Origin of Human Bipedalism: The Knuckle-Walking Hypothesis Revisited

BRIAN G. RICHMOND,[1*] DAVID R. BEGUN,[2] AND DAVID S. STRAIT[3]

[1]*Department of Anthropology, University of Illinois, Urbana, Illinois 61801*
[2]*Department of Anthropology, University of Toronto, Toronto, Ontario M5S 3G3, Canada*
[3]*Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, New York 11568*

ABSTRACT   Some of the most long-standing questions in paleoanthropology concern how and why human bipedalism evolved. Over the last century, many hypotheses have been offered on the mode of locomotion from which bipedalism originated. Candidate ancestral adaptations include monkey-like arboreal or terrestrial quadrupedalism, gibbon- or orangutan-like (or other forms of) climbing and suspension, and knuckle-walking. This paper reviews the history of these hypotheses, outlines their predictions, and assesses them in light of current phylogenetic, comparative anatomical, and fossil evidence. The functional significance of characteristics of the shoulder and arm, elbow, wrist, and hand shared by African apes and humans, including their fossil relatives, most strongly supports the knuckle-walking hypothesis, which reconstructs the ancestor as being adapted to knuckle-walking and arboreal climbing. Future fossil discoveries, and a clear understanding of anthropoid locomotor anatomy, are required to ultimately test these hypotheses. If knuckle-walking was an important component of the behavioral repertoire of the prebipedal human ancestor, then we can reject scenarios on the origin of bipedalism that rely on a strictly arboreal ancestor. Moreover, paleoenvironmental data associated with the earliest hominins, and their close relatives, contradict hypotheses that place the agents of selection for bipedality in open savanna habitats. Existing hypotheses must explain why bipedalism would evolve from an ancestor that was already partly terrestrial. Many food acquisition and carrying hypotheses remain tenable in light of current evidence. Yrbk Phys Anthropol 44:70–105, 2001.   © 2001 Wiley-Liss, Inc.

TABLE OF CONTENTS

"From the abundance and diversity of the game it might have appeared that every known species of bird and beast and reptile had sought here a refuge wherein they might take their last stand against the encroaching multitudes of men that had steadily spread themselves over the surface of the earth, wresting the hunting grounds from the lower orders, from the moment that the first ape shed his hair and ceased to walk upon his knuckles."
—Tarzan the Terrible, by Edgar Rice Burroughs. New York: Grosset & Dunlap, 1921.

One of the oldest questions in paleoanthropology, and one that continues to intrigue us within our discipline and in the public, concerns how and why the earliest members of the human family began to walk on two legs. Most paleoanthropologists agree that bipedalism is the key adaptation of the hominin[1] clade (Dart, 1925), but there is less agreement about the nature of the transition to bipedality. Numerous hypotheses have been offered regarding the selective agents underlying the origin of bipedalism (Rose, 1991, and references therein). Many of these hypotheses are dependent on the form of positional behavior from which bipedalism evolved. Identifying this ancestral form of locomotion has, therefore, been one of the central problems in the debate concerning hominin origins. As recently as 1986, Day (1986) stated that "we really have no clear idea of what form of locomotion, in what creature, preceded, or was immediately pre-adaptive for, upright posture and bipedal gait." Indeed, the debate will not be entirely settled without direct fossil evidence of both the earliest biped and its ancestor (and agreement on the taxonomic and phyletic positions of these fossils). However, evidence from phylogeny, the comparative anatomy of extant anthropoids, and the morphology of the earliest known hominins currently make some hypotheses more likely than others. Moreover, it is only with a detailed understanding of anthropoid locomotor anatomy that we will be able to reliably interpret the relevant fossils once they are recovered.

