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Review

The Hairless Mutation Hypothesis: a Driving Force of Humanization by Enforcing Bipedalism to Hold a Baby, by Allowing Immature Baby Delivery to Enlarge the Brain after Birth, and by Making Use of Fire to Get Meat and to Cook Foods

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Three characteristics, i.e., bipedalism, nakedness, and the family reproductive unit, distinguish humans from other primates. Once a hairless mutation was initially introduced, these three could be explained inseparately. All primates except humans can carry their babies without using their hands. A hairless mother would be forced to stand and walk upright to hold a baby. As her activities were markedly limited, the male partner had to collect food and carry it to her to keep their baby from starving. He must have been sexually accepted by her at any time as a reward for food. Sexual relations irrespective of estrus cycles might have strengthened the pair bond, leading to family formation. Savannahs appeared 2.5 million years ago (Ma), which forced hominins to terrestrial life, but the ground was full of danger and a larger brain became advantageous. Wildfires occurred frequently; naked hominins approached fire for warming, but soon must find burnt animals in the aftermath of wildfires. The taste of burnt meat must be a driving force for hominins to become meat-eaters. They must have learned how to control fire and how to repel hairy animals that hate fire. To compete with large carnivores with fangs and claws, they became not hunters but robbers. When robber hominins found that a carnivore had killed a prey animal, they approached the predator and repelled it away from the victim using fire, then claiming the prey intact. Major events such as the timing of global cooling, the appearance of savannahs, the appearance of early humans, decline of large predators, the manufacture of stone tools, and the start of cooking largely coincide at 2.5 Ma. Cooked meat must be tasty and easily digested, providing hominins with nutrients sufficient to enlarge the brain, while most large carnivores were forced to extinction. Thus, hairlessness created humans.

Key words: bipedality, extinction of carnivores, family formation, human robber hypothesis, hunter-gatherer, robber-gatherer

Three Major Characteristics of Humans

Bipedalism

There are several characteristics which separate humans from other primates such as bipedalism, practical hairlessness, a family as a social unit, a large neocortex, small canine teeth, uses of tools, fire, and language, culture, and civilization. Especially, bipedalism, practical hairlessness, and family as a social unit are considered to constitute basic key factors of the origin of humans. Other important characteristics such as a large neocortex and the use of tools and fire are considered to have achieved only after the establishment of bipedalism, which liberated hands from walking. Language is very likely to have emerged long after bipedalism, which allowed the brain to grow larger at the *Homo* stage. The basis of humanization, i.e., bipedalism, has remained a matter of interest for over a century. Typical hypotheses or ideas are listed in Table 1.

Most hypotheses or ideas listed in Table 1 are based on the assumption that humans evolved in dry savannahs, but our ancestors were arboreal denizens. Thus, a textbook says that all of these suggestions have their proponents, and none are universally accepted (12). Lovejoy (5) thought that provisioning must be critical for upright walking (Table 1). He wrote that five characters separate man from other hominins—a large neocortex, bipedalism, reduced anterior dentition with molar dominance, material culture, and the unique sexual and reproductive behavior. Human evolution, however, was not a direct consequence of brain expansion and material culture, but the unique sexual and

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Table 1. Typical hypotheses or ideas to explain the origin of human bipedalism

Hypothesis or idea	Reference
Use of tools compelled hominins to stand upright.*	Washburn, 1960 (1)
Bipedality might have evolved for food transport in a dry savannah habitat.*	Hewes, 1961 (2)
A terrestrial feeding posture was important for bipedalism.*	Jolly, 1970 (3)
Upright hominins were able to forage longer in the open sun.*	Wrangham, 1980 (4)
Provisioning must be critical for upright walking.†	Lovejoy, 1981 (5)
Upright posture and bipedal gait were useful for vigilance against predators.*	Day, 1986 (6)
Hominins were scavengers, and bipedalism was a necessary adaptation.*	Sinclair et al., 1986 (7)
In an open savannah, hominins had a thermoregulatory advantage.*	Wheeler, 1991 (8)
Bipedal threat display and appeasement behavior were important for peaceful resolution	Jablonski, Chaplin, 1993 (9)
Bipedal walking is less costly than quadrupedal knuckle-walking.‡	Sockol et al., 2007 (10)
The hairless mutation hypothesis: hairlessness enforced bipedalism while holding a baby with both hands.†	Sutou, 2012 (11)

*These are based on the assumption that humans evolved in dry savannahs, but early hominins lived in woodlands. †See the text. ‡Hominins were not knuckle-walkers.

