively through sweating by increasing the density of eccrine glands and losing fur, but other improved abilities to lose heat can be seen to a limited extent in *Australopithecus* (notably body shape) and then to a considerable extent in the genus *Homo*. Given the many functional roles of hominin locomotor and thermoregulatory capabilities, these adaptations must have evolved partly independently as a result of multiple selective pressures. However, there are several reasons to speculate that selection for long distance walking and then running also drove selection for more effective cooling. Two hypothetical scenarios best fit the evidence.

Hypothesis 1: Predator avoidance while walking in open habitats

One longstanding and very common hypothesis is that selection for living in more open, hot and arid habitats drove selection for hominins to become more efficient walkers in order to forage for more widely distributed food and simultaneously drove selection for more efficient heat dumping to cope with the thermoregulatory challenges of trekking in the heat. There are several problems with this popular hypothesis (often termed the savanna hypothesis). First, although the earliest hominins may have evolved in less densely forested habitats in which fruits were scattered in smaller, more distant patches and thus required more walking, the anatomy of the partial *Ardipithecus* skeleton and other early hominin fossils suggest that they were adapted for a combination of climbing plus bipedal walking. More data are needed on early hominin anatomy, but many adaptations for increased bipedal efficiency such as an adducted big toe or long legs, do not appear until later. In addition, although there is debate over how open the habitats of early hominins such as *Ardipithecus*, *Sahelanthropus* and *Orrorin* were, they were not open savannas without a substantial degree of tree cover (25, 26, 180).

Another problem with the savanna hypothesis as an explanation for the origins of bipedalism and fur loss is the inability to explain why these derived features evolved in just hominins and not in other mammals in the same habitats. As noted previously, some African ungulates did evolve elaborated apocrine sweat capabilities along with carotid retes and expanded nasal turbinates (34, 128). However, bipedalism is an unusual form of locomotion with substantial costs in terms of speed and stability, and which has evolved contingently only a few times. It is hard to imagine how other African mammals in open habitats would have benefited from switching to bipedal locomotion had they not been descended from African great apes. As discussed above, a reasonable hypothesis is that bipedalism was selected in early hominins primarily because they evolved from a knuckle-walking ancestor whose cost of transport was approximately four times greater than most other mammals, including humans (154). Alternatively or additionally, bipedalism may have evolved because

its benefits for feeding outweighed any costs for locomotion (32, 33, 163). In either case, incipient bipedalism is likely to have been intermediate in efficiency, and would not have necessarily entailed selection for enhanced abilities to cool. Put differently, selection for early bipedalism should not to be confused with later selection for more efficient bipedalism and possibly thermoregulation when hominins did eventually occupy very open habitats. Testing this hypothesis will require better data on the habitats and locomotor capabilities of early hominins.

Natural selection often favors efficiency, but an additional important selective factor for hominins in open habitats must have been predation. Bipedal hominins are necessarily slow because two legs generate approximately half as much power as four legs. The world's fastest sprinters can achieve top speeds slightly in excess of 10 m/s for only short durations, roughly half the speed of equivalent-sized quadrupeds with much shorter legs (52). It is thus reasonable to infer that hominins who had to forage by walking long distances in open habitats were easy prey for predators such as lions and sabertooth tigers. In this context, enhanced thermoregulatory abilities might have been strongly favored by natural selection because they would have enabled hominins to preferentially forage during the hottest times of the day when predators are generally constrained to rest and cannot run very far at high speeds. In other words, increased abilities to dump heat might have coevolved with increased walking efficiency to increase foraging safety and efficiency in hot, open habitats with sparsely distributed resources. Testing this hypothesis will be difficult, because its major prediction is that high densities of eccrine glands and lower densities of terminal hair evolved in the genus *Australopithecus* or possibly earlier. Also needed to test this hypothesis are better data on the habitats in which these hominins lived, as well as reliable estimates of their day ranges (see Ref. 116).

Hypothesis 2: Hunting and gathering

Another hypothesis that has received considerable attention is that selection for increased locomotor and thermoregulatory efficiency occurred primarily in the genus *Homo* because of the evolution of hunting and gathering. The hunting and gathering economic system is complex and multifactorial, involving a combination of long distance foraging, hunting, tool-making, and intense cooperation such as food-sharing and division of labor (74, 100). Although foraging and some degree of tool-using were almost certainly part of the australopith behavioral repertoire, there are multiple lines of archaeological and paleontological evidence that the hunting and gathering system evolved as a whole in the genus *Homo* (see Refs. 78 and 91). Species of *Homo*, especially starting with *H. erectus*, also differ morphologically from australopiths in many ways likely relevant to hunting and gathering.

Since the primary gait of hunter-gatherers is walking, the most common hypothesis invoked to explain these differences

is that the genus *Homo* was selected for long distance walking (trekking), which would have also favored sweating and fur loss in open habitats. Evidence to support this hypothesis includes many derived features in *H. erectus* that would have improved walking performance such as long legs, relatively larger lower extremity joints, and essentially modern feet (for review, see Ref. 2). Although we do not know when enhanced sweating and the loss of fur evolved, external noses, which play vital roles in heat and moisture exchange during walking (but not running) also first appear in the genus *Homo* (51). In addition, there is no question that the habitats in which early *Homo* evolved in Africa were hot, arid and open. Regardless of debates whether australopiths were inefficient, bent-hip-bent-kneed bipeds, it seems reasonable to hypothesize that there would have been strong selection among hunting and gathering hominins to walk as efficiently as possible and to tolerate thermal stress, especially if they were active during the midday to avoid predators (see above).

An additional, related hypothesis that is not entirely exclusive with selection for trekking is that there was strong selection in *Homo* for long distance running. As noted above, humans have superlative abilities to run long distances, in large part because of an extensive suite of adaptations for running that have little or no effect on walking performance. Such adaptations include elongated tendons such as the Achilles, relatively short toes, an expanded cranial portion of the gluteus maximus, a narrow waist, a nuchal ligament, and enlarged anterior and posterior semicircular canals (15, 92, 132, 155). In addition, running is considerably more thermogenic than walking, yet novel heat exchange adaptations make humans unique among mammals in being able to run long distances in hot conditions (89). It follows that although walking is unquestionably important in human evolution, walking alone is unable to explain the combination of unique locomotor and thermoregulatory adaptations that evolved in the genus *Homo*.

