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The Evolution of Hominid Bipedalism

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Abstract

Paleoanthropologists mark the divergence between apes and hominids with the adaptation of bipedalism five to six million years ago. In this paper, I argue that while the first upright hominids occurred in this time frame, the process of becoming a fully efficient biped took much longer and was not complete until *Homo erectus* at 1.8 million years ago. To provide context to the puzzle of how and why our ancestors evolved upright walking, I examine many of the prevailing theories of bipedal origins, including the aquatic ape hypothesis, the heat hypothesis, and the carrying hypothesis.

Introduction

Man is a biped without feathers —Plato (427 B.C.E.- 347 B.C.E.)

As I was hiking in Israel a couple of summers ago, my group approached a small stream that we needed to cross. There was a rock path, but the rocks were not easy to walk on— they were rounded and very slippery. After a couple of people ahead of me slipped, falling into the stream, I decided it would be best to use my arms for support. Using the idea that four points of contact for balance are better than two, I crawled across the rocks using all four of my limbs, with my hands leading the way. I made it across easily without falling in.

By using that form of locomotion to cross the stream, I took a five million year journey back to a time when all of my ancestors moved in that manner. Our closest primate relatives today, the chimpanzee and gorilla, still do not rely on upright walking, or bipedal walking, to get around. They are capable of standing and walking upright for periods of time, but their anatomy is not made for that kind of locomotion. The modern human body is wonderfully adapted to support bipedalism. We can walk for miles with ease. Why and how did this method of locomotion evolve in early humans?

Anthropologists use the adaptation of upright walking in hominids (early human ancestors) to mark their divergence from apes, a split occurring approximately five to six million years ago, though— as I argue later— fully efficient bipedalism was not complete until about 1.8 million years ago, in *Homo erectus*. Some early scholars saw larger brains and intelligence as the key to hominid origins (Gould 1977), but we know now that bipedalism evolved much earlier than the expansion of brain size.

Theories of bipedal origins use non-human primates as referential models for our common ancestor, since we cannot observe the behavior of extinct hominids. The chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) are the preferred models that anthropologists use. The bonobo is the best model for general physical appearance of the common ancestor. Figure 1 shows a physical comparison between the bonobo and Australopithecine, who was an early hominid.

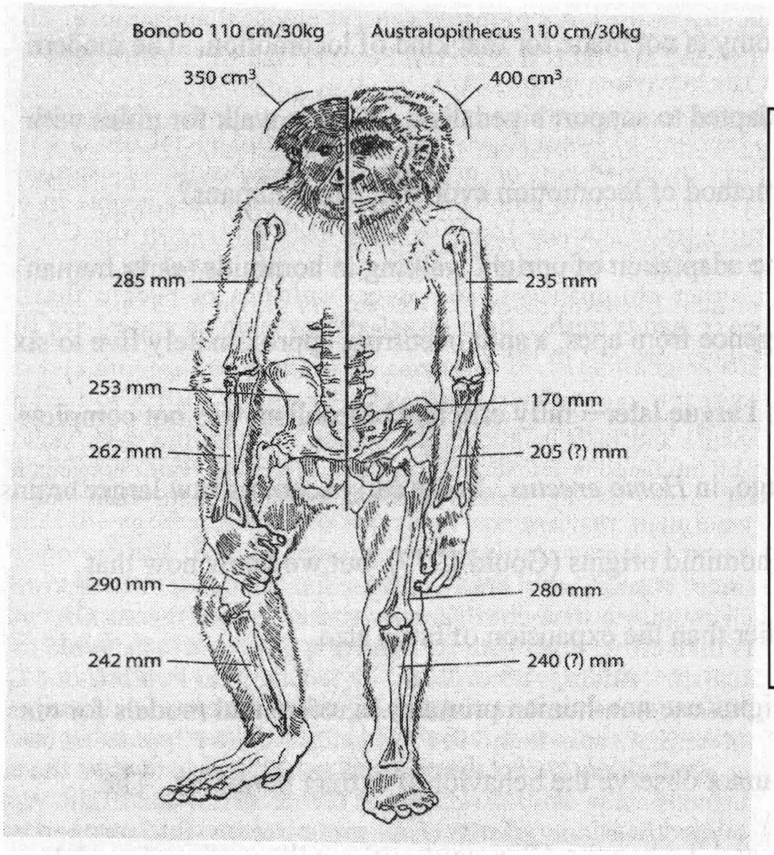

Figure 1: The body size proportions of the bonobo (left half) and Australopithecus (right half) are very similar. Notice the difference in pelvis bones between the two, and the bent knee posture of the bonobo.

