CHAPTER 14

Bipedal Locomotion

"The commonest explanation for the origin of human upright posture and gait relates these to tool and weapon using, and to offense and defense"
[Hewes, 1961, p. 692].

"...the origin of a bipedal form of locomotion was so fundamental a change, so replete with profound evolutionary potential, that we should recognize the roots of our humanity where they really are"
[R. Leakey and Lewin, 1992, p. 82].

"The evolution of hominid bipedalism is recognized as a crucial element in the hominization process. However, despite a voluminous literature, our ignorance concerning bipedalization is almost complete"
[Rose, 1991, p. 38].

Introduction. The earliest part of the hominin fossil record clearly reveals some sort of behavior performed in an upright, bipedal posture. The evidence is in the skull, the pelvis, the legs and feet. *What was that behavior?* Currently there is near-unanimous agreement that it was *locomotion*, and that the origin of our lineage is linked to the onset of bipedal walking.

Several 19th and early 20th century writers following Darwin [1871] called attention to our distinctive upright gait [Landau, 1991]. In the modern era, this became a central focus of human evolutionary studies. After Washburn [1950] asserted that bipedal locomotion was the first human adaptation, this idea gained such strong acceptance that bipedalism became a synonym for upright locomotion. It is now widely believed to represent the primordial hominin behavior and the initiating event in human evolution [Bartholomew and Birdsell, 1953; Hewes, 1961; Du Brul, 1962; Zihlman, 1978; Yamazaki, et al., 1979; Lovejoy, 1988; Corballis, 1991; Coppens, 1991; Langdon, et al., 1991; R. Leakey and Lewin, 1992; Tattersall, 1995; Wrangham and Peterson, 1996; Fleagle, 1999; Richmond and Strait, 2000; Wrangham, 2001; Richmond, et al., 2001; Videan and McGrew, 2001; D'Aout, et al., 2002; Ward, 2002; Kingdon, 2003; Stanford, 2003; Schmitt, 2003; Hilton and Meldrum, 2004; Crompton and Günther, 2004; Hart and Sussman, 2005; Thorpe, et al., 2007a; Richmond and Jungers, 2008; Parker and Jaffe, 2008; Pontzer, et al., 2009; Carvalho, et al., 2012].

If correct, this means the onset of bipedal locomotion signals the moment when our lineage diverged from its ancestors and set off in a new direction. It also indicates that an evolutionary explanation of this event is crucial to the understanding of hominin origins.

Nevertheless, after decades of speculation, the query of why hominins began to walk upright is still unanswered. It is widely acknowledged that no compelling explanation for bipedal locomotion has yet been proposed [Robinson, 1963; Rose, 1991; Langdon, et al., 1991; Stringer and McKie, 1996; Fleagle, 1999; Stanford, 1999; Kramer and Eck, 2000; Wrangham, 2001; D'Aout, et al., 2002; Kingdon, 2003; Steudel-Numbers, 2003; Schmitt, 2003; Preuschoft, 2004; O'Higgins and Elton, 2007; Sockol, et al., 2007; Sylvester and Kramer, 2008; Parker and Jaffe, 2008; Pontzer, et al., 2009; Carvalho, et al., 2012; Tattersall, 2012]. Why our unique two-legged gait evolved is an enigma. It is a fundamental question in the study of human evolution at the present time, but the answer remains elusive.

What were the bipedal proclivities of the hominin ancestor? Because the crucial fossils from the time of the hominin/chimpanzee divergence (6-7 Mya) are missing from the record (Chapter 2), paleoanthropologists have had to address the question indirectly. Two general approaches have been used.

The hypothetical ancestor. This method involves constructing a model of the last common ancestor's locomotion based on study of living arboreal apes that are adapted to clambering in trees, but also spend time on the ground. Tuttle proposed that traveling in arboreal contexts might have predisposed our hominin ancestors for bipedal locomotion by adapting them to vertical climbing on tree trunks or vines and bipedal travel on horizontal branches [1974, 1981, Tuttle, et al., 1991]. The concept that hominins were "preadapted" to terrestrial bipedal locomotion by upright adaptation to an arboreal setting gained wide support [Stern, 1977; Prost, 1980; Fleagle, et al., 1981; Rose, 1991; Senut, 1991; Richmond, et al., 2001]. In Prost's [1980] view, human bipedal gait arose from specialized climbing of vertical tree trunks; when hominins adopted terrestrial life they already had bipedal capacity. Fleagle and coauthors [1981] offer support for this idea. Senut [2006a, 2007] observed that fossil evidence indicated that early hominins lived in wooded habitats and their hominoid ancestors had been arboreal apes during the Miocene (~ 23-5 Mya). Some of these apes may have traveled bipedally on the ground, but not in the modern manner [Pickford, et al., 2002; Senut, 2006b; Nakatsukasa, et al., 2007; Harrison, 2010; Wood and Harrison, 2011]. Crompton and coauthors [2008] concluded that the last common panin/hominin ancestor was a mainly arboreal, orthograde, short-legged, long-armed ape capable of hand-assisted bipedality in trees, in a manner like that observed in modern orangutans. Hand-assisted bipedal locomotion in trees could have preadapted the ancestors of early hominins for habitual terrestrial bipedalism [Thorpe, et al., 2007a, b; Crompton, et al., 2008, 2010 and see below].