A potential explanation for these evolved capabilities is that there was also selection for the ability to hunt by chasing animals at running speeds over long distances in the heat, a strategy known as Persistence Hunting (PH). To appreciate the likely significance of PH, it is useful to consider that there is abundant evidence that early *Homo* was hunting large, mature bovids more than 2 million years ago without any of the deadly projectile technologies employed by recent hunter-gatherers (16, 42). Before the invention of stone points 500,000 years ago (184) and the bow and arrow less than 100,000 years ago (152), the most lethal weapons available to early *Homo* hunters were rocks and untipped wooden spears. Consequently, hunters would have needed to kill prey at close range, which is extremely dangerous and thus avoided (27). PH, however, takes advantage of human abilities to run long distances in hot conditions at speeds that require their prey to gallop, thus driving them into hyperthermia (15, 24). As documented by Liebenberg (86, 87), persistence hunts usually occur during peak heat, often in temperatures above 30°C, and focus on large prey, presumably because larger animals

generate relatively more body heat when running. Persistence hunts usually involve alternating chasing and tracking phases. During the chasing phase, runners run after their prey at a speed that makes the animal gallop and thus gain heat; during the tracking phase, which occurs after the prey has galloped away from the hunter, the hunter tries to follow and locate the animal, usually at a walking pace, while the prey seeks shade and rests. If the hunter can resume chasing the animal before it has recovered a normal core body temperature, then the prey's core body temperature will keep rising until it reaches a hyperthermic state, at which point the hunter can dispatch it from a close distance without danger or sophisticated weapons. Persistence hunting thus requires the hunter to be able to run at speeds that make quadrupeds gallop, to track, and to keep cool without dehydrating. Further, contrary to some misconceptions (112, 156), PH does not require the ability to run 35 to 40 km without stop, but instead involves roughly equal proportions of walking and running at moderate speeds over distances ranging from 15 to 40 km. The greatest physiological constraint for humans is water. Yet according to ethnographic accounts by Liebenberg (86, 87), Kalahari Bushmen are able to hunt this way without dehydrating in part by drinking copiously before starting a PH. When and to what extent runners carried water in containers such as ostrich eggshells or gourds is unknown. Note also that endurance running is only 30% to 50% more costly than walking (133), but that the energetic returns from hunting are typically orders of magnitude higher (100), especially for persistence hunting, which has a much higher success rate than bow and arrow hunting (87). Consequently, persistence hunting would have been a beneficial strategy among even energy-limited hunter gatherers.

Another hypothesized advantage for the evolution of derived endurance running and thermoregulatory capabilities in hominins is scavenging. All carnivores including modern hunter-gatherers sometimes scavenge, but competition for carcasses is intense and also requires speed and fighting (167). One hypothesis is that hominins first started to incorporate meat in their diet by scavenging for carcasses in open habitats, perhaps through cues such as circling vultures in the distance (15). Since hyenas, like other quadrupeds avoid running during the midday heat, hominins with the ability to run without overheating would have had an advantage scavenging for carcasses at times of low competition with other carnivores. This behavior is still practiced by modern hunter-gatherers (100, 108, 153), and might have been an important intermediate stage between foraging and hunting and gathering.

Like many evolutionary hypotheses, the PH and scavenging hypotheses are difficult to test rigorously, but they fit many lines of evidence. Most obviously, selection for scavenging and PH helps explain why many derived adaptations for endurance running appear at about the same time as the oldest evidence for meat-eating in human evolution (15). In addition, these adaptations also appear approximately when both meat-eating and bigger brains evolved. Perhaps the

ability to hunt released a constraint on selection for relatively larger brains, which require plentiful energy and fat, which are scarce resources. Additionally or alternatively, tracking during persistence hunting employs complex cognitive skills that would have benefited from more encephalization. The origins of the final component of this behavioral strategy—the ability to dump heat effectively from increased densities of eccrine glands and loss of fur—remains elusive. Without knowing the genes underlying these adaptations and when they evolved, it is not yet possible to test whether selection for improved heat exchange was driven by PH in *Homo*, was made possible by previous selection for long distance walking and predator avoidance in *Australopithecus*, or some combination of the two. Further, while selection for the ability to lose heat would have been important for male and female hunter-gatherers, it is not possible to test whether selection for endurance running was solely or primarily in males. Males who hunt more effectively have been shown to have higher reproductive success than less skilled hunters (see Ref. 100), but females can also run well. Although hunting is generally done by males not females (74), women who are not mothers (e.g., teenagers) might have benefited from the ability to scavenge or persistence hunt. Alternatively or additionally, adaptations for endurance running are not sex-linked.

Other selective forces

Despite the important interdependence between locomotion and heat exchange, other selective forces almost certainly played roles in the evolution of human bipedalism, fur loss, sweating and related adaptations. In addition to selection for feeding and foraging (discussed above), hypothesized selective forces on bipedalism have included food carrying and food-provisioning (96, 102), tool-using (35, 64, 173), the ability to see over tall grasses, and even swimming or wading (106, 187). Similarly, in addition to selection for dumping excess heat during locomotion, the evolution of fur loss (but not sweating) has been proposed to have arisen from selection against ectoparasites (110, 122, 123), sexual selection (35), and aquatic habitats (106, 187). It is beyond the scope of this review to evaluate these hypotheses, which have varying degrees of merit (for reviews, see Refs. 46, 60, 81, 91, 172). Although some of these selective forces (and probably others) were undoubtedly important factors in human evolution, it is important to emphasize that selection for efficient long distance walking and running must have been partly contingent on and entailed additional selection for improved abilities to dump heat. In the case of walking, bipedal hominins would have been at a severe disadvantage walking long distances if they could not have done so during times of peak heat when their inability to sprint rapidly would have placed them at high risk of predation from lions, saber-toothed cats and other carnivores. In addition, the ability to persistence hunt is fundamentally based on the ability to keep cool while running, which is extremely thermogenic.

Recent evolution and contemporary relevance

Although species in the genus *Homo* spread over much of the Old World during the Pleistocene, *H. sapiens* (modern humans) evolved in Africa between 200,000 and 300,000 years ago, and then subsequently dispersed into Eurasia, Oceania, and the New World over the last 100,000 years (78). As modern humans moved into new habitats with different ecologies and climatic conditions, they interbred a little with archaic human species such as Neanderthals (*H. neanderthalensis*) that had inhabited these regions for long periods of time, but for the most part modern humans replaced archaic humans (124, 140). Since the first modern humans were all African hunter-gatherers, primarily adapted to cope with walking and running long distances in hot, arid conditions, these pioneers must have faced serious thermoregulatory challenges as well as the need to change their locomotor behaviors as they dispersed into different environments. Moreover, because this period was the most intense period of the Ice Age, the Late Pleistocene, the most extreme challenges must have been those faced by early modern humans in highly seasonal temperate habitats.