In this paper, we briefly review the history of thought on the mode of positional behavior preceding bipedalism, compare relevant aspects of anthropoid forelimb functional anatomy, and assess existing hypotheses in the context of current evidence, with comments on their implications for the origin of bipedalism. We also discuss assumptions that underlie the reconstruction of the last common ancestor (LCA) of *Pan* and *Homo*, especially the use of parsimony to predict features present in the *Pan/Homo* LCA and the commonly held expectation that at least some ancestral (i.e., primitive) traits will be retained in descendents. Finally, we identify examples of how the identification of "adaptations" (i.e., products of natural selection) may be complicated, in some cases, by the epigenetic responses of bone to biomechanical activity during ontogeny. These assumptions, and the ways that researchers have tried to address the problem of what kind of creature gave rise to the earliest bipeds, are best understood in their historical context.

A CENTURY OF MODELS

Well over a century ago, Huxley (1863) concluded on the basis of comparative anatomy that African apes are humans' closest living relatives. This conclusion was shared by some of his contemporaries, including Darwin (1871) and Haeckel (1874). These authors did not speak directly to the problem of the antecedents of the earliest members of the human lineage, but rather were understandably focused on the more fundamental argument that humans share a close relationship with extant apes.

Keith (1903, 1923) was the first to offer an explicit hypothesis of the locomotor behaviors preceding bipedalism. Like Huxley and others before him, he was impressed by the anatomical similarities between humans and apes. Using an implicitly phylogenetic framework, Keith (1923) argued that early human bipedalism was preceded by a large-bodied orthograde "troglodytian" climbing mode of locomotion (Fig. 1), which itself evolved from a hylobatid-like brachiating ancestor. Keith was quickly joined by ardent proponents, notably Gregory (1916, 1927) and Morton (1926). Gregory (1927, p. 3) found in human anatomy "a veritable museum of relics of a former arboreal condition." Interestingly, Gregory (1927) noted that humans most closely resemble chimpanzees and gorillas in many respects, but at the time the terrestrial adaptations of the African apes were not well-understood.

A contemporary advocate of an arboreal ancestry, Morton (1926) argued that bipedalism evolved from a small-bodied, brachiating, hylobatid-like ancestor (Fig. 1). Although the model of Morton (1926) differed in important ways from the large-bodied "tro-