Table 2. Some hypotheses or ideas to explain the human hairlessness

Hypotheses or ideas	References
Sexual selection: females became hairless to attract males, or males favored naked females.*	T. Huxley (in Morgan, 2009 (13))
The body cooling hypothesis: nakedness was advantageous for hominins with a large brain, which is vulnerable to thermal damage.†	Wheeler, 1984 (14); 1985 (15)
The ectoparasite hypothesis: hominins shed their fur to rid their bodies of ectoparasites such as lice.‡	Pagel, Bodmer, 2003 (16)
The hairless mutation hypothesis: hairlessness triggered humanization by enforcing bipedalism while holding a baby with both hands.§	Sutou, 2012 (11)

*If nakedness was advantageous, at least a few other primates are expected to be naked. †The initial step in the denudation process did not occur in open hot environments, nor bipedalism preceded body-hair reduction (17). ‡A molecular clock analysis shows that human body lice originated approximately 72,000 years ago and suggests that clothing is a recent innovation in human evolution (18). §This is plausible, but there is no direct evidence.

reproductive behavior of man may be the sine qua non of human origin. Humanization must be achieved only after hominins became hairless and bipedalism, but he did not show why hominins became hairless and bipedal. My hairless mutation hypothesis suggests that a hairless mutation triggered humanization from the chimpanzee/human last common ancestor (CLCA) by enforcing bipedalism to hold a baby (11). Once a hairless mutation was initially introduced, bipedalism, practical hairlessness, and a family as a social unit became separately inexplicable.

Hairlessness

Hairlessness distinguishes humans from other primates. Lack of availability of skin or hair fossils must be the major reason for the scarcity of hypotheses and ideas about human nakedness. Some of them are listed in Table 2. Here again, none is conclusive as to the origin of human nakedness.

A family as a social unit

Monogamous family system of humans: The reproductive unit of humans is a family, which constitutes the basic unit of society and which clearly distinguishes humans from other primates. Reproductive units of primates are listed in Table 3. Chimpanzees form a closed reproductive unit consisting usually of 20–80 males and females who are promiscuous (19,20). Single-male and multimale groups exist among gorillas (21,22). The social organization of orangutans is a loose community. A typical reproductive unit consists of one male and one or more female clusters (23). Thus, the monogynous nature of a human family is unique, suggesting that the origin of the family is intrinsically associated with the origin of humans.

One of early hominins, *Ar. Ramidus*, had a reduced canine/premolar complex (24) and showed no sexual dimorphism in body size (25), meaning less male-to-male conflict and social aggression. If this was true for early hominins and a cooperative family was the basic unit of human society, no reasons exist to develop and maintain big, projecting canines and large, dimorphic

Table 3. Reproductive systems of great apes

Species	Reproductive unit	Reference
Humans	The basic unit is a family.	Morris, 1967 (28)
Chimpanzees	A closed unit usually consists of 20?80 males and females who are promiscuous.	Gagneux et al., 1999 (19); Vigilant et al., 2001 (20)
Gorillas	Troops tend to consist of one male, multiple females, and their offspring, but multimale troops exist.	Bradley et al., 2005 (21); Yamagiwa et al., 2003 (22)
Orangutans	A typical reproductive unit consists of one male and one or more female clusters.	Singleton, van Schaik, 2002 (23)

male bodies. The original monogamous family system seems to have been transferred to the descendant humans.

Australopitheccus afarensis was clearly bipedal (26) and was likely to be principally monogamous, as we are (27). Morris (28) wrote that we live in a culturally developed society, but the basic unit of the society remains the family, as was true in the early hunting and gathering days in savannahs. The family-based society must be dated back to early hominins. In addition, the mentality of family bonding is apparently expanded to human communities as human bonding. In this context, it is of interest to learn that 2- to 3-year old human children understand collaboration and sharing, while chimpanzees do not (29).