Modern humans in different regions coped in two ways. The most potent adaptations were obviously cultural, made possible by modern human abilities and proclivities to innovate, communicate, and cooperate. Cultural evolution led to a stunning variety of technologies and behaviors that have enabled hunter-gatherers to live in almost every habitat, including the arctic. Although innovations such as complex clothing and shelters (and eventually the agricultural and industrial revolutions) partially buffered humans from natural selection, they accelerated natural selection in other respects by enabling people to live in novel habitats and by increasing population sizes, hence the number of available mutations on which selection can act (62). For example, humans in the arctic would not have been selected to have relatively shorter limbs had not their clothing, harpoon technology and other innovations enabled them to survive in cold conditions in the first place. Although approximately 86% of the genetic variation in *H. sapiens* is within rather than between populations (7, 85), the combined result of cultural evolution and natural selection has been an integrated and interrelated combination of cultural and physiological adaptations that contribute to modern human diversity. Most of these regional variations reflect selection for disease and diet, but a few reflect selection for thermoregulation (92, 137).

In terms of adaptation for thermoregulation, the most conspicuous source of diversity is skin pigmentation, which is strongly correlated with UV levels, probably reflecting a trade-off between protecting the skin from radiation with inhibiting vitamin D synthesis (69). Another source of climate-related variation is body shape and size. The earliest modern humans who moved into Europe came from Africa, and thus it should be unsurprising that they were generally tall and relatively narrow, but over millennia selection drove

European populations towards more cold-adapted shapes with larger body masses and relatively shorter limbs (66). Other evidence for regional selection related to climate includes variations in nasal shape (189), and eccrine gland density (79, 174). Another candidate for ecogeographical selection is EDAR370A, an allele that arose in East Asia approximately 30,000 years ago that is associated with more numerous eccrine glands and thicker hair, but which also affects other traits such as incisor shape and breast size (73).

There is much less evidence for regional selection on locomotion. One well studied candidate is ACTN3, which affects the relative percentage of fast-twitch and slow twitch fibers, and which has a variant, R577X, that has been associated among some (but not all) populations with high percentages of fast twitch fibers better adapted for power and speed (188). It is possible that as some human populations experienced more selection for power relative to endurance as they moved into novel habitats or (more likely) became farmers. Additional candidates for selection on locomotion include relative heel length, toe length, and limb length (83, 115, 120, 132). Future research is needed to test these and other related hypotheses.

Conclusion

In conclusion, through a series of contingent events, many driven by climate change, hominins evolved a series of adaptations for bipedal walking and then running, which were probably the main impetus for additional selection for sweating, fur loss, and other adaptations for effective heat loss during vigorous activity. Regardless of differences within and between populations, all humans have remarkable abilities to walk and run long distances, and as a species we are generally well adapted for endurance. In addition, because of the endogenous heat gain caused by endurance activities, combined with our tropical origins, all humans are well adapted to lose heat. Despite some recent selection and much sophisticated technology, this unique and integrated suite of endurance and heat loss adaptations remain fundamental to human physiology.

Although we have learned much over the last few decades about the evolutionary history of human locomotion and thermoregulation, considerable additional research is needed. For one, there is a strong need for more fossils not just of early hominins, but also from the African great apes in order to test hypotheses about the anatomy of the LCA of humans and chimpanzees. We also need to develop better tools to test hypotheses about the nature of early hominin locomotion from fossils (e.g., from the structure of trabeculae within joints), and on the ecological contexts in which they were walking and running. The evolution of human thermoregulation is even more murky, largely because the really key physiological features that underlie them leave no fossil traces. The most promising avenues for research in this field will be to understand the genetic and developmental bases for the loss of fur and elaboration of sweat glands in humans, and then study the evolutionary history of these genes. And finally, we know

remarkably little about the recent evolution of these anatomical and physiological features within different modern human populations. Overall, an integrated, evolutionary approach to human locomotion and thermoregulation will help illuminate how and why humans are the way we are.

Acknowledgements

I am grateful to Dennis Bramble, David Carrier, Yana Kamberov, Bruce Morgan, Pardis Sabeti, Cliff Tabin, Sijia Wang, and Sara Wright for their insights and for many long discussions about the topics reviewed here.