(Figure taken from Falk 2000: 351)

The question of why bipedalism was selected for in our hominid ancestors has always baffled anthropologists. Many theories, from Morgan's aquatic ape hypothesis (1982) to Lovejoy's carrying hypothesis (1981), have created scenarios in the form of evolutionary narratives about how bipedalism might have produced a specific selective advantage. These theories often take the form of single-factor explanations for bipedalism, such as it allowed hominids to carry food, or see over visual barriers to see predators.

In this paper, I seek to resituate some prevailing presumptions of scholarship on the origins of hominid bipedalism, including the common assumption that early hominids were fully erect bipeds. Bipedalism evolved gradually— our earliest ancestors were probably very awkward walkers. I will first examine the historical backgrounds of thoughts on bipedalism and human evolution. After doing this, I will take a look at the anatomical changes that were associated with bipedal locomotion. Then I will critically assess seven of the most popular theories of bipedalism. Finally, I will add my own thoughts on how we should contextualize the evolutionary narratives regarding bipedalism.

A Historical Look at Human Origins and Bipedalism

Theories about human origins have classically focused on bipedalism, tool use, and brain size (Gould 1977). For a long time, there was an emphasis on progress from stupid small- brained apes that use no tools and walk on all fours to the pinnacle of a big brained, tool using, upright modern man. The modern big brain was the focus for theorists who thought that an enlarged brain allowed for bipedalism. In 1828, embryologist Karl Ernst von Baer wrote, "Upright posture is only the consequence of the higher development of the brain…all differences between men and other animals depend upon construction of the brain." (1828 von Baer, quoted in Gould 1977: 208).

The evolution of upright walking and big brains were linked as defining characteristics of mans' rise to glory in his dominance over other animals and the earth itself. Unfortunately for "progress" theorists, the current fossil record shows that bipedalism evolved a few million years before big brains and tool use, meaning that the first hominids were more ape-like in intelligence and behavior. They probably did not use many more tools than chimpanzees. This means that bipedalism was the first major adaptation that separated hominids from other apes. Hominid bipedalism evolved as a result of natural selection, approximately five million years ago.

Charles Darwin founded the theory of evolution by natural selection, which explains that some individuals are more reproductively successful than others (Darwin 1859). These individuals produce more viable offspring to pass on their genes to the next generation. Eventually, traits that give individuals certain advantages, such as bipedalism in hominids, will be selected for in greater numbers, and more individuals in a population will display these traits. Natural selection requires variation in a species, which can accounted for by gene flow, mutation, or genetic drift. It also requires environmental pressures, or filters, such as changing climate. These are the evolutionary means of how certain traits can be selected.

Darwin wrote specifically about human origins and bipedalism in his *Descent of Man, and Selection in Relation to Sex*: "If it be an advantage to man to stand firmly on his feet and to have his arms free… then I can see no reason why it should not have been advantageous to the progenitors of man to have become more erect or bipedal." (Darwin 1871, quoted in Stanford 2003:8). He believed that big brains, bipedalism, and tool use were linked. Darwin speculated that upright walking freed the hands to make and use tools, which led to increased cleverness. His ideas were impressive in light of the fact that they came without the rich fossil record that is known today, or the knowledge of the gene.

German evolutionist Ernst Haeckel did not need direct evidence for his theory of bipedal origins. He even created a scientific name for a fictional hominid ancestor, *Pithecanthropus alalus*, which means "the upright, speechless, small-brained ape-man" (Haeckel 1874, quoted in Gould 1977:210). Haeckel's theoretical hominid ancestor was remarkably similar to paleoanthropologists views today, that bipedalism pre-dated brain evolution. Haeckel's ancestor was so convincing, in fact, that when Du Bois discovered Java Man in the 1890's, he named it *Pithecanthropus erectus*. Du Bois later changed it to *Homo erectus* (Gould 1977).

Social theorist Friedrich Engels also discussed the connection between upright posture and becoming human. While Darwin saw continuity between humans and other animals, Engels saw a divide, relating to labor. Other animals simply had to use their own bodies for tools or weapons, but upright walking allowed for hominids to apply their labor to create weapons or tools (Engels 1876).

