

Body composition in *Pan paniscus* compared with *Homo sapiens* has implications for changes during human evolution

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The human body has been shaped by natural selection during the past 4–5 million years. Fossils preserve bones and teeth but lack muscle, skin, fat, and organs. To understand the evolution of the human form, information about both soft and hard tissues of our ancestors is needed. Our closest living relatives of the genus *Pan* provide the best comparative model to those ancestors. Here, we present data on the body composition of 13 bonobos (*Pan paniscus*) measured during anatomical dissections and compare the data with *Homo sapiens*. These comparative data suggest that both females and males (i) increased body fat, (ii) decreased relative muscle mass, (iii) redistributed muscle mass to lower limbs, and (iv) decreased relative mass of skin during human evolution. Comparison of soft tissues between *Pan* and *Homo* provides new insights into the function and evolution of body composition.

body composition | bonobo | *Pan paniscus* | human evolution | *Homo sapiens*

The human body has been shaped by natural selection during the past 4–5 million years. The large brain and expanded neurocranium of *Homo sapiens* (1,100–1,550 cm³) is triple the size of closely related chimpanzees (*Pan*, 275–420 cm³) and fossil australopithecines (e.g., *Australopithecus afarensis* AL-444, 550 cm³; *Australopithecus africanus* Taung, 382 cm³; and *Australopithecus sediba* MH1, 420 cm³) (1–6). Long lower limbs in humans accommodate habitual bipedality and contrast with the relatively short lower limbs of quadrupedal African apes. These changes in limb proportions can be tracked across millions of years of australopithecine and early *Homo* remains, (e.g., partial skeletons of *Au. afarensis* AL-288 “Lucy,” *Au. africanus* STS 14, *Homo erectus* WT 15000 “Nariokotome Boy”) (7–9).

Fossils, even relatively complete ones, preserve only bone, one component of body composition and a small proportion of body mass. The remaining muscle, skin, fat, and vital organs that make up the other 85% do not leave a record, although, separately and together, they underpin locomotor activity, energetics, health, and reproduction (10–14). There has been much speculation about their interrelationships. The “expensive tissue hypothesis” attempts to explain the threefold expansion of the human brain (15–18). It argues that because human brain tissue requires a disproportionately high energy supply, its increase during evolution necessitated a compensatory decrease in another component, the gastrointestinal tract (18). Another hypothesis suggests that body fat in australopithecines was as high as the body fat of modern hunter-gatherers (19). Tests of hypotheses about the evolution of body composition require a comparative database, one that includes the major tissues.

One way to fill in the missing information is to compare human body composition with the body composition of our closest living relatives, members of the genus *Pan* (20, 21). Few such comparative data are available on apes (but cf. 22–25). The rarity of apes in captivity, their long lives, and the logistics of obtaining relatively complete bodies for dissection pose challenges for accumulating a comparative sample. Here, we present a unique dataset

on the body composition of *Pan paniscus*, one of the two species of *Pan* (26). These data provide a comparison with *H. sapiens* and a basis for assessing evolutionary change in the major components of the body from an ape-like ancestor to modern humans.

Results

Muscle, bone, skin, and fat as a percentage of total body mass for six female and seven male adult *P. paniscus* individuals are shown in Table 1.

In body mass, females average 34,278.3 g and males average 42,676.3 g. The values differ significantly (ANOVA: $F_{1,11} = 9.498$, $P = 0.010$). Removal of the three captive-born individuals from the total sample does not change the significance of sexual dimorphism in body mass (ANOVA: $F_{1,8} = 8.806$, $P = 0.018$). The ranges included in this sample fall well within body masses that have been previously published for female and male wild *P. paniscus* (27). In this sample, sexual dimorphism in body mass is 80.3%, similar to previously published results for a *P. paniscus* sample (78.4%, $n = 18$) (28).

In brain size, females average 337.7 mL and males average 365.3 mL. The values differ significantly in this small sample (ANOVA: $F_{1,11} = 6.4$, $P = 0.028$). However, in a larger sample of 56 individuals, no significant sex difference is exhibited (3). Because both body mass and brain size are available for each individual (Table 1), we are able to calculate the ratio of brain size to body mass, which is higher for females than males (0.99 vs. 0.86), a catarrhine pattern for species with moderate to extreme sex differences in body mass (29).

Bone averages about 13% of body mass and shows little sex difference (females, 13.4%; males, 13.0%). Skin average is higher in females at 13.0% compared with males at 10.8%.

Significance

During human evolution, the body changed in shape, partially to accommodate bipedal locomotion. Concurrently, brain size underwent a three-fold increase recorded in evidence from fossils and from comparative anatomy of chimpanzees, *Homo sapiens*’ closest living relatives. Because soft tissues like muscle, skin, and fat do not fossilize, and little information is available on these components for the genus *Pan*, reconstructing tissue changes has primarily relied on what is known about humans. This study presents unique quantitative data on major body components of muscle, bone, skin, and fat of 13 bonobos (*Pan paniscus*) for interpreting evolutionary forces that have shaped the human form for survival in a savanna mosaic environment.