References

- Adelman S, Taylor CR, Heglund MC. Sweating on paws and palms: What is its function. *Am J Physiol* 229: 1400-1402, 1975.
- Aiello L, Dean MA. *An Introduction to Human Evolutionary Anatomy*. London: Academic Press, 1990.
- Al-Ramamneh D, Gerken M, Riek A. Effect of shearing on water turnover and thermobiological variables in German Blackhead mutton sheep. *J Anim Sci*. 89: 4294-4304, 2011.
- Almécija S, Tallman M, Alba DM, Pina M, Moyà-Solà S, Jungers WL. The femur of *Orrorin tugenensis* exhibits morphometric affinities with both Miocene apes and later hominins. *Nat Commun* 4: 2888, 2013.
- Baccaredda-Boy A. A note on the cutaneous arterial vessels of some primates. *Angiologica* 1: 209-212, 1964.
- Barak MM, Lieberman DE, Raichlen D, Pontzer H, Warrener AG, Hublin JJ. Trabecular Evidence for a human-like gait in *Australopithecus africanus*. *PLoS One* 8: e77687, 2013.
- Barbujani G, Magagnoli A, Minch E, Cavalli-Sforza LL. An apportionment of human DNA diversity. *Proc Natl Acad Sci U S A* 94: 4516-4519, 1997.
- Bennett MR, Harris JW, Richmond BG, Braun DR, Mbua E, Kiura P, Olago D, Kibunjia M, Omuombo C, Behrensmeyer AK, Huddart D, Gonzalez S. Early hominin foot morphology based on 1.5-million-year-old footprints from Ileret, Kenya. *Science*. 323: 1197-1201, 2009.
- Berge C, Penin X. Ontogenetic allometry, heterochrony, and interspecific differences in the skull of African apes, using tridimensional Procrustes analysis. *Am J Phys Anthropol* 124: 124-138, 2004.
- Biewener AA. Scaling body support in mammals: Limb posture and muscle mechanics. *Science*. 245: 45-48, 1989.
- Bobe R. Fossil mammals and paleoenvironments in the Omo-Turkana Basin. *Evol Anthropol* 20: 254-263, 2011.
- Bolognia JL, Jorizzo J, Schaffer J *Dermatology* (3rd ed). Philadelphia: WL Saunders, 2012.
- Borut A, Dmi'el R, Shkolnik A. Heat balance of resting and walking goats: Comparison of climatic chamber and exposure in the desert. *Physiol Zool* 52: 105-112, 1979.
- Bramble DM, Jenkins FA Jr. Mammalian locomotor-respiratory integration: Implications for diaphragmatic and pulmonary design. *Science* 262: 235-240, 1993.
- Bramble, DM, Lieberman DE. Endurance running and the evolution of *Homo*. *Nature* 432: 354-352, 2004.
- Braun DR, Harris JW, Levin NE, McCoy JT, Herries AI, Bamford MK, Bishop LC, Richmond BG, Kibunjia M. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Myr ago in East Turkana, Kenya. *Proc Nat Acad Sci USA* 107: 10002-10007, 2010.
- Brunet M, Guy F, Pilbeam D, Lieberman DE, Likius A, Mackaye HT, Ponce de León MS, Zollikofer CP, Vignaud P. New material of the earliest hominid from the Upper Miocene of Chad. *Nature* 434: 752-755, 2005.
- Brunet M, Guy F, Pilbeam D, Mackaye HT, Likius A, Aounta D, Beauvilain A, Blondel C, Bocherens H, Boisserie JR, De Bonis L, Coppens Y, Dejax J, Denys C, Duringer P, Eisenmann V, Fanone G, Fronty P, Geraads D, Lehmann T, Lihoreau F, Louchart A, Mahamat A, Merceron G, Mouchelin G, Otero O, Pelaez Campomanes P, Ponce De Leon M, Rage JC, Sapanet M, Schuster M, Sudre J, Tassy P, Valentin X, Vignaud P, Viriot L, Zazzo A, Zollikofer C. A new hominid from the upper Miocene of Chad, central Africa. *Nature* 418: 145-151, 2002.
- Bullard RW, Dill DB, Yousef MK. Responses of the burro to desert heat stress. *J Appl Physiol* 29: 159-166, 1970.
- Cabanac M. Selective brain cooling in humans: "fancy" or fact? *Fed Am Soc Exp Biol* 17: 1143-1146, 1993.