[1]Hominin is used here to indicate modern humans and taxa that are more closely related to modern humans to chimpanzees.
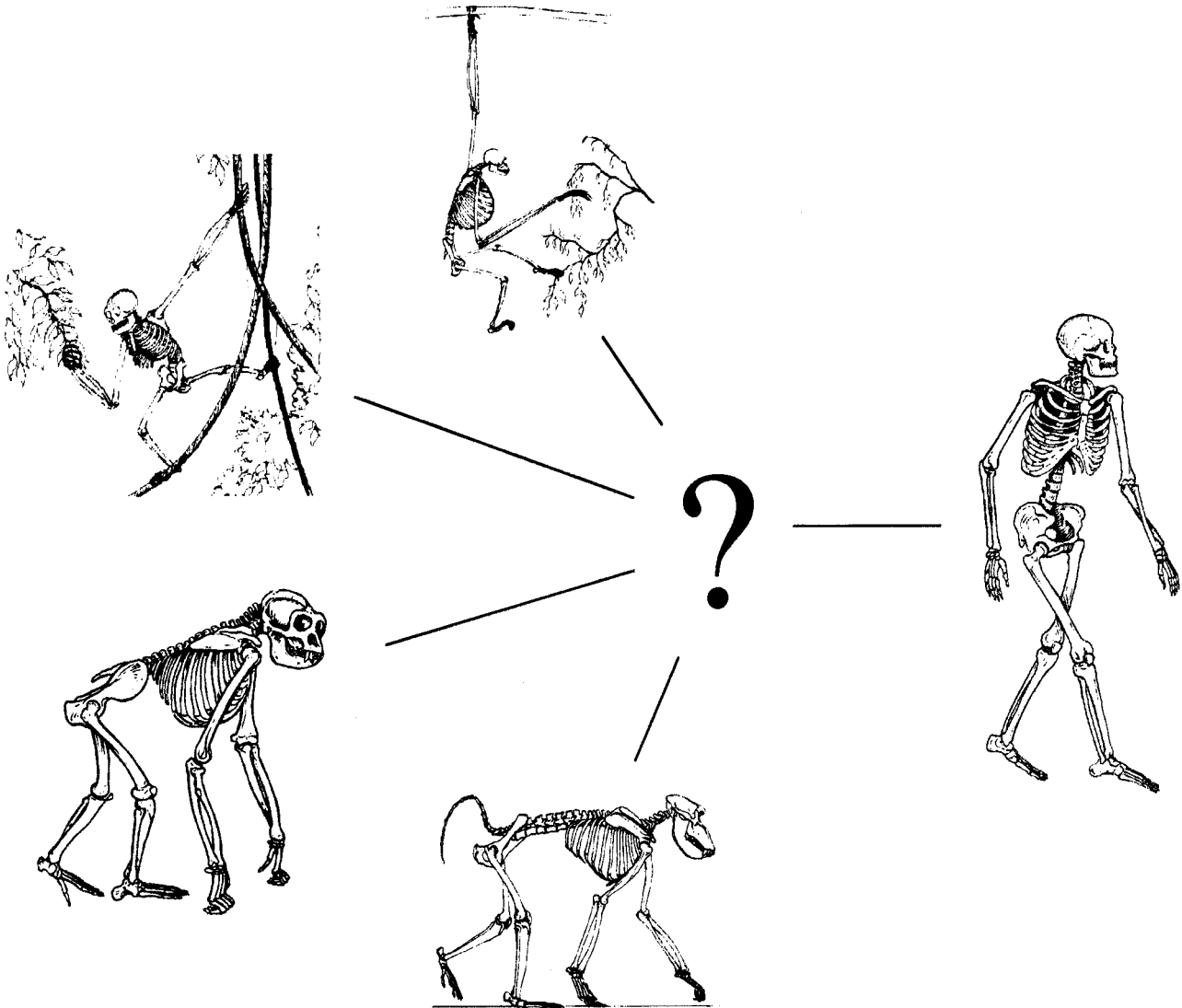
Fig. 1. Hypotheses on the form of locomotion that preceded bipedalism include hylobatian and climbing (antipronograde) arboreal models, as well as terrestrial models, including digitigrade and knuckle-walking hypotheses. Most researchers favor some rendition of large-bodied climbing, or knuckle-walking models.

glodytian" models favored by Keith and Gregory, these authors did not debate over the differences (Tuttle, 1974), probably because their models were broadly similar compared to contemporary competing theories (see below). Schultz (1930) also advocated an arboreal ape model, but one that was not as derived as hylobatids or extant great apes.

The "brachiationist" hypothesis was opposed by vociferous critics, including Boule (1912), Osborn (1927), Wood Jones (1916), and later Le Gros Clark (1940) and Straus (1949). Although they varied in the details of their views, these authors all believed humans to be more distantly related to apes and, thus, argued that humans and apes arose independently from a more primitive primate. For example, in an open debate with Gregory (1927) over ape-human relationships, Osborn (1927) contended that humans evolved from an early, albeit rather vaguely defined ancestor shared with apes. Similarly, Le

Gros Clark (1940) argued that, although humans and apes originated from a common ancestral stock, the ancestor had only an incipiently apelike skeleton. It may have been his influence that led Keith (1940), the architect of the "brachiationist" model, to abandon it in favor of a more generalized arboreal model (Tuttle, 1974).

Wood Jones (1916) championed one of the most extreme views in arguing for a very ancient split between humans and other primates. So early in primate evolution did humans diverge, Wood Jones (1964, p. 223–224) argued, that "right from that dawn period in which the Therapsida of the Triassic gave birth to the ancestors of the Mammals, the fore-limb of the mammalian stock from which Man sprang has been spared from the servile function of merely supporting the body weight in quadrupedal progression." In the view of Wood Jones (1929), the ancient split of the human lineage resulted in bipe-

dalism evolving from an arboreal and perhaps even vertical clinging ancestor. The hypothesis of Wood Jones (1929) is a stark example of the influence that phylogenetic hypotheses held over the debate about the origins of bipedalism.