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Table 1. Age, body mass, cranial capacity, and relative percentages of major tissues for 13 *P. paniscus* individuals

Individuals	Body mass, g	Brain, mL	Muscle, %	Muscle, % forelimb	Muscle, % hind limb	Bone, %	Skin, %	Fat, %
Females: identification								
no. and age, y								
PF1* 11.5	35,500	346	36.4	37.5	45.2	12.7	13.5	8.6
PF2 24	37,170	360	43.4	36.8	42.6	14.1	10.1 [†]	<1.0
PF3 24	30,500	358	44.1	32.7	47.1	13.5	12.0	1.2
PF4 33	31,400	316	30.1	35.9	43.6	13.9	14.0	3.8
PF5 54	35,100	326	33.7	38.5	40.5	13.4	12.1	<1.0
PF6 57	36,000	320	35.9	36.8	44.6	12.9	13.5	6.3
Males: identification								
no. and age, y								
PM1 11	36,364	324	48.0	33.0	46.9	13.2	n.a.	0.005
PM2* 15	53,070	359	51.2	34.6	47.4	12.1	10.8	0.004
PM3 21	40,900	333	56.1	34.2	47.7	12.7	9.9	0.006
PM4 22	36,500	360	48.6	35.4	49.5	13.7	10.6	0.002
PM5* 25	48,600	390	55.0	35.4	47.2	13.7	9.6 [†]	0.006
PM6 32	40,800	379	50.6	35.6	45.2	12.2	12.5	0.002
PM7 38	42,500	371	51.5	36.7	46.2	13.3	10.3	0.008

n.a., not available; PF, *paniscus* female; PM, *paniscus* male.

*Born captive.

[†]Minimum estimate due to necropsy damage.

Body fat among females that could be dissected from the necropsied trunk and limbs ranges from less than 1–8.6%, whereas all males had negligible amounts in these regions, less than 0.01%, an observation we noted during dissections. These fat estimates are minimum values (*Materials and Methods*).

Muscle in females averages 37.4% of total body mass, ranging from 30.1–44.1%. Males have more than half of their body mass as muscle, 51.6% on average, ranging from 48.0–56.1%. There is no overlap with females.

Although muscle mass differs between females and males, its distribution to the limbs is similar. Muscle acting on the upper limbs averages 36.4% of total muscle mass in females and 35.0% in males. Muscle acting on the lower limbs averages 44.0% in females and 47.2% in males (Table 1).

Discussion

Body Composition in *H. sapiens*.

Direct measure. Body composition data for *H. sapiens* are derived from both direct and indirect methods. Direct dissection distinguishes the main gross anatomical components of body composition. Only a few such studies are available on *H. sapiens* because manual separation of the components is tedious at best (30), and it is difficult to collect a representative sample. The most robust dissection results come from a Belgian study of 51 individuals (31, 32). Few were prime adults, and only a small number died accidentally. These conditions may have distorted the effects of age, poor health, or disease on body composition (cf. 32). Even with these drawbacks, the study is of interest because it measures all body components (muscle, bone, skin, and fat) for each individual, and therefore provides a basis for comparison with data collected in this study (Table 2).

The *H. sapiens* dissection data parallel the pattern of sex differences in the *P. paniscus* sample in that body mass overlaps slightly in women and men, although men are heavier and have more muscle and less fat. The Belgian sample on older *H. sapiens* may slightly underestimate the average percentage of muscle and slightly overrepresent the percentage of body fat, because both women and men from settled and industrial populations tend to lose muscle and gain fat as they age (14, 33–35).

Bone mass averages are similar in *Homo* and *Pan* samples, around 13%, although the Belgian group has a wider range.

Available information on other apes shows *Gorilla* and *Pongo* bone averages 12–13% (23–25).

Skin contributes the least mass to body composition in *H. sapiens* and, combined with muscle, comprises a lower percentage of body mass compared with those tissues in *P. paniscus*. Skin has a higher average in gorillas and orangutans at 14–15% (23–25).

The regional distribution of muscle in *H. sapiens* contrasts significantly with the regional distribution of muscle in *P. paniscus* and other apes. Of total muscle mass in *H. sapiens*, more than half acts on the lower limbs and only a fifth acts on the upper limbs (36, 37), whereas a third of *P. paniscus* muscle acts on the upper limbs (Fig. 1).

Indirect measure. Research on the body composition of *H. sapiens* receives considerable attention because it assists in assessing an individual's physical fitness, clinical health, and disease (diabetes, obesity, and amenorrhea), and growth and development (10, 34, 38, 39). Most of this research relies on the application of indirect, noninvasive methods on living subjects, such as anthropometry, bioelectrical impedance analysis (BIA), computed tomography and MRI scans, and dual-energy X-ray absorptiometry (10, 14, 34, 39, 40). Each indirect technique varies in its precision and in the

Table 2. Means and ranges of age, body mass, and percentage of tissue composition for bonobos and humans

Sample	Age, y	Body mass, kg	Muscle, %	Skin, %	Fat, %
<i>P. paniscus</i> F (n = 6)	34.0	34.3	37.4	13.0*	3.6 [†]
<i>P. paniscus</i> M (n = 7)	23.4	42.7	51.6	10.8 [‡]	0.005 [‡]
<i>H. sapiens</i> [§] F (n = 20)	75.5 22–94	57.3 32.0–75.4	28.6 16.8–39.0	5.6 3.1–9.0	36.3 9.4–54.1
<i>H. sapiens</i> [¶] M (n = 29)	56.6 26–87	62.4 38.5–88.9	39.4 27.3–45.5	6.1 4.4–9.5	20.3 5.2–30.2

F, female; M, male.

*Based on five females only.

[†]Minimum estimate (*Materials and Methods*).

[‡]Based on five males only.

[§]Predominantly older Belgium sample that died of natural causes (32).

[¶]Four males of unknown age. Two males were eliminated because they were preadult individuals.