How do primates carry their babies?: Figure 1A–F show how babies or infants of monkeys and apes are carried. They grasp mother's hair firmly soon after birth and are not thrown off even when mothers run on the bumpy ground or jump from branch to branch. This means that hair is the indispensable tool for monkeys and apes to carry babies or infants, and that their babies are born at matured stages grown enough to cling to their mothers for themselves. By contrast, a human mother is not hairy so that a baby cannot cling to her even if he or she is delivered at the matured stages as primate babies are. As a result, she is forced to hold her baby with both hands (Fig. 1G). This constitutes the most important and fundamental difference between humans and other primates at birth. The basic difference hinted me that hairlessness must be profoundly associated with human evolution. As a matter of course, when forelimbs were occupied to hold a baby, hindlimbs were used to upright walking. Here we can see the division of labor between forelimbs and hindlimbs, Thus, bipedalism, the very basic promoter of human evolution, was a inevitable gift of hairlessness.

The family formation enhanced by hairlessness: The hairless mutation hypothesis predicts that a hairless mother had to hold her baby with both hands and her attention was persistently paid to the baby (Fig. 1G). This must have intensified mother-baby bonding. However, her activities in a woodland area were greatly hampered so that she was difficult to collect enough food. The mother and baby would have starved to death if the partner male did not provide them with food. In other words, irresponsible and selfish males could not leave offspring. As a reward for food, the mother would have sexually accepted him at any time. Seasonless copulation with skin-to-skin contact must have reinforced the pair bond and contributed to form a family. When a family is the basic reproductive unit in a society, no sexual dimorphism is necessary. Consequently, the unique sexual and reproductive behavior of monomorphic humans, including monogamous and seasonless mating, lack of an externally recognizable estrous cycle, continual receptivity, and the large penis could be explained inseparably by introducing family as the original, basic nature of humans.

Not Gradual Modifications but Sudden Humanization from CLCA

Molecular and paleontological data suggest sudden human speciation: The African grate apes are our closest living relatives and molecular analyses indicate that humans separated from CLCA perhaps 5–7 Ma (30). Other genetic evidence shows that humanization occurred more recently than 6.3 Ma (31). Human (32,33) and chimpanzee (34) genomes were deciphered; the genomic difference between the two is 1.2% (35). When base changes of 1% require 10 million years (My), the time to a most recent common ancestor (TMRCA) is estimated as 6 My. Another analysis using 36 nuclear genes indicates that TMRCA is 5.4 ± 1.1 My (36). It is of great interest to learn that divergence between chimpanzee and human lice was estimated to occur 5.6 Ma (37).

The ages of early hominins, *Sahelanthropus tchadensis* (7–6 Ma) (38), *Orrorin tugenensis* (6.1–5.8 Ma) (39), and *Ardipithecus kadabba* (5.6 Ma) (40), are close to that of CLCA. Paleontologically and genetically determined ages overlap or match well, indicating that there was little or no intervening period between CLCA and the appearance of these early hominins. This means that humanization in essence had not been achieved gradually, but occurred suddenly. When 101 species were ana-

Fig. 1. Baby/child-carrying hairy primates, a lactating human mother, and a hairless dog. All primate mothers excepting those of humans carry their young without using their hands, even when moving through the jungle tree canopy; hair is a baby carrier (A–G). A, chimpanzees (courtesy of Mr. M. Nishizawa); B, gorillas (courtesy of the Ueno Zoological Gardens); C, orangutans (courtesy of Ms. H. Takahashi); D, gibbons (courtesy of the Parken Zoo, Sweden), E, golden snub-nosed monkeys (courtesy of Ms. M. Fukatsu); F, Japanese macaques (courtesy of Mr. T. Sakai); G, humans (courtesy of Dr. H. Shinozaki); and H, a Mexican hairless dog (courtesy of the Mutsugoro Animal Kingdom).

lyzed for speciation, approximately 80% species were found to emerge from a single, rare, stochastic event (41). Taken together, a hairless mutation could be the rare, stochastic event that enforced bipedalism, promoted family formation, and thereby triggered humanization.