In the early 1900's, Sir Arthur Keith did rigorous research on gibbons in Southeast Asia. He used gibbons as his model for the evolution of bipedalism (Keith 1903). Keith specifically looked at the shoulder anatomy of gibbons, which allows their upper arms fully rotate around their shoulder joints. This adaptation is known as brachiating shoulders, and is common in apes. He saw a brachiating shoulder joint as evidence for arm hanging behavior, which he thought was the characteristic of a common ancestor between chimps and humans.

American paleontologist Henry Fairfield Osborn and French anatomist Marcel Boule opposed Keith in viewing the gibbon as the common ancestor (Osborn 1928). They championed the chimpanzee as a better model of the evolution of bipedalism, since it is more similar to hominids in anatomy and behavior. Osborn and Boule were impressed with the knuckle-walking of the chimpanzee, which put it in a slightly elevated position, compared to a regular quadruped. Their knuckle-walking common ancestor school of thought was supported by Sherwood Washburn in the 1940's. He soon became the chief advocate of the knuckle-walking theory of human origins. In the 1950's and

1960's, Washburn created the field of biological anthropology, which merges the sciences of functional anatomy, genetics, and ecology (Stanford 2003). This is the field today that uses chimpanzee and other nonhuman primates' anatomy and behavior as models for a likely common ancestor, and human origins.

Anatomical Changes Associated With Bipedalism

There are many anatomical differences between apes that move quadrupedally and modern humans. Bipedalism is marked by several skeletal changes, many of which were adaptive compromises, meaning they came at certain costs to the hominids that evolved them. These include lower back problems due to pressures on the spine, knee problems, complicated childbirth resulting from a repositioned pelvis, and the greater chance of choking on food, which is a consequence of a lowered voice box. Nevertheless, bipedalism was strongly selected for in hominids, approximately five to six million years ago. What anatomical changes occurred in the shift from quadrupedal to bipedal locomotion?

The shape and structure of the pelvis is integral to discussing anatomical differences between quadrupedal nonhuman primates and bipedal hominids. The short, broad modern human pelvis has evolved from a taller, narrower pelvis of the chimpanzee or gorilla. Natural selection created a human pelvis providing a saddle-like support system for bipedal locomotion (Stanford 2003). The iliac blades create the saddle around the human waist, while in chimpanzees they lie flat against the back. This aids in climbing for chimpanzees because important climbing muscles attach to the iliac blade.

In humans the curved iliac blades provide stability and support for the weight of standing upright and walking. This shape allows for the attachment of the large gluteal muscles, which were also repositioned to support upright posture.

The hominid pelvis is strongly curved like the wall of a cup, as seen in Figure 2. The sacrum in the back is curved inward toward the large heart-shaped pelvic canal, which contrasts with the small pelvic canal and straight sacrum of apes (Tattersall and Schwartz 2001).

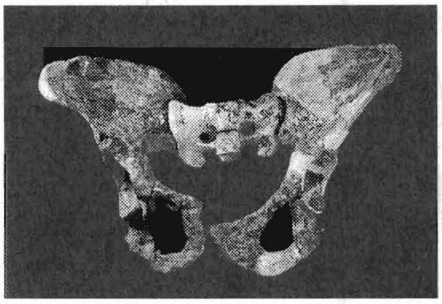

Figure 2— Sterkfontein (*Australopitchecus Africanus*) pelvis. The bladelike upper portions are short, and deep from front to back. The pelvis is expanded toward the back and flared to the side. (Tattersall and Schwartz 2001).

There were many changes in the legs and feet that allow humans to walk bipedally. The human foot is transverse and longitudinally arched, while the chimpanzee foot lacks these arches. Humans have non-opposable big toes that help in propulsion while walking. Human toes are also much straighter than those of the chimpanzee or gorilla. The weight-bearing heel bone, or calcaneus, is much larger in humans. Also, humans have fully extendable legs due to a lockable knee joint, and a natural knock-kneed stance, which differs from the chimpanzee bow-legged stance (Nickels 2003). Additionally, the human femur attaches at an inward angle to the pelvis, which makes the knees lie underneath the body (Tattersall and Schwartz 2001). As a result of this orientation, humans can stand upright for hours without much energy expenditure. Humans exert only seven percent more energy standing up than lying down (Stanford 2003). Quadrupeds burn much more energy when standing, because their legs need to stay flexed, which requires using more muscles to keep their balance.