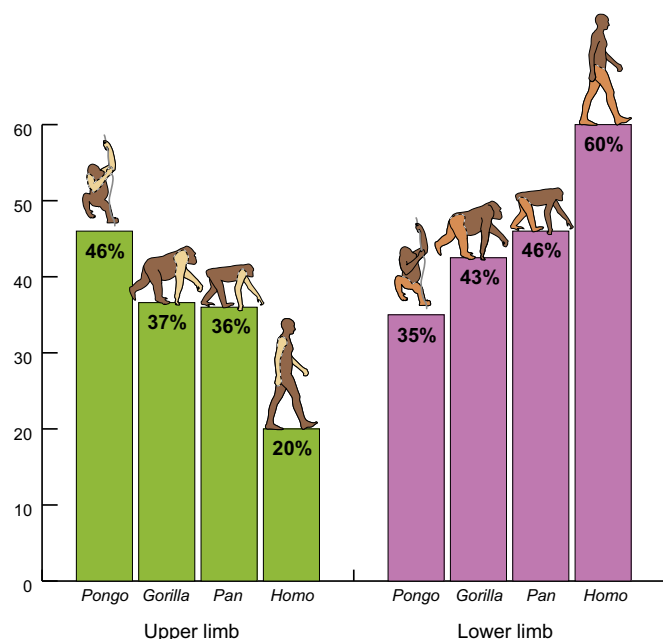


Fig. 1. Percentage of muscle distribution to upper and lower limbs in *Pongo pygmaeus*, *Gorilla gorilla*, *P. paniscus*, and *H. sapiens*.

robusticity of the samples (cf. 38), and no one technique can independently measure all body tissues of the same individual. Based on average physical dimensions derived from anthropometric measurements on thousands of individuals from Western populations, Albert Behnke developed a theoretical “reference woman” and “reference man” (14) to use as a comparative framework. The reference woman, between 20 and 24 y of age, has 36% muscle of total body mass, 12% bone, and 24–31% fat, and the reference man has 43% muscle and 12–20% fat (14, 41, 42). Averages for body fat, typically 25% for women and 15% for men, are proposed as a basis for evaluation in diverse groups, such as athletes and underweight or obese individuals (14).

Body fat is a particular focus of study because of its wide-ranging implications for an individual’s nutritional status and activity level. Furthermore, body fat can be relatively easy to measure in individuals in the field using anthropometry and BIA. Studies on non-Western populations are particularly useful because they provide the environmental and cultural context to evaluate the effects of subsistence activities, caloric level, and seasonal shortage of food on weight fluctuations, typically in body fat (19, 43–48) (Table 3).

Hadza hunter-gatherers, who live in a savanna-woodland habitat in northern Tanzania, have a high activity level, because both women and men traverse the landscape daily to collect food they bring back to camp, and exhibit lower levels of body fat than the Behnke model (19.0% females and 10.6% males). Ariaal pastoral nomads, camel herders in the desert of northern Kenya, live in conditions of chronic undernutrition and have low average body fat (6.2%), indicating acute undernutrition (49). The Turkana pastoral nomads in northern Kenya also experience chronic undernutrition and carry a relatively high disease burden. Male body fat (5.7%) is near the lowest threshold sustainable for humans (39).

Settled populations have fewer precarious food shortages and lower activity levels and slightly higher fat reserves than their nomadic counterparts. The Ariaal, who live at higher altitudes as cattle herders and farmers, have less food stress and somewhat higher body fat than their nomadic counterparts, although still low (7.7%). The settled Turkana men have significantly more body fat (9.1%) than the Turkana nomads, in part due to better nutrition.

An urban population in Harare, Zimbabwe is intermediate in nutrition and activity between settled Kenyan populations and Western populations (34, 50). The Zimbabwe men are mildly underweight, with average body fat at 14.8%, but are not under severe nutritional stress. An urban population sample of healthy adults in Geneva, Switzerland shows men with 19.7% average body fat, similar to the direct dissection data from the Belgium study (32) (20.3%, Table 3) but higher than estimated for the Behnke model, whereas the Geneva women had body fat (28.8%) within the range calculated for the Behnke model (24–31%).

These studies demonstrate that the contribution of body fat to body composition varies broadly depending on subsistence base and seasonal caloric intake, activity level, and sex. Lower overall body fat in the Hadza nomads compared with settled populations may reflect seasonal fluctuations of resources in this environment. Fat reserves in ecologies where caloric intake fluctuates provide a useful survival strategy (43, 51). Urban dwellers have lower activity levels and more consistent access to food than do hunter-gatherer or nomadic populations, as well as higher body fat. Even with severe nutritional stress and high activity levels, men in non-Western societies maintain body fat. Human body fat values as low as 4–6% lead to cannibalization of muscle tissue for body maintenance, and thus have a negative impact on health (39).

Implications for Human Evolution.

Body fat. The negligible measurable fat in all seven *P. paniscus* males was unexpected, overriding captivity, age, and body mass. Among wild chimpanzees, there is little indication of an ability to mobilize fat stores during times of caloric restriction, a key adaptive feature found in orangutans and possibly to a lesser degree in gorillas (24, 52, 53). Without selection pressure for storage fat, and with over half of body mass in muscle, the male *P. paniscus* does not easily accumulate body fat, even under optimal circumstances of captivity. Remarkably, none of the males and females manifested detrimental health as a consequence of having little fat, in stark contrast to *H. sapiens*.

There is evidence in female *P. paniscus* that fluctuation in body fat is associated with reproductive history. Individual *paniscus* female 1 (PF1) with the most body fat was lactating at the time of death and had considerable fat in her breasts, trunk, and limbs. Individual *paniscus* female 4 (PF4) died within 1 wk after giving birth to a full-term offspring, her first, and had notable fat deposits in the trunk and limbs. Individual *paniscus* female 3 (PF3) had no offspring or pregnancies during her life, had remarkably low levels of dissectable fat, and stood out as having the highest percentage of muscle mass among the females (44.1%, Table 1). Body fat is also sexually dimorphic in some monkeys, as well as in gorillas and orangutans (23–25), and has a demonstrated role in reproduction (54–56). The same is true for *H. sapiens* (19, 43–48).