21. Cabanac M, Brinnet H. Beards, baldness, and sweat secretion. *Eu J Appl Physiol Occup Physiol* 58: 39-46, 1988.
22. Cabanac M, Caputa M. Natural selective cooling of the human brain: Evidence of its occurrence and magnitude. *J Physiol* 286: 255-264, 1979.
23. Carey JW, Steegman, AT Jr. Human nasal protrusion, latitude and climate. *Am J Phys Anthropol* 56: 313-319, 1981.
24. Carrier D. Energetic paradox of human running and hominid evolution. *Curr Anthropol* 25: 483-495, 1984.
25. Cerling TE, Levin NE, Quade J, Wynn JG, Fox DL, Kingston JD, Klein RG, Brown FH. Comment on the paleoenvironment of *Ardipithecus ramidus*. *Science* 328: 1105-1106, 2010.
26. Cerling TE, Wynn JG, Andanje SA, Bird MI, Korir DK, Levin NE, Mace W, Macharia AN, Quade J, Remien CH. Woody cover and hominin environments in the past 6 million years. *Nature* 476: 51-56, 2011.
27. Churchill SE. Weapon technology, prey size selection and hunting methods in modern hunter-gatherers: Implications for hunting in the Palaeolithic and Mesolithic. *Arch Papers Am Anthropol Assoc* 4: 11-24, 1993.
28. Churchill SE, Holliday TW, Carlson KJ, Jashashvili T, Macias ME, Mathews S, Sparling TL, Schmid P, de Ruiter DJ, Berger LR. The upper limb of *Australopithecus sediba*. *Science* 340: 1233-1237, 2013.
29. Churchill SE, Shackelford LL, Georgi JN, Black MT. Morphological variation and airflow dynamics in the human nose. *Am J Hum Biol* 16: 625-638, 2004.
30. Cole P. Modification of inspired air. In: Proctor DF, Andersen HP, editors. *The Nose: Upper Airway Physiology and the Atmospheric Environment*. Amsterdam: Elsevier Biomedical Press, 1982, pp. 351-375.
31. Courtiss EH, Gargan TJ, Courtiss GB. Nasal physiology. *Ann Plast Surg* 13: 214-223, 1984.
32. Crompton RH, Li Y, Thorpe SK, Wang WJ, Savage R, Payne R, Carey TC, Aerts P, Van Elsacker L, Hofstetter A, Gunther MM, D'Aout K, De Clerq D. The biomechanical evolution of erect bipedality. *Cour Forsch Inst Senckenberg* 243: 115-126, 2003.
33. Crompton RH, Vereecke EE, Thorpe SK. Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *J Anat* 212: 501-543, 2008.
34. Daniel PM, Dawes JDK, Pritchard MML. Studies of the carotid rete and its associated arteries. *Phil Trans R Soc Lond B* 237: 173-208, 1953.
35. Darwin CR. *The Descent of Man, and Selection in Relation to Sex*. London: John Murray, 1871.
36. Dawson TJ, Blaney CE, Munn AJ, Krockenberger A, Maloney SK. Thermoregulation by kangaroos from mesic and arid habitats: Influence of temperature on routes of heat loss in eastern grey kangaroos (*Macropus giganteus*) and red kangaroos (*Macropus rufus*). *Physiol Biochem Zool* 73: 374-381, 2000.
37. Dawson TJ, Robertshaw D, Taylor CR. Sweating in the kangaroo: A cooling mechanism during exercise, but not in the heat. *Am J Physiol* 227: 494-498, 1974.
38. deMenocal PB. Climate and human evolution. *Science* 331: 540-542, 2011.
39. DeSilva JM, Holt KG, Churchill SE, Carlson KJ, Walker CS, Zipfel B, Berger LR. The lower limb and mechanics of walking in *Australopithecus sediba*. *Science* 340: 1232-1237, 2013.
40. Dill DB, Edwards HT, Talbot JH. Studies in muscular activity: VII. Factors limiting the capacity for work. *J Physiol* 77: 49-62, 1932.
41. Dingwall HL, Hatala KG, Wunderlich RE, Richmond BG. Hominin stature, body mass, and walking speed estimates based on 1.5 million-year-old fossil footprints at Ileret, Kenya. *J Hum Evol* 64: 556-568, 2013.
42. Dominguez-Rodrigo M. Hunting and scavenging by early humans: The state of the debate. *J World Prehist* 16: 1-54, 2002.
43. Ellis RA, Montagna W. The skin of primates VI. The skin of the gorilla (*Gorilla gorilla*). *Am J Phys Anthropol* 20: 79-85, 1962.
44. Falk D. *Braindance* (2nd ed). Gainesville: University Press of Florida, 2004.
45. Falk D. Constraints on brain size: The radiator hypothesis. In: Kaas JH, Preuss TM, editors. *The Evolution of Primate Nervous Systems*. Oxford: Elsevier Press, 2007, pp. 347-354.
46. Fleagle, JG. *Primate Adaptation and Evolution* (3rd ed). San Diego: Academic Press, 2013.
47. Folk GE Jr. *Textbook of Environmental Physiology* (2nd ed). Philadelphia: Lea and Febiger, 1974.
48. Folk GE Jr, Semken HA Jr. The evolution of sweat glands. *Int J Biometeorology* 35: 181-186, 1991.
49. Foster F, Collard M. A reassessment of Bergmann's rule in modern humans. *PLoS One* 8: e72269, 2013.
50. Franciscus RG, Long JC. Variation in human nasal height and breadth. *Am J Phys Anthropol* 85: 419-427, 1991.
51. Franciscus RG, Trinkaus E. Nasal morphology and the emergence of *Homo erectus*. *Am J Phys Anthropol* 75: 517-527, 1988.
52. Garland T Jr. The relation between maximal running speed and body-mass in terrestrial mammals. *J Zool* 199, 157-170, 1983.