A single mutation can induce hairless animals with scalp hair: Ectodermal dysplasias (EDs) are congenital disorders characterized by changes in ectodermal structures involving alterations in hair, teeth, nails, sweat glands, cranial-facial structure, digits and other parts of the body. Clinically, 64 genes are responsible for EDs (42). The downless (*dl*) gene mutation in mice is an example. Affected mice have defective hair follicle induction, lack sweat glands, and have malformed teeth. The *dl* gene is a member of the tumor necrosis factor (*Tnf*) receptor (*Tnfr*) family, of which ligand is likely to be the product of the tabby (*Ta*) gene (43). The human *DL* homologue supports this finding (44). Darwin (45) noticed the close relationship between the hair and teeth in the naked Turkish dog, and wrote ''it can be only slightly accidental.'' Indeed, Mexican, Peruvian, and Chinese crested hairless dogs lack the hair and teeth. This phenotype is called canine ectodermal dysplasia (CED). A frameshift mutation in a member of the forkhead box transcription factor family (*FOXI3*) gene was found to be responsible for CED (46). The three hairless dogs have hair on the head (Fig. 1H), as we have. Mexican hairless dogs have hair on the tail. Chinese crested dogs have long hair not only on the head but also on the tail and the lower part of the legs.

A mutation in the *hr* gene is responsible for hairless cats called Sphynx. A hairless chimpanzee named Cinder suffered from alopecia universalis (47). Her company did not discriminate against her. Nude mice have a mutation in the *nu* locus in the chromosome 11, and are hairless and devoid of the thymus (48). By contrast, a Burmese family suffered from congenital hypertrichosis lanuginose—a kind of hypertrichosis characterized by excessive growth of hair—were extremely hairy and the traits were autosomal dominant (49). They lacked teeth. Some examples shown above exemplify that hairless or hairy animals including humans can be produced by a single mutation. A gene plays a role as a member of genetic networks; it sometimes or even frequently shows pleiotropic effects. The full set of ED genes might contain a locus associated with hairless humans with scalp hair as dogs (Fig. 1H). This mutation is probably dominant and its expression could accompany other traits such as modifications of dentition and sweat glands.

Evolution from Hominins to Humans

Early hominins were bipeds, but arboreal denizens: Typical hominin and human species are listed in Table 4. It is commonly received that we *Homo sapiens* deviated from CLCA, which is estimated to have existed between 5 and 7 Ma. The earliest fossil of the human lineage close to CLCA is *S. tchadensis* (38). Associated fauna imply that the fossils are 6–7 Ma and that they lived close to a lake but not far from a sandy desert (50). Analysis of the basicranium—examination of the connection of the spinal column and scal—shows that *S. tchadensis* was an upright biped (51). The femoral morphology of *O. tugenensis* 6 Ma from Kenya exhibits bipedalism (39,52). Another earlier species of *Ar. kadabba* was dated to 5.2–5.8 Ma. The proximal foot phalanx supports bipedalism (40). *Ar. ramidus* might have lived ca. 6–4 Ma (53). ''Ardi'' was an *Ar. ramidus* woman who lived in the Afar Rift region of northern Ethiopia 4.4 Ma (25). Her well preserved and reconstructed skeleton, together with a large collection of animal and plant fossils (more than 15,000) around her (54), provides reliable information as to human evolution. She was 120 cm tall and weighed 50 kg. Her brain was small (300–350 cm^3), similar to that of a present female chimpanzee. *Ar. ramidus* males and females had

Table 4. More than two hominin species had been usually coexisted. All were bipeds