Table 3. Means and SDs of percentage of body fat for selected human groups, adults only, divided by sex when available

Population	Body fat, %	Method	Sample size, <i>n</i>
Hadza nomads (51) in Tanzania	19.0 ± 7.0 F	BIA	235 (F)
	10.6 ± 3.2 M		238 (M)
Ariaal nomads (49) in Kenya	6.2 ± 3.1 M	BIA	49
Ariaal settled (49) in Kenya	7.7 ± 3.8 M	BIA	52
Turkana nomads (33) in Kenya	5.7 ± 2.1 M	SK	132
Turkana settled (33) in Kenya	9.1 ± 3.6 M	SK	90
Urban (50) in Zimbabwe	14.8 ± 6.8 M	BIA	103
Urban (34) in Switzerland	28.8 ± 6.6 F	BIA	2,490 (F)
	19.7 ± 5.6 M		2,735 (M)

SK, skinfolds.

In the course of human evolution from early australopithecines onward, the ability to store and mobilize body fat must have played an increasing role in successful reproduction (43, 44, 57, 58), coupled with the shift to bipedal locomotion (59). We posit that early australopithecine females, such as *P. paniscus*, put on more body fat than the males and had the ability to vary their adiposity with reproductive cycles. We conclude that body fat was sexually dimorphic in australopithecines, as it is for *P. paniscus*, variable in females but consistently low in males: as high as 8–10% in females and 2–3% in males. Although Wells (19) suggests that both female and male australopithecines had 11–13% body fat, our data suggest, to the contrary, it is unlikely that male australopithecines approached the level of body fat found in male Hazda hunter-gatherers.

It may be that in early *Homo* and *H. erectus*, with the increase in brain size (60) and body mass (61), fat began to play a more significant role in female reproduction. As the early *Homo* species expanded out of Africa, the ability to put on, store, and mobilize body fat provided a clear adaptive advantage for both females and males as a backup against extremes of food availability in a variety of environments, as well as mitigating adverse effects on pregnancy and lactation in females. Although body fat for males may not be as critical for reproduction as it is for females, we suspect that male *H. erectus* would have needed an estimated 7–8% body fat as a buffer against “seasonal hunger” (43, 45, 46). In order for females of ancestral species of *Homo* to nourish larger brained infants without the extended developmental period characteristic for *H. sapiens* (62), they probably needed additional body fat, in the range of 12–14%.

Increased body fat during human evolution reflected more than one selective pressure. Females experienced increased nutritional demands for successful reproduction and for maintenance of a high level of activity, walking several miles a day collecting and carrying food and dependent infants (cf. 44). These needs were compounded by pronounced seasonal variation in food sources characteristic of the tropical savanna mosaic (63) and the unpredictability of new environments as early *Homo* species expanded their home ranges regionally and geographically.

Muscle. Muscle is overall the heaviest body tissue in *P. paniscus* and underpins locomotor function (14, 54, 65). Muscle mass is notably sexually dimorphic, with females ranging between 30.1% and 44.1% and males ranging between 48.0% and 56.1%, and no overlap between the sexes. *H. sapiens* individuals are not as muscular as *P. paniscus* individuals, with females averaging around 29–36% and males averaging 39–43% with some overlap, although males generally have more muscle than females.

Chimpanzees and bonobos are quadrupedal on the ground and in the trees; they climb, hang, and reach in all directions to collect fruit and leaves. The upper limbs of great apes are well-muscled. Human locomotion, in contrast, relies on the lower limbs for propulsion, braking, and balance (66), and more than half of muscle mass is devoted to those functions. The upper limbs counter body rotation during forward progression (67) but do not bear body weight and have much less muscle (Fig. 1).

As the earliest hominins made the transition from quadrupedal to habitual bipedal locomotion, while still maintaining climbing function, muscle mass decreased, mainly in the upper limbs. Having effective motor function with less muscle mass would seem to be a paradox. However, human bipedal locomotion is less costly than chimpanzee bipedal or quadrupedal locomotion (68).

An increase in muscle mass to the lower limbs and a decrease to the upper limbs must have taken place by 3 million years ago. Fossils of this age provide strong evidence for bipedal behavior, including restructured pelvic and lower limb bones, reshaped vertebrae, and footprints reflecting a heel-toe strike and non-divergent hallux of the australopithecines (e.g., 6–8). Limb lengths and proportions of AL-288 (*Au. afarensis*) are consistent with a distribution of muscle mass altered from the distribution of muscle

mass of the ape ancestors. Femur length in this *Au. afarensis* at 280 mm (8) is similar to *P. paniscus* femur length at 290 mm (69, 70), whereas the shorter AL-288 humerus at 235 mm falls below the *P. paniscus* average at 285 mm (69, 70). The humeral/femoral index in AL 288 of 84 thus indicates a shift to a more human index of 75, reduced from the bonobo index of 98 (8, 70). This index signals that *Au. afarensis* deemphasized the upper limbs in locomotion, a conclusion concordant with our proposal of a decrease in overall muscularity.

Because the longer lower limbs of *H. erectus* WT 15,000 (9) approached the condition of *H. sapiens*, muscle mass must have decreased further in the shoulder and upper limbs and increased in the hip and thigh. A restructured body with relatively longer legs and additional muscle to maximize lower limb function contributed to an energetically efficient biped. At this point in human evolution, the changes in the locomotor system of *Homo* further facilitated long-distance bipedal walking and running (71) as species of this genus dispersed out of Africa to distant regions in central and south Asia.