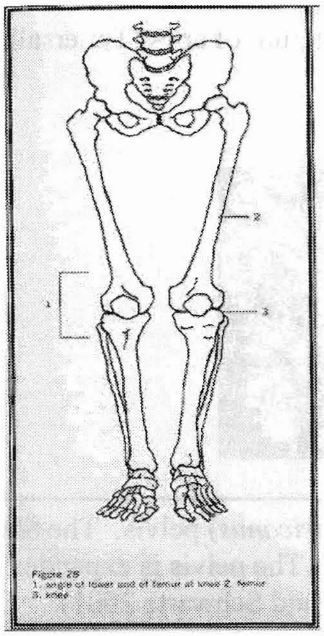

Figure 3— The human knees lie underneath the body when humans stand upright. In quadrupeds, the angle of knees is straighter (Tattersall and Schwartz 2001).

The spine changed from an arch-shape in chimpanzees to an S-shape in humans, allowing humans to maintain a center of gravity above their feet, while offering maximum mobility (Stanford 2003). The human spine has four main curves, as seen in Figure 4. These changes did not happen all at once— earlier bipeds had differently structured spines than later bipeds, such as *Homo erectus*. The earliest hominids had an extra vertebra in the lower back, which may have been a precursor to the development of the lumbar curve (Walker and Shipman 1997). This suggests the earliest hominids probably walked bipedally in a different style from modern humans.

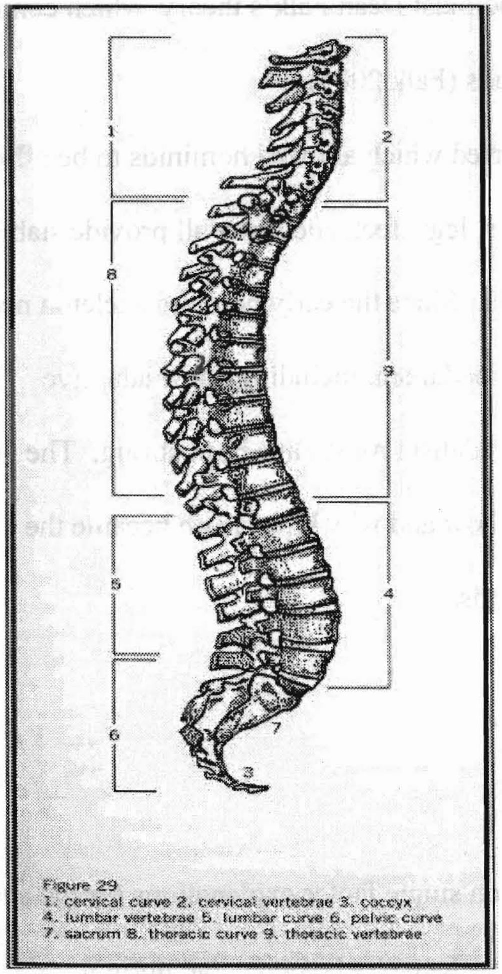

Figure 4— The human vertebral column is curved in the neck vertebrae (1), thoracic vertebrae (8), lumbar vertebrae (5), and sacral vertebrae (6). (Tattersall and Schwartz 2001).

Changes higher up in the skeleton involved a centered foramen magnum in bipeds, as opposed to one that was in a more posterior position in apes. Also, the voice box, or larynx, is much lower in humans than in apes. This increases the risk of choking while eating.

Another change associated with bipedalism relates to heat control and the circulatory system. Upright walkers need to get blood up to the brain, which means they have to fight against the forces of gravity. There was a rerouting of the circulatory system somewhere in the evolution of bipedalism that allowed hominids to get blood up to their brains. This is important in anthropologist Dean Falk's theory, which connects bipedalism to increased brain size in hominids (Falk 2004).

Numerous anatomical changes occurred which allowed hominids to be efficient upright walkers. These changes in the pelvis, legs, feet, and spine all provide stability and support for standing and walking upright. Since the early hominid skeleton needed to be so drastically restructured to support bipedalism, including a few adaptive compromises, the selective pressures for bipedalism must have been strong. The next section will examine various theories about how and why bipedalism became the preferred method of transportation in hominids.