Hominins or humans	Species	Time (Ma)	Height (m)	Weight (kg)	Brain (cm^3)
Early hominins	*Sahelanthropus tchadensis*	6–7	150		320–380
	Orrorin tugenensis	6.1–5.8			
	Ardipithecus kadabba	5.6			
	Ar. ramidus	4.4	120	50	300–350
Archaic hominins	*Australopithecus anamensis*	4.2–3.9		33–51	
	Au. afarensis	3.9–2.9	107–152	29–45	380–430
	Au. bahrelghazali	3.5–3			
	Au. africanus	3.03–2.04	115–138	30–41	420–500
	Au. garhi	3–2			450
	Au. sediba	1.78–1.95	130		420
	Kenyanthropus platyops	3.5–3.2			350
Megadont archaic hominins	*Paranthropus aethiopicus*	2.6–2.3			410
	P. boisei	2.1–1.1	124–137	34–49	530
	P. robustus	2–1.5	110–132	32–40	530
Early humans	*H. rudolfensis**	2.4–1.6	150–160	51–60	790
	*H. habilis**	2.4–1.5	100–131	32–37	500–800
	*H. georgicus**	1.8	150		600–780
Pre-modern humans	*H. ergaster**	1.8–1.3	160–180	56–66	700–1,100
	H. electus	1.9–0.14	179		950–1,100
	Homo antecessor	1.2–0.8	160–180	90	1,000–1,150
	H. heidelbergensis	0.5–0.2	175	62	1,100–1,400
	Denisova hominins	−0.04			
	H. neanderthalensis	0.23–0.024	157–165	80	1,450
	H. floresiensis	−0.017	106	25	426
Modern humans	*H. sapiens*	0.2–	170	70	1,350

*These might belong to a single *Home* lineage, *Homo electus* (65).

a reduced canine/premolar complex (24) and showed no sexual dimorphism in body size (25), suggesting no or less social aggression. She lived in woodlands with small patches of forest. She was probably omnivorous, ate nuts, insects, snails, and small animals, and did not feed much in the open grassland. Importantly, she was apparently a biped; i.e., our ancestors walked upright before they evolved a larger brain. She had the opposable big toe, clearly demonstrating that she was an arboreal denizen (55). She had no characteristics of the suspension, vertical climbing, and knuckle-walking that present chimpanzees and gorillas have (56). These findings definitely deny the idea that inhabitation of grassland or open savannahs was the driving force of the origin of upright walking (Table 1). The skull and teeth of *Ar. ramidus* resemble those of *S. tchadensis*. In fact, *S. tchadensis*, *O. tugenensis*, and *Ar. kadabba* are similar to each other overall (25), and they might belong to a single genus (57). Their living periods overlap at least in part. These findings suggest that *Ar. ramidus* is the fourth member of the early hominin genus. Even if that is not so, Ardi must by and large represent images of our ancestors soon after separation from CLCA. Consequently, early hominins were bipedal from the beginning.

Archaic hominins were bipeds before brain enlargement: Early hominins were followed by archaic hominins (4.2–1.1 Ma) such as *Australopithecus* and *Paranthropus* species (Table 4). *Ar. Ramidus* and *Au. anamensis* (58) were separated by only ca. 0.2 My, but the difference between the two groups is discrete. Especially, early hominins had the opposable big toe, but archaic hominins had the more adducted one in line with other four lateral toes. By transformation from an ape-like foot to a modern human-like one, the foot is changed to act as a propulsive lever rather than a grasping tool. Plentiful fossils of *Au. afarensis* are available. Lucy was a female *Au. afarensis* who lived 3.18 Ma. Over 40% of Lucy's skeleton was recovered. Although her foot was not recovered, her pelvic structure clearly shows that Lucy was a biped (5). Her brain size was less than 400 cm^3, indicating that bipedalism outstripped enlargement of the brain. Another well preserved skeleton of Selam or Dikika Baby, a 3-year-old *Au. afarensis* girl who lived 3.32 Ma and whose brain size was 330 cm^3, also supports bipedalism before brain enlargement (59). Hominin footprint fossils 3.6 Ma at Laetoli in Tanzania demonstrated directly bipedalism of *Au. afarensis* (60). The Laetoli hominins walked with weight transfer like the economical extended limb bipedalism of humans, which is more ergonomically efficient than ape-like bipedalism (61). Lucy seemed to have flat feet, but some archaic hominins had arched feet (62). The StW 573 specimen called 'Little Foot' belongs to neither *Au. afarensis* nor *Au. africanus*, but to an *Australopithecus* species (63). The date of Little Foot has not been firmly determined and varies from 4, 3.3, and 2.2 Ma. Whereas the big toe is medially diverged and mobile, the foot is adapted apparently for bipedalism (64). These fossils indicate that Australopithecines were adapted to bipedal locomotion if not perfect.