Skin. African apes' hairy skin constitutes between 10% and 16% of their total body mass (24, 25). Long hair shafts and follicles grow in a relatively thick epidermis. This epidermis has patchy, inconsistent areas of pigmentation under the body hair. Eccrine sweat glands, common on the hairless palms and soles of all primates, are also present on chimpanzees' hairy trunk and limbs (72–74). However, these sweat glands do not respond to heat stimulation (73).

Human skin accounts for only a small fraction of body mass: 6% on average. *H. sapiens* is unique among primates in that its eccrine sweat glands respond to thermal stimulation (74) triggered by external heat from direct solar radiation and from heat internally generated by muscle action during walking and running. The sweat glands give off moisture, and through evaporation, they cool the body. Reduced hair shafts and smooth skin facilitate the evaporation process. Hair shafts are so reduced over most of the body that the skin appears naked (74).

Human skin is uniformly pigmented. However, in the absence of ape-like hair covering, UV radiation can penetrate the epidermis, cause damage to the DNA, interrupt protein production, and destroy vitamins in the body (75). Pigmentation throughout the skin forms a protective shield against radiation (74, 75). The functional complex of skin shields the body from UV damage through pigmentation and, through sweating, acts to moderate overheating, thereby enabling long-distance walking and work effort even in hot regions with direct sunlight (76).

Most populations of *Pan* live in forest or woodland habitats with tolerable ambient temperatures. However, some populations endure in hot, dry areas, with open grasslands and limited tree cover (77–81). These chimpanzees can travel freely in the open terrestrial areas during the wet season when air temperatures are tolerable, but during the dry season when temperatures are high, their activities are restricted to areas with shade. At Fongoli, Senegal, at the hottest times of the year, chimpanzees retreat into caves as shelters, where temperatures are significantly cooler than in open habitats (81).

Behavioral and anatomical adaptations to heat stress must have been initiated early in human evolution, concurrent with the initial expansion of australopithecine species across several savanna mosaic regions in eastern and southern Africa. To exploit open, high-sunlight areas without continuous tree cover, the australopithecines must have begun to develop the ability to maintain year-round use of all parts of their range, facilitated by an air-conditioning sweating mechanism (82). Keeping the body and especially the brain cool was essential for survival in this new habitat (83).

The functional complex of eccrine gland secretion, reduced hair shafts on trunk and limbs, and continuous pigmentation must have been fully developed by early *Homo* species, as they walked and ran long distances, fully exploited resources of the savanna mosaic, and expanded their geographic range out of Africa.

Once prominent hair shafts became reduced and the skin surface became “naked,” sensory and immune functions of skin may have increased significantly compared with our primate relatives. Bare skin heightens the sense of touch over the body and plays an important role in human bonding and communication. The skin’s surfaces harbor multiple species of microorganisms and create an ecosystem that contributes to the health of the human species (e.g., 84–86). Even in early *Homo*, these profound changes in the skin probably approached those changes found in modern humans. Such adaptive features freed early *Homo* from temperature- and activity-level restrictions and allowed bipedal hominins to exploit regions of the African savanna mosaic not previously available to their great ape relatives.

Summary and Conclusions

Comparison of the body composition of *P. paniscus* with the body composition of *H. sapiens* helps elucidate the human body’s evolutionary history. The savanna mosaic with mixed vegetation, seasonal rainfall, and fluctuating food availability presented challenges for evolving hominins. Habitual bipedal locomotion and an increase in daily travel allowed early hominins to forage more broadly over terrestrial landscapes, even with limited shade. The combinations of habitat, caloric, reproductive, and health-related selective pressures acted on body components of fat, muscle, and skin.

In the changing environment, different body tissues adapted in particular ways. Increased ability to store fat in both females and males served as a buffer during seasonal fluctuations and unpredictable food resources. For females, storing fat enhanced effective pregnancy and lactation to nourish larger brained infants without extended developmental periods. Decreased muscularity accompanied the new method of locomotion. Muscle redistributed to the hip and thigh for efficient bipedalism. Reorganized and reduced skin tissue evolved to facilitate heat dissipation, cellular protection, and immune function.

The fossil record preserves primarily cranial, facial, and dental remains and relatively few postcranial bones that, together, represent only 15% of body mass. Comparing the body composition of our closest living relatives with the body composition of *Homo sapiens*, we can address the other 85% and extend our perspective on how natural selection has shaped the human body.

Materials and Methods

Sample. Our research did not involve live animals or experiments. We collected the individuals after death for dissection. Thirteen captive adult *P. paniscus* individuals from zoos and research institutions died of natural causes and were made available for postmortem study over a 35-y period. The individuals were maintained in social groups. One female and two males were born captive. Ages are estimated for wild-born individuals. Body weights during life or at necropsy are available, along with some information on reproductive history.

Methods of Dissection. All individuals were frozen after death and dissected unpreserved. Twelve were dissected in the Zihlman Anthropology Laboratory, University of California, Santa Cruz, and one was dissected in the Field Museum of Natural History in Chicago. Veterinary necropsies before dissection usually removed thoracic and abdominal contents and the brain. One individual, *paniscus* male 1 (PM1), had the skin removed before dissection.

Another individual, *paniscus* female 3 (PF3), was not necropsied and was dissected completely intact.

Dissection proceeds segment by segment: forelimbs (arm, forearm, and hand), hind limbs (thigh, leg, and foot), and head and trunk. From each segment, the major tissues (skin, muscle, and bone) are separated and weighed immediately (24, 25, 87). Muscle mass encompasses all skeletal muscle from the limbs, torso, and masticatory muscles. It does not include facial, eye, or diaphragm muscles, so that the total muscle represents a minimum. Total bone mass includes the weight of the skull; all limb, hand, and foot bones; and the trunk, including ribs, vertebrae, and pectoral and pelvic girdles. Skin (epidermis and dermis) is treated as a major tissue and weighed separately.