53. Gisolfi CV, Sato K, Wall PT, Sato F. In vivo and in vitro characteristics of eccrine sweating in patas and rhesus monkeys. *J Appl Physiol Respir Environ Exerc Physiol* 53: 425-431, 1982.
54. Groves CP. *A Theory of Human and Primate Evolution*. Oxford: Oxford University Press, 1989.
55. Guy F, Lieberman DE, Pilbeam D, Ponce de Leon M, Likius A, Mackaye HT, Vignaud P, Zollikofer CP, Brunet M. Morphological affinities of the *Sahelanthropus tchadensis* (Late Miocene hominid from Chad) cranium. *Proc Natl Acad Sci USA* 102: 18836-18841, 2005.
56. Hahn I, Scherer PW, Mozell MM. Velocity profiles measured for airflow through a large-scale model of the human nasal cavity. *J Appl Physiol* 75: 2273-2287, 1993.
57. Haile-Selassie Y, Saylor BZ, Deino A, Levin NE, Alene M, Latimer BM. A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature* 483: 565-569, 2012.
58. Haile-Selassie Y, Suwa G, White TD. Hominidae. In: Haile-Selassie Y, WoldeGabriel G, editors. *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia*. Berkeley: University of California Press, 2009, pp. 159-236.
59. Harcourt-Smith W, Aiello LC. Fossils, feet and the evolution of human bipedal locomotion. *J Anat* 204: 403-416, 2004.
60. Harcourt-Smith W. The origins of bipedal locomotion. In: Henke W, Tattersall I, editors. *Handbook of Paleoanthropology*. Berlin: Springer, 2007, pp. 1483-1518.
61. Harrison RJ, Montagna W. *Man*. New York: Appleton-Century-Crofts, 1969.
62. Hawks J, Wang ET, Cochran GM, Harpending HC, Moyzis RK. Recent acceleration of human adaptive evolution. *Proc Natl Acad Sci U S A* 104: 20753-20758, 2007.
63. Heglund NC, Taylor CR. Speed, stride frequency and energy cost per stride. How do they change with body size and gait? *J Exp Biol* 138, 301-318, 1988.
64. Hewes G. Food transport and the origin of Hominid bipedalism. *Am Anthropologist* 63: 687-710, 1961.
65. Hiley PG. The thermoregulatory responses of the galago (*Galago crassicaudatus*), the baboon (*Papio cynocephalus*) and the chimpanzee (*Pan troglodytes*) to heat stress. *J Physiol* 254: 657-671, 1976.
66. Holliday TW. Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evol* 32: 423-448, 1997.
67. Holton NE, Yokley TR, Butaric LN. The morphological interaction between the nasal cavity and maxillary sinuses in living humans. *Anat Rec* 296: 414-426, 2013.
68. Hunt KD. The evolution of human bipedality: Ecology and functional morphology. *J Hum Evol* 26: 183-203, 1994.
69. Jablonski NG, Chaplin G. Epidermal pigmentation in the human lineage is an adaptation to ultraviolet radiation. *J Hum Evol* 65: 671-675, 2013.
70. Jenkinson DM, Robertshaw D. (Studies on the nature of sweat gland 'fatigue' in the goat. *J Physiol* 212: 455-465, 1971.
71. Johnson GS, Elizondo RS. Thermoregulation in *Macaca mulatta*: A thermal balance study. *J Appl Physiol* 46: 268-277, 1979.
72. Jungers WL. Relative joint size and hominid locomotor adaptations with implications for the evolution of hominid bipedalism. *J Hum Evol* 17: 247-265, 1988.
73. Kamberov YG, Wang S, Tan J, Gerbault P, Wark A, Tan L, Yang Y, Li S, Tang K, Chen H, Powell A, Itan Y, Fuller D, Lohmueller J, Mao J, Schachar A, Paymer M, Hostetter E, Byrne E, Burnett M, McMahon AP, Thomas MG, Lieberman DE, Jin L, Tabin CJ, Morgan BA, Sabeti PC. Modeling Recent Human Evolution in Mice by Expression of a Selected EDAR Variant. *Cell* 152: 691-702, 2013.
74. Kelly RL. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Clinton Corners, New York: Percheron Press, 2007.
75. Kimbel WH, White TD, Johanson DC. Cranial morphology of *Australopithecus afarensis*: A comparative study based on a composite reconstruction. *Am J Phys Anthropol* 64: 337-388, 1984.
76. Kingston JD. Shifting Adaptive Landscapes: Progress and challenges in reconstructing early hominid environments. *Yrbk Phys Anthropol* 50: 20-58, 2007.
77. Kivell TL, Schmitt D. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proc Natl Acad Sci U S A* 106: 14241-14246, 2009.
78. Klein RG. *The Human Career: Human Biological and Cultural Origins* (3rd ed). Chicago: University of Chicago Press, 2009.
79. Knip AS. Ethnic studies on sweat gland counts. In: Weiner, JS, editor. *Physiological Variation and Its Genetic Basis*. London: Taylor and Francis, 1977, pp. 113-123.
80. Kuno Y. *Human Perspiration*. Springfield, IL: Charles C Thomas, 1956.
81. Langdon DH. Umbrella hypotheses and parsimony in human evolution: A critique of the Aquatic Ape Hypothesis. *J Hum Evol* 33: 479-494, 1997.
82. Lebatard AE, Bourlès DL, Durringer P, Jolivet M, Braucher R, Carcaillet J, Schuster M, Arnaud N, Monié P, Lihoreau F, Likius A, Mackaye