Theories of Bipedal Origins

Twentieth century theorists focused on single factor explanations for the evolution of bipedalism. These theories promoted one selective advantage that upright walking would have given hominids, and based their models on that advantage. These single factor theories include the vigilance hypothesis (Dart 1926), the aquatic ape hypothesis (Hardy 1960, Morgan 1982), the heat hypothesis (Wheeler 1984), the energetic efficiency hypothesis (Rodman and McHenry 1980), the carrying hypothesis (Lovejoy 1981, 1984) and the lowly origin hypothesis (Jolly 1970; Kingdon 1997). While these theories have their supporters, it seems unlikely than any one event led hominids to adapt bipedalism. Also, the fossil record does not support any single behavior being the catalyst for the change to upright walking.

Other theories have focused on multiple factor explanations of the origins of bipedalism, such as Craig Stanford's meat eating and food gathering hypothesis (Stanford 2003). This theory is more plausible than many of the single factor theories, but it is still problematic.

The Vigilance Hypothesis

Raymond Dart's vigilance hypothesis described a situation where early hominids who stood upright would have the benefit of seeing over tall savanna grass (Dart 1926). This would allow them to see predators from a distance. Additionally, their other sense organs would be elevated with bipedalism.

This hypothesis has fallen from favor mainly because animals do not need to be bipedal to display vigilance behavior. For example, Chimpanzees, other nonhuman primates, and squirrels all can stand upright to get a better view of their surroundings. Elaine Videan and W.C. McGrew tested the vigilance hypothesis and many others with captive chimpanzees and bonobos (Videan and McGrew 2001, 2002). They found that the introduction of visual barriers did not change the bipedality of either species. The apes just ignored the barriers. The authors note that further testing should be done with a more compelling stimulus for vigilant behavior, such as a predator. Regardless, the vigilance hypothesis is not a popular one anymore.

The Aquatic Ape Hypothesis

The aquatic ape hypothesis was created by Alastair Hardy and championed by Elaine Morgan (Hardy 1960; Morgan 1982). They claimed that there was an aquatic phase in human evolution when our ancestors lived on the seacoast. In this aquatic phase, bipedalism evolved from upright hominids wading in the shallow waters. For (circumstantial) evidence, Morgan notes humans' high level of subcutaneous fat which may have aided in buoyancy, controlled breathing that would have helped deep dives, relative hairlessness, and hands that would be perfect for eating shellfish. This hypothesis has been completely discredited (Fitch 2002; Pond 1991). It relies on explanations of adaptations that could have happened for a number of reasons.

The Heat Hypothesis

Peter Wheeler's heat hypothesis describes a thermoregulatory advantage that bipedal hominids would have had over their quadrupedal peers (Wheeler 1984). It illustrates a situation where hominids became bipedal on the grasslands of the African savannah. By standing up, they will be exposed to cooler air, because air moves faster the further it is from the ground. Wheeler suggests that an evaporative cooling system, sweat, also evolved. Most importantly, upright posture would minimize the solar radiation on the body at noon.

There are many criticisms of this hypothesis. Bipedalism probably did not evolve in open savannah grasslands— it evolved in partially forested areas (see Stanford 2003; Kingdon 2003). A shift in hominids' thermoregulatory system did occur, it can not be determined that it was the cause of bipedalism. Regarding the cooler air, Wheeler mentions that upright hominids would have only benefited from it if the surrounding vegetation was a specific height, approximately one meter. This makes it unlikely that cooler air was a factor. It is true that the solar radiation at noon would be minimized, because only the top of the head is exposed directly, but what about other times of the day? The sun's rays are the strongest between 10:00 a.m. and 4:00 p.m., but it is not directly overhead at those times. Additionally, thermoregulation might have played a part in the evolution of bipedalism, but it can not be singled out as the primary factor.

The Energetic Efficiency Hypothesis

The increased efficiency of transportation has been noted as a possible cause of the shift to bipedalism (Rodman and McHenry 1980). These authors concluded that human bipedal walking is at least as efficient as quadrupedal locomotion in general, and more efficient than chimpanzee quadrupedality specifically. A major problem with the energetic efficiency model of bipedalism is that early hominids did not have the morphological adaptations necessary for efficient bipedalism (Steudel 1996). It would be counterintuitive to assume that they would evolve an awkward new form of locomotion.