Remaining tissue (or “other”) is designated as “undifferentiated” in human dissections (31) and includes connective tissue, nerves and blood vessels, fascia, ligaments, and trunk contents removed at necropsy (e.g., brain, organs, viscera), as well as the diaphragm, tongue, larynx, hyoid and associated structures; gastrointestinal tract; reproductive organs; and interdigitated adipose and fat in bone marrow, spinal cord, and internal organs. Fat that is associated with trunk contents and cannot be dissected and weighed separately is included in this category.

During dissection, body fat that can be separated from the trunk and limbs, including s.c. fat separated from the skin, is weighed and recorded; it does not include fat associated with abdominal contents, which are removed during necropsy, or fat tissue in the head, hands, and feet. The measured fat represents only a minimum of storage fat and serves as a point of comparison among the sampled individuals as an indicator of fatness rather than an accurate representation of total body fat.

The volume of the brain case is measured as a proxy for brain size. The cranium is filled with mustard seeds, tilted to distribute them throughout, tapped twice to settle its contents, and then filled to the plane of the foramen magnum rim. The seed is then poured into a flask and recorded to the nearest milliliter. The measurement is performed three times, and the mean is taken.

Analysis. Each component tissue is calculated relative to the individual’s total body mass (Table 2).

Further analysis of total muscle mass (100%) is calculated to determine its distribution to the body. All of the forelimb muscles plus the rotator cuff (infraspinatus, supraspinatus, subscapularis, and teres minor) and trunk muscles that act on the shoulder joint and attach on the humerus (latissimus dorsi, teres major, and pectoralis major) are calculated as a percentage of total muscle mass. Similarly, muscles from the hind limbs plus muscles that act on the hip joint and attach on the femur (gluteus maximus, medius, and minimus as well as obturator externus and internus, gemelli, quadratus femoris, and iliopsoas) are taken as a percentage of total muscle mass. The remaining percentage includes muscles from the trunk and head.

Means and SDs are calculated for body mass and brain size by sex, and ANOVA between the sexes is undertaken. $P < 0.05$ is taken as significant.

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- Holloway R, Yuan M (2004) Endocranial morphology of A.L. 444-2. *The Skull of Australopithecus afarensis*, eds Kimbel W, Rak Y, Johanson D (Oxford Univ Press, New York), pp 123–135.
- Hambly WD (1947) Cranial capacities, a study in methods. *Fieldiana Anthropol* 36(3): 25–75.
- Cramer DL (1977) Craniofacial morphology of *Pan paniscus*. A morphometric and evolutionary appraisal. *Contrib Primatol* 10:1–64.
- Zihlman AL, Stahl D, Boesch C (2008) Morphological variation in adult chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Côte d’Ivoire. *Am J Phys Anthropol* 135(1):34–41.
- Falk D, Clarke R (2007) Brief communication: New reconstruction of the Taung endocast. *Am J Phys Anthropol* 134(4):529–534.

- Berger LR, et al. (2010) *Australopithecus sediba*: A new species of *Homo*-like australopithecine from South Africa. *Science* 328(5975):195–204.
- Robinson JT (1972) *Early Hominid Locomotion and Posture* (Univ of Chicago Press, Chicago).
- Johanson DC, Taieb M (1976) Plio-Pleistocene hominid discoveries in Hadar, Ethiopia. *Nature* 260(5549):293–297.
- Walker A, Leakey RE, eds (1993) *The Nariokotome Homo erectus Skeleton* (Harvard Univ Press, Cambridge, MA).
- Holliday M (1978) Body composition and energy needs during growth. *Postnatal Growth Neurobiology*, Human Growth: A Comprehensive Treatise, eds Falkner F, Tanner J (Plenum, New York), Vol 2, pp 117–139.
- Wang ZM, Pierson RN, Jr, Heymsfield SB (1992) The five-level model: A new approach to organizing body-composition research. *Am J Clin Nutr* 56(1):19–28.