- HT, Vignaud P, Brunet M. Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali* Mio-Pliocene early hominids from Chad. *Proc Natl Acad Sci U S A* 105: 3226-3231, 2008.
83. Lee SS, Piazza SJ. Built for speed: Musculoskeletal structure and sprinting ability. *J Exp Biol* 212: 3700-3707, 2009.
 84. Lewis OJ. *Functional Morphology of the Evolving Hand and Foot*. Oxford: Oxford Univ. Press, 1989.
 85. Lewontin RC. The Apportionment of human diversity. *Evol Bio* 6: 391-398, 1972.
 86. Liebenberg L. *The Art of Tracking: The Origin of Science*. Claremont, South Africa: David Philip Publishers, 2001.
 87. Liebenberg L. Persistence hunting by modern hunter-gatherers. *Curr Anthropol* 47: 1017-1026, 2006.
 88. Lieberman DE. *The Evolution of the Human Head*. Cambridge MA: Harvard University Press, 2011.
 89. Lieberman DE. *The Story of the Human Body: Evolution, Health and Disease*. New York: Pantheon, 2013.
 90. Lieberman DE, Bramble DM. The evolution of marathon running: Capabilities in humans. *Sports Med* 37: 288-290, 2007.
 91. Lieberman DE, Raichlen DA, Pontzer H, Bramble DM, Cutright-Smith E. The human gluteus maximus and its role in running. *J Exp Biol* 209: 2143-2155, 2006.
 92. López Herráez D, Bauchet M, Tang K, Theunert C, Pugach I, Li J, Nandineni MR, Gross A, Scholz M, Stoneking M. Genetic variation and recent positive selection in worldwide human populations: Evidence from nearly 1 million SNPs. *PLoS One* 4: e7888, 2009.
 93. Lovejoy CO. The origin of man. *Science* 211: 341-350, 1981.
 94. Lovejoy CO, Heiple KG, Burstein AH. The gait of *Australopithecus*. *Am J Phys Anthropol* 38: 757-779, 1973.
 95. Lovejoy CO, Latimer B, Suwa G, Asfaw B, White TD. Combining prehension and propulsion: The foot of *Ardipithecus ramidus*. *Science* 326: 72e1-72e8, 2009b.
 96. Lovejoy CO, Suwa G, Spurlock L, Asfaw B, White TD. The pelvis and femur of *Ardipithecus ramidus*: The emergence of upright walking. *Science* 326: 71e1-71e6, 2009a.
 97. MacLatchy L, Gebro D, Kityo R, Pilbeam D. Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *J Hum Evol* 39: 159-183, 2000.
 98. Mahoney SA. Cost of locomotion and heat balance during rest and running from 0 to 55° in a patas monkey. *J Appl Physiol* 49: 789-800, 1980.
 99. Marks JG, Miller J. *Lookingbill and Marks' Principles of Dermatology* (4th ed). Philadelphia: Saunders, 2006.
 100. Marlowe FW. *The Hadza: Hunter-Gatherers of Tanzania*. Berkeley: Univ. California Press, 2010.
 101. Martin RD. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* 293: 57-60, 1981.
 102. McGrew WC. *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press, 1992.
 103. Meiri S, Dayan T. On the validity of Bergmann's rule. *J Biogeogr* 30: 331-351, 2003.
 104. Montagna W. The skin of nonhuman primates. *Am Zool* 12: 109-124, 1972.
 105. Montagna W, Yun JS. The skin of primates XV. The skin of the chimpanzee (*Pan satyrus*). *Am J Phys Anthropol* 21: 189-203, 1963.
 106. Morgan E. *The Aquatic Ape: A Theory of Human Evolution*. New York: Stein and Day, 1982.
 107. Niinimaa V. Effect of nasal or oral breathing route on upper airway resistance. *Acta Oto-Laryngologica* 95: 161-166, 1983.
 108. O'Connell JF, Hawkes K, Blurton Jones NG. Hadza scavenging: Implications for Plio-Pleistocene hominid subsistence. *Curr Anthropol* 29: 356-363, 1988.
 109. Olson LG, Strohl KP. The response of the nasal airway to exercise. *Am Rev Respir Dis* 135: 356-359, 1987.
 110. Pagel M, Bodmer W. A naked ape would have fewer parasites. *Proc Roy Soc B: Biol Sci* 270: S117-S119, 2003.
 111. Passey BH, Levin NE, Cerling TE, Brown FH, Eiler JM. High-temperature environments of human evolution in East Africa based on bond ordering in paleosol carbonates. *Proc Natl Acad Sci U S A* 107: 11245-11249, 2010.
 112. Pickering TR, Bunn HT. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J Hum Evol* 53: 434-438, 2007.
 113. Pickford M, Senut B. Millennium ancestor, a 6-million-year-old bipedal hominid from Kenya. *Comptes rendus de l'Académie des Sciences de Paris, série 2a*, 332: 134-144, 2001.
 114. Pilbeam D, Young N. Hominoid Evolution: Synthesizing Disparate Data. *Comptes Rendus Palevol* 3: 303-319, 2004.
 115. Pontzer H. Predicting the energy cost of terrestrial locomotion: A test of the LiMb model in humans and quadrupeds. *J Exp Biol* 210: 484-494, 2007.
 116. Pontzer H. Relating ranging ecology, limb length, and locomotor economy in terrestrial animals. *J Theor Biol* 296: 6-12, 2012.
 117. Pontzer H, Raichlen DA, Rodman PS. Bipedal and quadrupedal locomotion in chimpanzees. *J Hum Evol* 66: 64-82, 2014.
 118. Pontzer H, Rolian C, Rightmire GP, Jashashvili T, Ponce de León MS, Lordkipanidze D, Zollikofer CP. Locomotor anatomy and biomechanics of the Dmanisi hominins. *J Hum Evol* 58: 492-504, 2010.
 119. Pontzer HD, Wrangham RW. The ontogeny of ranging in wild chimpanzees. *Int J Primatol* 27: 295-309, 2006.
 120. Raichlen DA, Armstrong H, Lieberman DE. Calcaneus length determines running economy: Implications for endurance running performance in modern humans and Neandertals. *J Hum Evol* 60: 299-308, 2011.
 121. Raichlen DA, Gordon AD, Harcourt-Smith WE, Foster AD, Haas WR. Laetoli footprints preserve earliest direct evidence of human-like bipedal biomechanics. *PLoS One* 5: e9769, 2010.
 122. Rantala M. Human nakedness: Adaptation against ectoparasites? *Int J Parasitol* 29: 1987-1989, 1999.
 123. Rantala M. Evolution of nakedness in *Homo sapiens*. *J Zool* 273: 1-7, 2007.
 124. Reich D, Patterson N, Kircher M, Delfin F, Nandineni MR, Pugach I, Ko AM, Ko YC, Jinam TA, Phipps ME, Saitou N, Wollstein A, Kayser M, Pääbo S, Stoneking M. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *Am J Hum Genet* 89: 516-528, 2011.
 125. Richmond BG, Begun DR, Strait DS. Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Yrbk Phys Anthropol* 44: 71-105, 2001.
 126. Richmond BG, Jungers WL. *Orrorin tugenensis* femoral morphology and the evolution of hominin bipedalism. *Science* 319: 1662-1665, 2008.
 127. Roach NT, Venkadesan M, Rainbow MJ, Lieberman DE. Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*. *Nature* 498: 483-486, 2013.
 128. Robertshaw D. Sweat and heat exchange in man and other mammals. *J Hum Evol* 14: 63-73, 1985.
 129. Robertshaw D. Mechanisms for the control of respiratory evaporative heat loss in panting animals. *J Appl Physiol* 101: 664-668, 2006.
 130. Robertshaw D, Taylor CR. A comparison of sweat gland activity in eight species of East African bovines. *J Physiol* 203: 135-143, 1969.
 131. Rodman PS, McHenry HM. Bioenergetics and the origin of hominid bipedalism. *Am J Phys Anthropol* 52: 103-106, 1980.
 132. Rolian C, Lieberman DE, Hamill J, Scott JW, Werbel W. Walking, running and the evolution of short toes in humans. *J Exp Biol* 212: 713-721, 2009.
 133. Rubenson J, Heliam DB, Maloney SK, Withers PC, Lloyd DG, Fournier PA. Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses. *J Exp Biol* 210: 3513-3524, 2007.
 134. Ruff CB. Climatic Adaptation and Hominid Evolution: The Thermoregulatory Imperative. *Evol Anthropol* 2: 53-60, 1993.
 135. Ruff CB, Trinkaus E, Walker A, Larsen CS. Postcranial robusticity in *Homo*. I: Temporal trends and mechanical interpretation. *Am J Phys Anthropol* 91: 21-53, 1983.
 136. Ruxton GD, Wilkinson DM. 2011. Avoidance of overheating and selection for both hair loss and bipedality in hominins. *Proc Natl Acad Sci U S A* 108: 20965-20969, 2011.
 137. Sabeti PC, Schaffner SF, Fry B, Lohmueller J, Varilly P, Shamovsky O, Palma A, Mikkelsen TS, Altshuler D, Lander ES. Positive natural selection in the human lineage. *Science* 312: 1614-1620, 2006.
 138. Sakethkoo K, Kaplan I, Sackner MA. Effect of exercise on nasal mucous velocity and nasal airflow resistance in normal subjects. *J Appl Physiol* 46: 369-371, 1979.
 139. Sanders WJ. Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *J Hum Evol* 34: 249-302, 1998.
 140. Sankararaman S, Mallick S, Dannemann M, Prüfer K, Kelso J, Pääbo S, Patterson N, Reich D. The genomic landscape of Neanderthal ancestry in present-day humans. *Nature*. doi: 10.1038/nature12961, 2014.
 141. Sato F, Owen M, Matthes R, Sato K, Gisolfi CV. Functional and morphological changes in the eccrine sweat gland with heat acclimation. *J Appl Physiol* 69: 232-236, 1990.
 142. Sato K, Leidal R, Sato F. Morphology and development of an apoeccrine sweat gland in human axillae. *Am J Physiol* 252: R166-R180, 1987.
 143. Scherer PW, Hahn II, Mozell MN. The biophysics of nasal airflow. *Otolaryngologic Clin N Am* 22: 265-278, 1989.
 144. Schmidt-Nielsen K. The physiology of the camel. *Scient Am* 201: 140-151, 1959.
 145. Schmidt-Nielsen K. *Desert Animals: Physiological Problems of Heat and Water*. Oxford: Clarendon Press, 1964.
 146. Schmidt-Nielsen K, Bretz WL, Taylor CR. Panting in dogs. *Science* 169: 1102-1104, 1970.
 147. Schmitt D. Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *J Exp Biol* 206: 1437-1448, 2003.