However, chimpanzees and cebus monkeys are able to move bipedally with no greater energetic costs than moving quadrupedally, and they lack the morphological changes that even the early hominids had (Leonard and Robertson 1997). Those authors speculate that the early pelvis and lower limb adaptations of the australopicines would have reduced the costs for terrestrial bipedal locomotion. It is difficult to determine the exact energetic benefits of early hominid bipedality, because only fragments of fossils do not give a very clear picture. While upright walking for humans today is much more energetically efficient than chimpanzee terrestrial locomotion, saying that was the single factor in the evolution of bipedalism is impossible.

The Carrying Hypothesis

Owen Lovejoy's carrying hypothesis was partially a reaction against the energetic efficiency model of the origins of bipedalism (Lovejoy 1981, 1984). He questioned the efficiency hypothesis because developing a new form of locomotion would be inefficient, since the common ancestor's bones would have been made for quadrupedal walking and running. He wrote "For efficiency or endurance to have been the favored feature of bipedality, a lower limb completely adapted to bipedality would have had to have appeared almost instantly in our ancestors, a genetic impossibility" (Lovejoy 1984:24). The fossil record supports a longer period of bone readjustment to create a hominid that walked efficiently bipedally. Since energetic efficiency can not solve the bipedalism puzzle, Lovejoy created a carrying hypothesis, based on sexual selection.

The powerful selective advantage that he saw in bipedalism was its relation to carrying food. As the East Africa climate was drying five million years ago, sources of food, such as fruit trees, were growing farther apart. Hominids would have to walk farther and farther to gather food. This would be disadvantageous to females trying to raise their young. The solution to this problem, according to Lovejoy, is the monogamous male partner who would gather food for his mate. This occurred simultaneously with the adaptation of concealed ovulation in hominid females, which meant that males would not know when they were sexually receptive. Monogamous relations began so males would be sure that their women were not involved with other men. The male would provision for his female, and he would carry the food. He was able to carry it because his hands were free, because he was walking bipedally.

Lovejoy's carrying hypothesis is provocative, but is criticized for a number of reasons. It shares a similar problem with Wheeler's heat hypothesis— it is looking more likely that bipedalism evolved in the forest and not in the savannah. Also, rather than hominid females lost their sexual swellings, it is believed that chimpanzees and bonobos evolved them after their ancestry diverged from humans (Stanford 2003). Additionally, the fact that early hominids were monogamous is disputed. Lovejoy cites the lack of canine dimorphism in *Australopithecus afarensis* to suggest that it was monogamous, but other indications of monogamy, such as body size dimorphism in early hominids, suggest a polygamous mating system like that of the chimpanzee.

Upright walking probably emerged as a result of a number of factors working together, since there was such a strong selective pressure for it. These factors most likely included a change in environment and a resulting change in food supplies, which created an advantage for hominids who could walk bipedally.

The Squat-feeding Hypothesis

Jonathan Kingdon's book *Lowly Origins: Where, When, and Why Our Ancestors First Stood Up*, focuses on the origin of bipedalism (2003). Kingdon is a zoologist who grew up Africa, which gives him a unique perspective on African ecosystems. His intimate knowledge of East African coastal forests allows him to give a detailed analysis of where upright walking likely emerged. He points to those coastal forests as drier and more seasonal locations where there were more ground-level plants. This is where his squatting hypothesis materializes: with specific groups of apes exploiting the rich forest floor and adapting to feeding in a squatting position. These adaptations included pelvic and lower limb adjustments, which prepared them for bipedality (p. 127).

Notice that this hypothesis solves Lovejoy's problem of necessary skeletal changes for efficient bipedalism in early hominids. Kingdon's model suggests that as apes squatted on the ground, their waists gained flexibility for swiveling the upper body from side to side. This led to pelvic anatomical changes such as lowering of the iliac blades and broadening of the sacrum, which together were "an essential precondition for balanced standing," (p. 21). This squat feeding also would lessen the weight bearing capacities of the arms. Under these conditions, Kingdon sees quadrupedal locomotion gradually becoming less efficient as upright walking.

After creating his theory of bipedalism, Kingdon belatedly discovered Clifford Jolly's squat feeding hypothesis (Jolly 1970). This is very similar to Kingdon's, except Jolly's emphasizes squat-feeding in open grassland and hominid ancestors consuming seeds, while Kingdon's takes place on the forest floor and has the hominid ancestors consuming fruit. Nevertheless, Kingdon's ideas are provocative and convincing. The hypothesis of squat feeding pre-adapting hominids for bipedalism solves many of the problems from which other theories suffer.