Straus (1949) more explicitly argued that humans originated from an above-branch monkey-like ancestor. This view stemmed in part from his belief that humans diverged early from an anthropoid stock. Straus (1949) focused on similarities in hand anatomy shared between humans and cercopithecoids, and the ways in which human hand anatomy is distinct from that of modern apes.

In the 1960s, phylogeny continued to played a critical role in these debates. With the advent of molecular systematics (Goodman, 1963; Sarich and Wilson, 1967), it became clear that humans share a close relationship with the African apes (vindicating earlier anatomists such as Huxley, Keith, Gregory, and others). Washburn (1967) was quick to incorporate this phylogenetic information into the model of hominin ancestry by proposing a knuckle-walking stage between large-bodied orthograde arboreality and hominin bipedality (Fig. 1). Aside from phylogenetic evidence, however, Washburn (1967) presented very few data to support a knuckle-walking hypothesis. The only anatomical evidence offered by Washburn (1967) was the relative absence of hair on the middle phalanges of humans and African apes. However, Tuttle (1974) noted that, in humans, depilitation is more prevalent in the toes than in the fingers, but this does not suggest that human ancestors once practiced a form of "pedal knuckle-walking."

So why did Tuttle (1974), who identified knuckle-walking bone, muscle, and ligament specializations, not advocate a knuckle-walking ancestor? Tuttle (1974) was not convinced by existing arguments that modern human hands retained any evidence of a knuckle-walking heritage. At the time, Tuttle (1975) favored a phylogeny in which humans diverged prior to an orangutan/African ape clade, thus making a knuckle-walking ancestor of all great apes and humans very unlikely. Furthermore, the best early hominin fossil hand evidence at the time, the bones from several individuals collectively known as OH7, lacked any clear signs of knuckle-walking adaptations (Tuttle, 1969a). However, Tuttle (1969a) noted that the relevant metacarpal and radius morphology was not preserved. The subsequent discovery that metacarpal heads of *Australopithecus* lacked knuckle-walking structures, while many aspects of the skeleton point to arboreal climbing adaptations, seemed to confirm this view (Tuttle, 1981).

Molecular systematists were not the first to suggest an especially close relationship between chimpanzees and humans. Weinert (1932) suggested that humans and chimpanzees share a common ancestor, with gorillas, orangutans, and gibbons more distantly related. It appears that Weinert (1932) may have been correct, but perhaps for the wrong reasons. Adolf Schultz, one of the most accomplished and knowledgeable comparative primate anatomists of the 20th century, was extremely critical of the conclusion of Weinert (1932) and the reasoning behind it. Schultz (1936) criticized the categorical descriptions by of Weinert (1932) of great ape and human anatomy that failed to take into account normal ranges of variation and patterns of growth and development. For example, Schultz (1936) responded to the assertion of of Weinert (1932) that only African apes and humans have a fused os centrale (see below) by pointing out that the os centrale is occasionally fused in *Pongo* and *Hylobates*, and occasionally unfused in *Pan*. Schultz (1936) presented a compelling anatomical case for a great ape clade to the exclusion of humans. The comparative anatomical study of Schultz (1936) may be one of the reasons that the knuckle-walking hypothesis has not enjoyed as much support as other hypotheses over the last few decades.

With the phylogenetic relationships of extant hominoids essentially resolved today, and with a growing fossil record, the debate about the origins of bipedalism was influenced heavily, in the last decades of the 20th century, by studies in biomechanics. Most researchers abandoned ideas of a small-bodied hominin predecessor, including the hylobatid-like brachiation hypothesis. It is important to note that the meaning of "brachiation" changed during this debate. When referring to a "brachiating" ancestor, early workers generally meant locomotion involving the hands placed in postures above the body, or "hand-over-hand suspensory locomotion" (Lewis, 1989, p. 86). Indeed, Tuttle (1969a, p. 953) noted that of the extant great apes, "the chimpanzee is generally considered by brachiationists the form that most closely resembles the prototypic large-bodied ape near the base of hominid phylogeny," but with the critical difference that no terrestriality, including knuckle-walking, is included in the "brachiationist" model. Today, the term "brachiation" typically refers specifically to the pendulum-like, sometimes ricochetal, arm-swinging locomotion practiced by extant hylobatids (Hunt et al., 1996).