12. Goran MI, Malina RM (1999) Fat distribution during childhood and adolescence: Implications for later health outcomes. *Am J Hum Biol* 11(2):187–188.
13. Wells JCK (2001) A critique of the expression of paediatric body composition data. *Arch Dis Child* 85(1):67–72.
14. McArdle WD, Katch WD, Katch VL (2014) *Exercise Physiology: Energy, Nutrition and Human Performance* (Williams & Wilkins, Baltimore), 8th Ed.
15. Hladik CM, Chivers DJ, Pasquet P (1999) On diet and gut size in non-human primates and humans: Is there a relationship to brain size? *Curr Anthropol* 40(5):695–697.
16. Hladik CM, Pasquet P (2002) The human adaptations to meat eating: A reappraisal. *Hum Evol* 17(3–4):199–206.
17. Roberts AM, Thorpe SK (2014) Challenges to human uniqueness: Bipedalism, birth and brains. *J Zool (Lond)* 292(4):281–289.
18. Aiello LC, Wheeler P (1995) The expensive-tissue hypothesis: The brain and digestive system in human and primate evolution. *Curr Anthropol* 36(2):199–221.
19. Wells JCK (2010) *The Evolutionary Biology of Human Body Fatness* (Cambridge Univ Press, Cambridge, UK).
20. Prüfer K, et al. (2012) The bonobo genome compared with the chimpanzee and human genomes. *Nature* 486(7404):527–531.
21. Rieueux A, et al. (2014) Improved calibration of the human mitochondrial clock using ancient genomes. *Mol Biol Evol* 31(10):2780–2792.
22. Zihlman A (1984) Body build and tissue composition in *Pan paniscus* and *Pan troglodytes* with comparisons to other hominoids. *The Pygmy Chimpanzee*, ed Susman RL (Plenum, New York), pp 179–200.
23. Morbeck ME, Zihlman AL (1988) Body composition and limb proportions in orangutans. *Orangutan Biology*, ed Schwartz J (Oxford Univ Press, New York), pp 285–297.
24. Zihlman AL, McFarland RK (2000) Body mass in lowland gorillas: A quantitative analysis. *Am J Phys Anthropol* 113(1):61–78.
25. Zihlman AL, McFarland RK, Underwood CE (2011) Functional anatomy and adaptation of male gorillas (*Gorilla gorilla gorilla*) with comparison to male orangutans (*Pongo pygmaeus*). *Anat Rec (Hoboken)* 294(11):1842–1855.
26. Coolidge H (1933) *Pan paniscus*, pygmy chimpanzee from south of the Congo River. *Am J Phys Anthropol* 18(1):1–59.
27. Coolidge H, Shea B (1982) External body dimensions of *Pan paniscus* and *Pan troglodytes* chimpanzees. *Primates* 23(2):245–251.
28. Cramer D, Zihlman A (1978) Sexual dimorphism in pygmy chimpanzees. *Behavior, Recent Advances in Primatology*, eds Chivers D, Joysey K (Academic, New York), Vol 1 pp 487–490.
29. Bolter DR, Zihlman AL (2003) Morphometric analysis of growth and development in wild-collected vervet monkeys (*Cercopithecus aethiops*), with implications for growth patterns in Old World monkeys, apes and humans. *J Zool (Lond)* 260(1):99–110.
30. Pitts GC (1963) Studies of gross body composition by direct dissection. *Ann N Y Acad Sci* 110(1):11–22.
31. Clarys JP, Martin AD, Drinkwater DT (1984) Gross tissue weights in the human body by cadaver dissection. *Hum Biol* 56(3):459–473.
32. Clarys JP, et al. (1999) Human body composition: A review of adult dissection data. *Am J Hum Biol* 11(2):167–174.
33. Campbell B, Gray PB, Leslie P (2005) Age-related changes in body composition among Turkana males of Kenya. *Am J Hum Biol* 17(5):601–610.
34. Kyle UG, Genton L, Slosman DO, Pichard C (2001) Fat-free and fat mass percentiles in 5225 healthy subjects aged 15 to 98 years. *Nutrition* 17(7–8):534–541.
35. Young CM, Blondin J, Tensuan R, Fryer J (1963) Body composition studies of “older” women, thirty to seventy years of age. *Ann N Y Acad Sci* 110:589–607.
36. Theile F (1884) Determinations of weights during the development of the muscle system and of the skeleton of man with a biographical sketch by W Hir. *Proceedings of the Kaiser Leopold-Carolin German Academy of Sciences* (E. Blockmann, Dresden), pp 133–472.
37. Clarys JP, Marfell-Jones MJ (1986) Anthropometric prediction of component tissue masses in the minor limb segments of the human body. *Hum Biol* 58(5):761–769.
38. Duran DL, et al. (2008) Body composition methods: Comparisons and interpretations. *J Diabetes Sci Technol* 2:1139–1146.
39. Norgan NG (1997) The beneficial effects of body fat and adipose tissue in humans. *Int J Obes Relat Metab Disord* 21(9):738–746.
40. Heymsfield SB, Lohman T, Wang Z, Going SB (2005) *Human Body Composition* (Human Kinetics, Champaign, IL), 2nd Ed.
41. Abernathy RP, Black DR (1996) Healthy body weights: An alternative perspective. *Am J Clin Nutr* 63(3, Suppl):448S–451S.
42. Katch VL, et al. (1980) Contribution of breast volume and weight to body fat distribution in females. *Am J Phys Anthropol* 53(1):93–100.
43. Ellison PT (2001) *On Fertile Ground* (Harvard Univ Press, Cambridge, MA).
44. Pond C (1997) The biological origins of adipose tissue in humans. *The Evolving Female: A Life-History Perspective*, eds Morbeck ME, Galloway A, Zihlman AL (Princeton Univ Press, Princeton), pp 147–162.
45. Lee R (1979) *The !Kung San: Men, Women and Work in a Foraging Society* (Cambridge Univ Press, Cambridge, UK).
46. Jenike M (2001) Nutritional ecology: Diet, physical activity and body size. *Hunter-Gatherers: An Interdisciplinary Perspective*, Biosocial Society Symposium Series, eds Panter-Brick C, Layton RH, Rowley-Conway P (Cambridge Univ Press, Cambridge, UK), pp 205–238.
47. Truswell A, Hansen J (1976) Medical research among the !Kung. *Kalahari Hunter-Gatherers. Studies of the !Kung and Their Neighbors*, eds Lee RB, DeVore I (Harvard Univ Press, Cambridge, MA), pp 166–194.