I have two concerns regarding Kingdon's hypothesis. I wonder if squat-feeding would provide a strong enough selective pressure for skeletal adjustments that would support a new method of locomotion. Also, this hypothesis makes bipedalism occur in too short a time frame, since Kingdon argues that squat-feeding led to all the pre-adaptations necessary for bipedal standing and walking. The fossil record shows that bipedalism evolved more gradually than he suggests.

The Meat-eating Hypothesis

Craig Stanford presents his model of bipedalism in a book written for a popular audience, titled *Upright: The Evolutionary Key to Becoming Human*. Stanford's ideas arise from his extensive experience studying chimpanzees and gorillas in feeding situations. His hypothesis merges the environmental change of widening food patches and the consumption of meat by hominids as the impetus for the evolution of bipedalism (Stanford 2003). He explains the environment in East Africa five to six million years ago as having a declining rainfall and a higher degree of seasonality, which led to more open forests, instead of closed, dense forests. The distribution of foods changed, as fruit trees became more dispersed. Hominids gradually increased their frequency of bipedalism to move around the greater distances between food sources (p. 120).

Stanford describes a situation where different groups of new hominids evolved slightly different strategies for food gathering and hunting, which accounts for the anatomical differences found in different hominid species. The second half of Stanford's theory emphasizes how the search for meat continued to enhance and refine bipedalism.

Stanford is an expert on the predator-prey relationship between chimpanzees and red colobus monkeys (Falk 2000). He uses that relationship to propose a model for early hominid hunting and meat eating. Different groups of chimpanzees hunt in different capacities, depending on the environmental factors. Hunting varies in dry or wet seasons, according to the amount of plant food available. His research of the Kasakela community of chimpanzees at Gombe shows that sometimes they will prefer larger home ranges, and sometimes smaller ones (Stanford 1996). Since climate varied for the early hominids, sometimes they would be faced with larger home ranges. This meant they would have to forage and hunt farther, which is where Stanford sees the link to bipedalism. Efficient bipedal long-distance walking would have allowed them to spend more time searching for meat than their ape cousins. Gradually, their anatomy became more refined for this walking. Simultaneously, other hominids may have chosen other foraging strategies, such as remaining in the trees, which would explain the differences in anatomy between different species of early hominids.

Thus, as some hominids searched for more meat, they became better walkers. Stanford explains that meat eating which result from bipedalism was integral for the later evolution of intelligence and behaviors such as tool use.

Stanford has been criticized for not giving credit to his predecessors for the environmental change/ widening food patches hypothesis. This theory went back to Darwin (1872) and Haeckel (1874), and it is a major part of Rodman and McHenry's energetic efficiency hypothesis (1980).

What separates Stanford from the others is his emphasis on meat eating, setting him up for criticism from scholars who question how important hunting and meat eating were to the early hominids. They reference the bonobo, who eats much less meat than the chimpanzee. However, bonobos have been seen begging for meat from an adult who had captured a small animal in the wild, which shows they share a little bit of the taste for meat with chimpanzees (Falk 2000). Whether the early hominids hunted or scavenged is another criticism of Stanford, who advocates a hunting model. The idea of early hominids hunting has fallen from favor recently in anthropology. It is more accepted that they primarily scavenged for meat. Even if this was so, Stanford's model would still work since hominids would still be traveling farther distances to find meat.

Analysis and Discussion

It is important to remember that evolution occurs at the level of the individual, not the group. Narratives explaining selective pressures that favored bipedalism need to keep this in mind and cautiously use the selective pressures that they champion. When trying to figure out why our ancestors evolved upright walking, we need to look at the smaller picture of how a new form of locomotion affected the individual, before we examine the larger picture.

While entertaining to read, these evolutionary narratives leave something to be desired. It seems unlikely that any single factor would be strong enough to select for the drastic anatomical changes that are associated with the shift to bipedalism. As anthropologist Robert Foley (1995) insists, it is necessary to look at the evolutionary scenario holistically. This means we must examine the conditions, causes, constraints, and consequences in hominid evolution. Conditions would include the environmental factors that set the stage for new forms of foraging. The causes are selective pressures, which might consist of the selection for energetic efficiency in hominids walking upright. Constraints might comprise the older forms of locomotion, which were previously selected for a reason. For example, arboreal locomotion, moving around efficiently in trees, would protect early hominids from predators on the ground. Finally, the consequences of bipedalism need to be part of the picture. These would include the eventual increase in brain size, and freed hands that were able to make and use tools.