The modern chimpanzee model. Chimpanzee bipedal walking has been studied in wild and captive animals. These investigations show that upright walking in chimpanzees bears little resemblance to the way modern humans walk. Thus it is a questionable model that may even obscure understanding [Senut, 2007; Crompton, et al., 2008; Lovejoy, et al., 2009b, g].

Chimpanzees rarely use upright gait, and then only in short bursts [Hunt, 1992, 1996; Doran, 1992; Stanford, 2003]. They are not adapted for it [Hunt, 1992; Richmond, et al., 2001].

Their common gait on the ground is quadrupedalism, supported by the knuckles of the hands and the plantar surface of the feet. Hip and knee joints are flexed and the pelvis is oriented horizontally, with the iliac blade well in front of the hip joint. In this configuration the gluteus medius and minimus are able to rotate the femur which can be extended beyond the vertical at the hip joint by the hamstring and gluteus maximus muscles to produce forward propulsion. However, when the animal stands upright, the pelvis is oriented vertically, producing instability because the long iliac blade raises the sacroiliac joint high above the hip joint [Robinson, 1972]. The hamstrings and gluteus maximus cannot fully extend the femur and the trunk is bent forwards [D'Aout, et al., 2002]. To compensate for the tilt, the knees have to be flexed, which requires strong contraction of hip and knee extensors to prevent collapse [Tuttle, et al., 1979; Kimura, et al., 1983]. When the femur is maximally extended, rotation by the gluteus medius and minimus is lost [Zihlman and Brunker, 1979], limiting the ability to swing forward the opposite side of the pelvis. The abducted femur and angle of the knee joint position the foot outwardly [Jenkins, 1972]. Mobility of hip, knee, ankle and foot joints adds instability [Robinson, 1972]. The hallux, deployed sideways, cannot exert forward thrust, and the other toes, long and curved, cannot be extended fully [Elftman and Manter, 1935; Robinson, 1972]. As weight shifts from heel to toes, the foot collapses at the midtarsal joint, wasting energy [Elftman, 1944].

Chimpanzees walk upright with short steps, feet wide apart, and minimal hip rotation [Zihlman and Brunker, 1979]. Leg, hip, and torso tend to swing forward as a unit on the unsupported side. The upper body leans markedly toward the supported side to bring the center of mass over the support leg [Elftman, 1944; Tuttle, et al., 1979]. Asymmetric motions of the arms are required to maintain balance [Tardieu, et al., 1993] and there is great variability in the gait. Chimpanzee bipedalism (1-1.7 m/sec) [Tardieu, et al., 1993; Kimura, 1996] is about ten times slower than the estimated top speed of quadrupedalism [Kortlandt, 1980].

Which model works best? Did upright walking in the modern manner arise in the trees before hominins emerged from their ape ancestry? This cannot be the full story because the fossil record, described below, shows that adaptation for bipedal locomotion continued for several million years *after* onset of the hominin lineage. Did hominin bipedal gait arise in an arboreal ancestor that commonly used quadrupedalism on the ground? This also seems questionable, based on the chimpanzee model. Explication of the evolution of human upright walking in either case will require the identification of a behavior that provided profound reproductive advantages to produce such an eccentric mode of locomotion.

Modern human bipedal locomotion. Modern humans are clearly adapted for bipedal locomotion. The behavior is instinctive and appears within two years of birth. Energy expended per unit distance traversed is minimized [Saunders, et al., 1953; Ralston, 1976]. Upright stance requires only slight, intermittent muscle action to maintain balance, due to extensive skeletal remodeling [Elftman and Manter, 1935; Weidenreich, 1947; Tuttle, et al., 1979; Reeser, et al., 1983]. The heels rest on the ground; the legs are extended at hip and knee joints; the vertebral column is curved alternately forward and back; the skull is balanced on top of the spine, and the center of mass has descended to the level of the hip joint in a plane passing through the foramen magnum, hip, knee and ankle joints [Robinson, 1972; Tardieu, 1992]. Normal walking speed is about 1.25 m/sec [Ralston, 1976; Steudel, 1996], comparable to chimpanzee bipedal walking, but top running speed is about 25% slower than full speed chimpanzee quadrupedal running.

Human bipedal walking is steady, rhythmic, and bilaterally symmetrical, with each step a replica of preceding ones (Figure 15). One leg swings forward, accepts the weight of the body, then produces forward acceleration as it extends, thrusting into the ground behind the hip joint while the opposite leg swings forward. Vertical and transverse displacements are small and in phase with one another, reducing energy expenditure. Efficiency is enhanced by slight rotations of the thorax and hips around the vertical axis [Zihlman and Brunker, 1979; Tardieu, et al., 1993]. The pelvis rotates 4° on the support leg to position the swinging foot in the midline while the femur on the swing side rotates externally to point the foot straight ahead [Saunders, et al., 1953; Zihlman, 1978]

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