48. Howell N (2010) *Life Histories of the Dohu !Kung: Food, Fatness, and Well-Being Over the Life-Span* (Univ of California Press, Berkeley, CA).
49. Campbell B, O'Rourke MT, Lipson SF (2003) Salivary testosterone and body composition among Aka males. *Am J Hum Biol* 15(5):697–708.
50. Lukas WD, Campbell BC, Ellison PT (2004) Testosterone, aging, and body composition in men from Harare, Zimbabwe. *Am J Hum Biol* 16(6):704–712.
51. Sherry DS, Marlowe FW (2007) Anthropometric data indicate nutritional homogeneity in Hadza foragers of Tanzania. *Am J Hum Biol* 19(1):107–118.
52. Knott C (1998) Changes in orangutan caloric intake, energy balance and ketones in response to fluctuating fruit availability. *Int J Primatol* 19(6):1061–1079.
53. Knott C (2005) Energetic responses to food availability in the great apes: Implications for hominin evolution. *Seasonality in Primates*, Studies of Living and Extinct Human and Non-Human Primates, eds Brockman DK, van Schaik CP (Cambridge Univ Press, New York), pp 351–378.
54. Altmann J, Schoeller D, Altmann SA, Muruthi P, Sapolsky RM (1993) Body size and fatness of free-living baboons reflect food availability and activity levels. *Am J Primatol* 30:149–161.
55. Dittus WP (2013) Arboreal adaptations of body fat in wild toque macaques (*Macaca sinica*) and the evolution of adiposity in primates. *Am J Phys Anthropol* 152(3):333–344.
56. McFarland R (1997) Female primates: Fit or fat? *The Evolving Female: A Life History Perspective*, eds Morbeck ME, Galloway A, Zihlman AL (Princeton Univ Press, Princeton), pp 163–175.
57. Wells JCK (2012) The capital economy in hominin evolution. *Curr Anthropol* 53(Suppl):S466–S478.
58. Antón SC, Potts R, Aiello LC (2014) Human evolution. Evolution of early Homo: An integrated biological perspective. *Science* 345(6192):1236828.
59. Zihlman A (1997) Women's bodies, women's lives: An evolutionary perspective. *The Evolving Female: A Life History Perspective*, eds Morbeck ME, Galloway A, Zihlman AL (Princeton Univ Press, Princeton), pp 185–197.
60. Spoor F, et al. (2015) Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early Homo. *Nature* 519(7541):83–86.
61. Ruff C, Walker A (1993) Body size and body shape. *The Nariokotome Homo erectus Skeleton*, eds Walker A, Leakey R (Harvard Univ Press, Cambridge, MA), pp 234–265.
62. Kelley J, Bolter D (2013) Growth, development and life history in hominin evolution. *Companion to Paleoanthropology*, ed Begun D (Wiley-Blackwell, Oxford), pp 97–117.
63. Bourliere F, Hadley M (1970) The ecology of tropical savannas. *Annu Rev Ecol Syst* 1:125–152.
64. Zihlman AL, McFarland R (1999) Should muscle have most favored tissue status? *Am J Phys Anthropol* 108(Suppl):285.
65. Grand TI (1977) Body weight: Its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am J Phys Anthropol* 47(2):211–240.
66. Zihlman AL, Bruner L (1979) Hominid bipedalism: Then and now. *Yearb Phys Anthropol* 22:132–162.
67. Eftman H (1939) The function of the arms in walking. *Hum Biol* 11(4):529–535.
68. Sokol MD, Raichlen DA, Pontzer H (2007) Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc Natl Acad Sci USA* 104(30):12265–12269.
69. Zihlman AL, Cramer DL (1978) Skeletal differences between pygmy (*Pan paniscus*) and common chimpanzees (*Pan troglodytes*). *Folia Primatol (Basel)* 29(2):86–94.
70. Zihlman AL (1979) Pygmy chimpanzee morphology and the interpretation of early hominids. *S Afr J Sci* 74(4):165–168.
71. Bramble DM, Lieberman DE (2004) Endurance running and the evolution of Homo. *Nature* 432(7015):345–352.
72. Montagna W (1972) The skin of primates. *Am Zool* 12(1):109–124.
73. Montagna W, Yun JS (1963) XV. The skin of the chimpanzee (*Pan satyrus*). *Am J Phys Anthropol* 21(2):189–203.
74. Montagna W (1985) The evolution of human skin. *J Hum Evol* 14:3–22.
75. Jablonski N (2013) *Skin: A Natural History* (Univ of California Press, Berkeley, CA), 2nd Ed.
76. Zihlman AL, Cohn B (1988) The adaptive response of human skin to the savanna. *Hum Evol* 3(5):397–409.
77. Baldwin P, McGrew W, Tutin C (1982) Wide-ranging chimpanzees at Mt. Assirik, Senegal. *Int J Primatol* 3(4):367–385.
78. Nishida T (1989) A note on the chimpanzee ecology of the Ugalla area, Tanzania. *Primates* 30(1):129–138.
79. Hunt K, McGrew W (2002) Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. *Behavioural Diversity in Chimpanzees and Bonobos*, eds Boesch C, Hohmann G, Marchant L (Cambridge Univ Press, Cambridge, UK), pp 35–51.
80. Ogawa H, Idani G, Moore J, Pintea L, Hernandez-Aguilar A (2007) Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *Int J Primatol* 28(6):1397–1412.
81. Pruett JD (2007) Evidence of cave use by savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: Implications for thermoregulatory behavior. *Primates* 48(4):316–319.
82. Laporte LF, Zihlman AL (1983) Plates, climate, and hominoid evolution. *S Afr J Sci* 79(3):96–110.
83. Falk D (1990) Brain evolution in Homo: The “radiator” theory. *Behav Brain Sci* 13:333–344.
84. Pennisi E (2012) Microbiology. Microbial survey of human body reveals extensive variation. *Science* 336(6087):1369–1371.
85. Trivedi B (2012) Microbiome: The surface brigade. *Nature* 492(Suppl 7429):S60–S61.
86. Hurlley S, Hines PJ, Mueller KL, Culotta E (2014) Skin. From bench to bedside. Introduction. *Science* 346(6212):932–933.
87. Zihlman AL, Underwood CE (2013) Locomotor anatomy and behavior of patas monkeys (*Erythrocebus patas*) with comparison to vervet monkeys (*Cercopithecus aethiops*). *Anat Res Int* 2013:409534.