The process of the hominids developing bipedalism was a gradual one. The early hominids, including australopithecines and *Homo habilis*, probably walked more like upright chimpanzees than fully efficient bipeds. It is not until *Homo erectus* approximately 1.8 million years ago that we see anatomical structures that would indicate highly efficient bipedalism. In 1984 a team of paleoanthropologists led by Alan Walker discovered a nearly complete *Homo erectus* skeleton in Kenya. This was an extraordinary find because most hominids fossils are just small bone fragments. Walker's find was a juvenile, who is now referred to as "Nariokotome boy." Nariokotome boy had narrow hips and long-necked femurs, which would have helped him maintain his balance and be a very efficient walker and runner (Walker and Shipman 1997).

Two aspects of Nariokotome boy's anatomy shed light on the gradualness of the evolution of bipedalism. The first suggests that *Homo erectus* were more efficient bipeds than earlier hominids, and the second suggests that they may have walked differently from modern humans. An interesting feature of Nariokotome boy's anatomy is his inner ear. The semicircular canal in the inner ear helps regulate balance, so it is very important in upright walking. Anthropologist Fred Spoor found Nariokotome boy's inner ear more developed than any earlier hominids, who had ape-like inner ears. This suggests *Homo erectus* was a more efficient and modern walker than his predecessors (Spoor 1994). The second interesting anatomical feature of Nariokotome boy was that his spine still contained an extra lumbar vertebrae. This is a feature retained from earlier hominids.

Modern humans only have five vertebrae in their lower backs. Additionally, the vertebrae in the spine had less surface area, and thus less weight bearing capacity than modern human vertebrae (Walker and Shipman 1997). Taken together, these features of Nariokotome boy's anatomy show that *Homo erectus* walked differently from earlier hominids, but not exactly the same as modern humans. Thus, *Homo erectus* were the first highly efficient bipeds, and they show the gradual change that occurred in the evolution of bipedalism.

The fact that the gradual evolution of efficient biped hominids happened over millions of years makes many evolutionary narratives explaining how this occurred seem impractical. Any story describing how early hominids "broke camp at dawn, and knew the hunt would be a difficult one today…" is oversimplifying a complex situation. It would be more beneficial to examine the refinement of bipedalism that occurred between early hominids such as the Australopithecines, and *Homo erectus*. This refinement must have been affected by a number of factors, including a change in environment and a resulting change in food resources. I think it is very possible that bipedalism evolved five to six million years ago along the coastal forests like Kingdon suggests (Kingdon 2003), and was refined in the next few million years in the savannah environments that many other scholars have advocated (Dart 1926; Lovejoy 1981; Wheeler 1984)[1]. If this is the case, then some of the single factor theories, such as the carrying hypothesis, may have contributed to the refinement of bipedalism in intermediate hominids, such as *Homo habilis*. If a few of these single factor theories worked together, they could have provided the selective pressures necessary for the anatomical changes in the later bipeds.

[1] Miocene, Pliocene, and Pleistocene habitats fluctuated drastically, which resulted in some hominids' feeding patches to become more dispersed. This required more traveling on the ground between clumps of trees, as the African climate became drier and grassier (Kingdon 2003).

I believe that the evolution of bipedalism must have also been associated with foraging or hunting, because such strong selective pressures that realigned the hominid anatomy must have been caused by a universal behavior such as food acquisition and consumption. Is it a coincidence that fully refined bipedalism occurred around the same time that we see the increased consumption of red meat, with *Homo erectus* 1.8 million years ago?

Bipedal walking must have provided hominids with certain benefits, or else it would not have evolved. These benefits might have included freeing of the hands to carry food items, or efficiency of moving long distances. Whatever the selective pressures were, it took awhile for fully efficient upright walking hominid to come forward. The evolution of bipedalism is a dividing line between humans and apes, and theories of how it emerged are very important for understanding how we became human. I would like to see more theories about the refinement of bipedalism from the early hominids to *Homo erectus*. Their fully refined bipedalism set the stage for advanced tool use and increased brain size in hominids. Factors explaining how and why it evolved are useful in figuring out the evolutionary picture that explains how we stood up for ourselves and separated ourselves from our primate cousins.

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