Split of upper and lower bodies of archaic hominins: *Au. afarensis* Lucy 3.2 Ma had a mosaic structure of the upper and lower body. The upper body consisting of a small head and long arms with long fingers is primitive and ape-like. However, the lower body is clearly bipedal. *Au. sediba* 2 Ma also shows the split features of upper and lower bodies (66). This means that evolution from early hominins to archaic ones was applied mostly to the lower body, and the upper body remained rather primitive (see Fig. 1 in Ref. 67). The reason for the split evolution between the two body parts may be explained by the selective pressure from their lifestyle. Early hominins probably spent most of their lives in trees and were sometimes forced to walk on the ground to move from tree to tree and collect foods. Archaic hominins must not have been allowed to live mainly in trees, because arboreal regions regressed in association with climate change in the Pliocene epoch (5.332–2.588 Ma). Then they had to collect foods largely on the ground. They might have to catch vivid insects and small animals and have to scavenge from kills made by predators such as large cats and dogs, from which they would have had to flee quickly and frequently to trees nearby. Therefore, trees must have provided them with refuge and places to make nests. Effective walking and running was becoming a major selective advantage for archaic hominins to evolve human-like bipedalism according to the terrestrial principles, whereas the upper body remained ape-like according to the arboreal principles. A large brain was advantageous for the terrestrial life that was full of danger. However, it was practically impossible for them to have a big brain case in addition to the long upper limbs with the massive and limber shoulder girdles. Most critically, they did have insufficient tools and ability to get nutrition sufficient to support a large brain.

Bipedalism Helped Immature Baby Delivery, Allowing the Brain to Enlarge after Birth

Selective pressure to have a big brain: Archaic hominins were followed by early humans such as *H. rudolfensis*, *H. habilis*, and *H. georgicus* (Table 4). Climate change might have compelled early humans to shift their major life from woody lands to more savannah-like openly lands, but terrestrial life was full of dangers. They had to be vigilant for predators, approach of which would be communicated vocally among family or group members. Development of communication capability and methods must be advantageous. Weapons made of stone and wood must be effective in order to defend early humans against their natural enemies. Stone tools were useful to dig edible roots, to cut meat, and to break bones. A larger brain was therefore advantageous to the terrestrial life. To have a larger brain, a nutritional supply was indispensable; a vegetarian life must be difficult to support it. Foods rich in lipids and proteins, such as meat, were favored. To get meat, fire must be used to expel carnivores and to steal prey (67). Fire is useful to cook foods, which are easily digestible. To control and manipulate fire, a larger brain was favored, too. There were two strategies to get a big brain: one was to widen the birth canal and deliver a mature baby, and the other was to deliver an immature baby and rear it after birth. Thanks to bipedalism, humans could adopt the second strategy, because mothers would be able to hold an immature baby with both hands (68). To explain how humans have achieved a big brain, a new idea was put forward as the human robber hypothesis (67).

Coincidence of climate change and appearance of early humans: The earth entered a phase of global cooling about 3 Ma. This cooling is thought to have spurred the disappearance of forests and the spread of grasslands and savannahs. Australopithecines (4.2–1.8 Ma) lived in fairly wooded, well-watered regions and were thought to be collector-gatherers because their body structures were not suitable for use by scavengers or hunters. Instead, they would rather be the victims of carnivores. Their brain sizes were around 400 cm^3. Those of early humans (2.4–1.5 Ma) were approximately 600–800 cm^3. Consequently, transition from hominins to humans was accompanied by a brain size shift. Hernandez and Vrba (69) investigated palaeoclimatic change using mammal fauna as environmental indicators. They showed that biomes in the Turkana Basin changed from semi-evergreen rain forest to deciduous woodland and savannah during the middle-late Pliocene (3.3–2.58 Ma). Savannahs have been continuously present from 2.5 Ma onwards. This inference matches fairly well with the appearance of early humans 2.4 Ma and the start of decline of large carnivores shown by Werdelin and Lewis (70).