The focus has shifted instead to whether bipedalism was preceded by exclusively or nearly exclusively climbing and suspensory behaviors (Tuttle, 1969a, 1974; Stern, 1975), including vertical climbing (Prost, 1980; Fleagle et al., 1981; Stern and Susman, 1981; Ishida et al., 1985; Senut, 1988), in a large-bodied ape, or whether the ancestral condition included a significant terrestrial (Gebo, 1996; Sarmiento, 1998), possibly knuckle-walking component (Washburn, 1967; Corruccini, 1978; Shea and Inouye, 1993; Begun, 1993a, 1994, in press; Richmond and Strait, 2000, 2001d). Arguments for suspensory/climbing ancestors (Fig. 1) grew out of a better understanding of the biomechanics involved in these locomotor strategies, and the striking biomechanical similarities between climbing and bipedalism (e.g.,

Fleagle et al., 1981). In addition, these hypotheses are supported by the many apelike arboreal traits present in early hominin fossils (e.g., Tuttle, 1981; Stern and Susman, 1983; Senut and Tardieu, 1985; Hunt, 1998).

Advocates of a terrestrial ancestor (Fig. 1), on the other hand, cite numerous terrestrial traits shared between hominins and African apes to the exclusion of Asian apes (Sarmiento, 1994, 1988; Gebo, 1992, 1996). A few researchers have suggested that palmigrade terrestriality preceded bipedalism (Delmas, 1972; Hotton et al., 1984). Others argue that traits specific to knuckle-walking are shared between African apes and extant humans (Corruccini, 1978; Corruccini and McHenry, 2001; Begun, 1993a, 1994) or African apes and fossil hominins (Richmond and Strait, 2000; Corruccini and McHenry, 2001), and therefore indicate that the common ancestor of African apes and humans was a knuckle-walker. At present, there are numerous hypotheses but no consensus regarding what mode of locomotion preceded hominin bipedalism. How can we test these various hypotheses?

Fossil evidence of this transition will be of the utmost importance in ultimately identifying the locomotor mode preceding bipedalism. However, it is also critical that we sufficiently understand functional anatomy of anthropoid locomotion so that we can reliably interpret the locomotor behavior of these fossils. Below, we review the current evidence that bears on the debate over this ancestral locomotor mode. The phylogeny of great apes and humans, in combination with the functional anatomy that modern humans and fossil hominins share with extant primates, allows us to reject some hypotheses, and address the merits and deficiencies of others.

MAJOR HYPOTHESES AND PREDICTIONS

Of the many hypotheses discussed over the last century, a handful of them have been seriously considered over the last couple of decades. The expectations of each hypothesis will be briefly outlined below, and then considered in light of current evidence. Many anatomical features match predictions of more than one hypothesis, and not all modes of positional behavior are mutually exclusive of one another. However, each hypothesis has some unique predictions.

The logical bases for the predictions of the various models are not often made explicit. Arguments over most models, including those outlined below, include the explicit or implicit assumption that hominins retain unmodified or little-modified skeletal locomotor adaptations of their prebipedal ancestors. For example, a number of authors have noted that the hypothesis of a knuckle-walking ancestor is weakened by the absence of knuckle-walking features in the metacarpals of *Australopithecus afarensis* (also known as *Praeanthropus afarensis*; Strait et al., 1997; Groves, 1999) (see "Current Evidence," below); the underlying expectation is that metacarpal

knuckle-walking adaptations should persist in *A. afarensis* despite the fact that this species almost certainly did not knuckle-walk.