148. Schultz AA. The density of hair in primates. *Hum Biol* 3: 303-317, 1931.
149. Schwartz GG, Rosenblum LA. Allometry of primate hair density and the evolution of human hairlessness. *Am J Phys Anthropol* 55: 9-12, 1981.
150. Semaw S, Simpson SW, Quade J, Renne PR, Butler RF, McIntosh WC, Levin N, Dominguez-Rodrigo M, Rogers MJ. Early Pliocene hominids from Gona, Ethiopia. *Nature* 433: 301-305, 2005.
151. Shea BT. Ontogenetic allometry and scaling: A discussion based on the growth and form of the skull in African apes. In: Jungers WL, editor. *Size and Scaling in Primate Morphology*. New York: Plenum Press, 1985, pp. 175-206.
152. Shea JJ. The origins of lithic projectile point technology: Evidence from Africa, the Levant, and Europe. *J Arch Sci* 33: 823-846, 2006.
153. Shostak M. *Nisa, the Life and Words of a 'Kung Woman*. Cambridge, MA: Harvard University Press, 1981.
154. Sockol MD, Raichlen D, Pontzer HD. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc Natl Acad Sci U S A* 104: 12265-12269, 2007.
155. Spoor F, Wood BA, Zonneveld F. Implications of early hominid labyrinthine morphology for the evolution of human bipedal locomotion. *Nature* 369: 645-648, 1994.
156. Steudel-Numbers KL, Wall-Scheffler CM. Optimal running speed and the evolution of hominin hunting strategies. *J Hum Evol* 56: 355-360, 2009.
157. Stitt JT, Hardy JD. Thermoregulation in the squirrel monkey (*Saimiri sciureus*). *J Appl Physiol* 31: 48-54, 1971.
158. Susman RL, Brain TM. New first metatarsal (SKX 5017) from Swartkrans and the gait of *Paranthropus robustus*. *Am J Phys Anthropol* 77: 7-15, 1988.
159. Susman RL, de Ruiter DJ. New hominin first metatarsal (SK 1813) from Swartkrans. *J Hum Evol* 47: 171-181, 2004.
160. Susman RL, Stern JT Jr, Jungers WL. Arboreality and bipedality in the Hadar hominids. *Folia Primatol* 43: 113-156, 1984.
161. Taylor CR, Heglund NC, Maloiy GM. Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J Exp Biol* 97: 1-21, 1982.
162. Taylor CR, Rowntree VJ. Temperature regulation and heat balance in running cheetahs: A strategy for sprinters? *Am J Physiol* 224: 848-851, 1973.
163. Thorpe SKS, Holder RL, Crompton RH. Origin of human bipedalism as an adaptation for locomotion on flexible branches. *Science* 316: 1328-1331, 2007.
164. Tilkens MJ, Wall-Scheffler C, Weaver TD, Steudel-Numbers K. The effects of body proportions on thermoregulation: An experimental assessment of Allen's rule. *J Hum Evol* 53: 286-291, 2007.
165. Trinkaus E. Neanderthal limb proportions and cold adaptations. In: Stringer CB, editor. *Aspects of Human Evolution*. London: Taylor Francis, 1981, pp. 187-224.
166. Turner A. The evolution of the guild of larger terrestrial carnivores during the Plio-Pleistocene in Africa. *Geobios* 23: 349-368, 1990.
167. Van Valkenburgh B. The dog-eat-dog world of carnivores: A review of past and present carnivore community dynamics. In: Stanford CB, Bunn HT, editors. *Meat-Eating and Human Evolution*. Oxford: Oxford University Press, 2001, pp. 101-121.
168. Vignaud P, Düringer P, Mackaye HT, Likies A, Blondel C, Boiserie JR, De Bonis L, Eisenmann V, Etienne ME, Geraads D, Guy F, Lehmann T, Lihoreau F, Lopez-Martinez N, Mourer-Chauviré C, Otero O, Rage JC, Schuster M, Viriot L, Zazzo A, Brunet M. Geology and palaeontology of the Upper Miocene Toros-Menalla hominid locality, Chad. *Nature* 418: 152-155, 2002.
169. Vogel S. *Comparative Biomechanics: Life's Physical Word* (2nd ed). Princeton: Princeton University Press, 2013.
170. Vogt A, McElwee K, Blume-Peytavi U. Biology of the hair follicle. In: Blume-Peytavi U, Tosti A, Whiting D, Trüeb R, editors. *Hair Growth and Disorders*. Berlin: Springer, 2008, pp. 1-22.
171. Walker A, Shipman P. *The Ape in the Tree: An Intellectual and Natural History of Proconsul*. Cambridge, MA: Harvard University Press, 2005.
172. Ward CV. Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? *Yrbk Phys Anthropol* 35: 185-215, 2002.
173. Washburn SL. Tools and human evolution. *Sci Am* 203: 63-75, 1960.
174. Weiner JS. Variation in Sweating. In: Weiner JS, editor. *Physiological Variation and Its Genetic Basis*. London: Taylor and Francis, 1977, pp. 125-137.
175. Wheatley JR, Amis TC, Engel LA. Oronasal partitioning of ventilation during exercise in humans. *J Appl Physiol* 71: 546-551, 1991.
176. Wheeler PE. The evolution of bipedality and loss of functional body hair in hominids. *J Hum Evol* 13: 91-98, 1984.
177. Wheeler PE. The loss of functional body hair in man: The influence of thermal environment, body form and bipedality. *J Hum Evol* 14: 23-28, 1985.
178. Wheeler PE. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: The contribution of increased convective heat loss and cutaneous evaporative cooling. *J Hum Evol* 21: 107-115, 1991.
179. Wheeler PE. The influence of the loss of functional body hair on the water budgets of early hominids. *J Hum Evol* 23: 379-388, 1992.
180. White TD, Ambrose SH, Suwa G, Su DF, DeGusta D, Bernor RL, Boisserie JR, Brunet M, Delson E, Frost S, Garcia N, Gaiourtsakis IX, Haile-Selassie Y, Howell FC, Lehmann T, Likies A, Pehlevan C, Saegusa H, Semperebon G, Teaford M, Vrba E. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. *Science* 326: 87-93, 2009.
181. White TD, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, WoldeGabriel G. *Ardipithecus ramidus* and the paleobiology of early hominids. *Science* 326: 75-86, 2009.
182. White TD, Suwa G, Asfaw B. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371: 306-312, 1994.
183. Whittow GC. *Comparative Physiology of Thermoregulation. II Mammals*. New York: Academic Press, 1971.
184. Wilkins J, Schoville BJ, Brown KS, Chazan M. Evidence for Early Hafted Hunting Technology. *Science* 338: 942-946, 2012.
185. Wolpoff MH. Climatic influence on the nasal aperture. *Am J Phys Anthropol* 29: 405-423, 1968.
186. Wood B, Harrison T. The evolutionary context of the first hominins. *Nature* 470: 347-352, 2012.
187. Wrangham R, Cheney D, Seyfarth R, Sarmiento E. Shallow-water habitats as sources of fallback foods for hominins. *Am J Phys Anthropol* 140: 630-642, 2009.
188. Yang N, MacArthur DG, Gulbin JP, Hahn AG, Beggs AH, Eastale S, North K. ACTN3 genotype is associated with human elite athletic performance. *Am J Hum Genet* 73: 627-631, 2003.
189. Yokley TR. Ecogeographic variation in human nasal passages. *Am J Phys Anthropol* 138: 11-22, 2009.
190. Yousef MK, Dill DB. Energy expenditure in desert walks: Man and burro *Equus asinus*. *J Appl Physiol* 27: 681-683, 1969.
191. Zenker W, Kubik S. Brain cooling in humans – anatomical considerations. *Anat Embryol* 193: 1-13, 1996.
192. Zollikofer CP, Ponce de León MS, Lieberman DE, Guy F, Pilbeam D, Likies A, Mackaye HT, Vignaud P, Brunet M. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 434: 755-759, 2005.