Humans must have been neither scavengers nor hunters, but robbers: Wildfires were frequent in arid climates. As early humans had no hair to be burnt, they must have willingly approached the flames and smoke. There must be lots of opportunities to find victims of burnt animals that smelled good and tasted nice. They must have become meat-eaters. Sooner or later, they must have known that hairy animals did not approach a burning fire. Hominins must gradually have become familiar with fire and learnt how to control fire. Soon they must have learnt how to repel beasts using fire.

Werdelin and Lewis (70) published an important report recently. They divided carnivorous fossils into large animals of more than 21.5 kg and those of smaller ones. When their functional richness and functional evenness were analyzed in eastern Africa at a 0.5 Ma time span from 3.5 Ma to 1.5 Ma, those of the large carnivores consisting of 29 species decreased rapidly from around 2 Ma to the present, while those for small carnivores, consisting of 49 species, increased. As this decline coincides closely with the appearance of *Homo* species, the authors conclude that the invasion of humans into the carnivore niche space played a critical role in the decline of large carnivores' functional richness. I readily agree with and support this so-to-speak 'human invader' hypothesis.

Here, let me ask if early humans were hunters. It seems very difficult for them to because hunters when grazing herbivores were able to run faster than bipedal humans who were equipped with stone arms. Moreover, would they have been able to compete for the niche space against carnivorous predators such as saber-toothed cats? I do not think so; early humans might have become scavengers at best. However, there was a more cunning way to get meat neatly, i.e., to become neither hunters nor scavengers, but to become robbers. When early humans found that a predator had killed a game animal, they approached the beast with fire, repelled the animal, and robbed it of the intact prey animal. A stone or club attack can be sustained by hairy beasts. They might even counterattack early humans. Hairy beasts must be instinctively vulnerable and unable to resist fire, however. Stealing prey animals must have delivered a more severe blow to carnivores than being competitors as hunters, because the energy to capture a prey animal comes to yield nothing. Taken together, I put forward the human robber hypothesis (67) that explains the rapid decline of large carnivores than the human invader hypothesis (70) or the human hunter hypothesis does. Therefore, our ancestors must be not hunter-gatherers, but bobber-gatherers.

Humans stole not only meat but also shelter: Hairlessness is disadvantageous in a usual sense because hairless animals have difficulty in maintaining body warmth, protecting their body from injury, defending the skin from ultraviolet light, and avoiding rain in part. Oil-coated hair of animals is water-repellent and they can shake raindrops off the hair. Hairless humans were certainly miserable on rainy days. Trees were not good rain shields, while dens or natural caves were ideal refuges. Importantly, these were effective in protecting them from attacks by predators. Beasts and predators were, however, the earlier inhabitants than humans. Once early humans had knowledge and techniques to control fire, they were able to smoke out hairy beasts from caves easily. We know that caves are good places to excavate high-quality human fossils. Most probably, humans were robbers not only of meat but also of shelter. Thus, the human robber hypothesis well explains the downhill decline of large carnivores reported by Werdelin and Lewis (70).

Stone tools and fire, enhancers of brain enlargement: Australopithecines lived in wooded, well-watered regions. They must have encountered wildfires only rarely and would not be good fire users. Early humans would have had many chances to encounter wildfires in savannahs from around 2.5 Ma on. They must find burnt bodies of animal victims in the ruins of wildfires. The roasted meat was tasty and readily digestible. The taste of cooked meat must have been a driving force compelling early humans to become meat-eaters and consequently robbers as described above. To be robbers, alert vigilance, verbal warnings, and dexterous hands to make stone tools and to control fire must have been helpful. For this, a larger brain was inevitably advantageous and selective. Fire was indispensable to rob carnivorous predators of animal victims (67). Stone tools were also indispensable to dissect the victims and to break bones for the bone marrow. Usefulness of fire was fully achieved using stone tools, occurrences of which are dated between 2.6–2.5 Ma (71,72). The dates largely coincides with the climate change to savannahs, appearance of early humans, and decline of large carnivores, although natural stones might have been used much earlier. At the present time, wild bearded capuchin monkeys use stones to open seeds by placing them on stone or wood surfaces and then pounding them with rocks (73). Bone fossils with cut marks were dated back to as early as 3.4 Ma (74). When was fire first used by hominins? "The answer is that fire was first controlled anywhere from about 230,000 years ago to 1.4 or 1.5 Ma, depending on which evidence you accept as definitive (75). Analyses of burnt bone and plant ash remains at the site of Wonderwerk Cave, South Africa, indicates that fire was used approximately 1.0 Ma (76). Possibly burnt bones were recovered from Member 3 (approximately 1.0–1.5 Ma) in the Swartkrans cave, South Africa (77). Abundant remains of *Australopithecus robustus* (2.2–1.2 Ma) and *Homo erectus* (1.8–0.14 Ma) were found in the older Members 1 (1.8 Ma) and 2 (1.5 Ma) at the cave, but no evidence of fire use was detected. These findings indicate that fire was controlled by humans at 1.5 Ma at best. Such are the fossil records. Reduced feeding time and molar size were analyzed and the results suggest that food processing originated after the evolution of *Homo*, before or around 1.9 Ma (78). As early humans appeared around 2.4 Ma, there is the possibility that cooking started 2.4 Ma. The dating is not unchangeably fixed. Considering that charred bones made in the field might be difficult to remain as fossils, use of fire is expected to date back to much earlier than 1.5 Ma.

Roughly speaking, our brain occupies 2% of our body and consumes 20% of its energy. Nutrients of high quality including n-6 and n-3 essential fatty acids in addition to animal-derived proteins are needed to develop the brain (79). Marine and estuarine ecosystems might have provided hominins with the appropriate stimulus to develop a large brain (80). Foods thus provided less competitively include invertebrates, molluscs, small or slow-moving fish, and marine algae. These might have contributed to enlarge the human brain to some extent, but the main nutrients were apparently obtained from animal meat when we consider that savannahs became a major landscape 2.5 Ma, that humans with an enlarged brain started to appear around 2.4 Ma, that stone tools appeared 2.5–2.6 Ma, and that large carnivores started to decline during 2.5–2.0 Ma. It is plausible that early humans started to use and control fire approximately 2.5 Ma to expel carnivores, to get meat, to cook it, and consequently to enlarge the brain. Fire and stone tools were very likely to have acted synergistically to provide the human brain with nutrients.

Discussion

This review is a summary of previous papers. Humanization was triggered by a hairless mutation that enforced bipedalism (11), which in turn allowed hominins to deliver an immature baby and rear it after birth (68). Hairlessness let hominins to approach fire, which provided them with methods to get meat and to cook it, supplying sufficient nutrients to enlarge the brain (67).

Solar energy is fixed by plants through photosynthesis. Herbivores consume the plants to make their bodies, which are then consumed by carnivores. Activities of both herbivores and carnivores are supported by ATP, which is produced mainly by the oxidative phosphorylation process in mitochondria. Production and consumption of ATP are mild processes. By contrast, fire releases the solar energy fixed in plants all of a sudden. When early hominins obtained knowledge and techniques how to control fire, firearms were in their hands. Fire was so powerful that large carnivores with claws and fangs could not resist early hominins. Hominins used fire not only to rob carnivores of meat but also of shelters. Cooked foods were more or less sterile, tender, easily digestible, and nutritious, allowing hominins to enlarge the brain and to spare time that might be used for creation. We need neither gigantic robust jaws nor long canine teeth any more. When humans radiated out from Africa to Europe and Asia in pursuit of prey animals, they must have accompanied fire as their most precious inheritance and legacy. Indeed, "we humans are the cooking apes: the creatures of the flame (81)".

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