"Retentions" do indeed occur on many biological levels (e.g., molecular, developmental, or structural). The fact that descendents resemble their ancestors is a basic consequence of the historical nature of biological evolution (Williams, 1992). Adaptations can significantly alter ancestral morphologies, but natural selection can only act on "available" anatomical structures. Some adaptations may be retained because their usefulness in ancestral taxa may persist in descendent taxa (e.g., bipedalism in *Homo erectus* and *Homo sapiens*). Some morphology may be "retained" and exapted for new purposes. Other aspects of morphology may be retained for no apparent reason (often referred to as phylogenetic "lag"). Modern humans retain morphology (such as a globular humeral head, laterally facing scapula, and broad chest) from apelike ancestors. Although these features are associated with climbing and suspension in anthropoids, modern humans do not employ these characteristics in the functional roles for which these traits evolved.

One of the questions that is typically not addressed concerns how much phylogenetic "lag" is reasonable, or how long we should expect descendent taxa to retain adaptations to ancestral locomotor behaviors that were abandoned in the descendents. Most researchers would expect the earliest bipeds to retain some aspects of the locomotor adaptations of their immediate nonbipedal ancestors. Some researchers are open to the possibility that such retentions, although perhaps altered, may be present in *Australopithecus*, or even modern humans, millions of years after the origins of bipedalism (Corruccini, 1978; Corruccini and McHenry, 2001; Tuttle, 1981; McHenry, 1984; Latimer, 1991; Begun, 1993a; Shea and Inouye, 1993; Gebo, 1996; Ward et al., 1999a; Richmond and Strait, 2000). These authors reason that, because natural selection acts on existing morphology, traces of former adaptations can persist in descendents. Thus, there is no clear "time limit" on the retention of ancestral traits (e.g., pentadactyly). It should be noted that this issue is not the same as the debate over the *functional significance* of primitive retentions, such as whether or not the "arboreal" traits retained in *Australopithecus* are indicative of arboreal locomotion (e.g., Stern and Susman, 1983; Tuttle, 1981; Latimer, 1991; Richmond, 1999). In other words, a key aspect about the debate over the origin of bipedalism is the persistence of primitive retentions, not their biological role.

The major hypotheses on the forms of locomotion preceding bipedalism, and their predictions, are outlined below. In each case, a particular mode of locomotion is not viewed as being the only positional behavior practiced by the ancestor of hominin bipeds; rather, it is viewed as being an

important component of a locomotor repertoire (Rose, 1991).

Arboreal quadruped ancestor

The arboreal quadruped hypothesis posits that bipedalism evolved from an ancestor adapted to above-branch, pronograde (relatively level trunk) quadrupedalism, much like that observed in most living anthropoids. During above-branch locomotion, the limbs are held under (ventral to) the pronograde body, and typically move in a parasagittal plane. The elbow and knee are generally flexed, arguably to bring the body mass closer to the support. The shoulder and hip undergo greater parasagittal excursions than observed during terrestrial locomotion in order to accommodate a compliant substrate (Schmitt, 1994). However, the shoulder and hip show relatively little mobility, especially in abducted postures, and aspects of their morphology (e.g., large humeral tubercles that project superior to the head) reflect this lack of mobility (Fleagle, 1998). The hands and feet typically have digit lengths intermediate between those of terrestrial monkeys and suspensory/climbing apes. Many of them also have long, divergent first digits to enable effective grasping of smaller substrates. Arboreal quadrupeds generally range from small to medium body size. Above-branch quadrupedalism is more problematic for large-bodied primates because their size relative to the size of typical branches creates difficulties in balance, and may exceed the strength of the support (however, some primitive fossil hominoids appear to have been pronograde arboreal quadrupeds, despite large size). The limbs of arboreal quadrupeds are subequal in length (the hindlimb is typically a bit longer) and are not long relative to body mass compared to other primates (Jungers, 1985).

The arboreal quadruped hypothesis therefore predicts that the ancestor of bipeds would have most of the characteristics outlined above. This hypothesis would be supported if the earliest bipeds retain some of these characteristics as well, such as small-medium body mass, short limbs relative to body size, intermediate finger and toe lengths combined with relatively long first digits, a narrow rib cage with an anteriorly facing scapula, characteristics of the shoulder and wrist associated with stability (vs. mobility), and an elbow reflecting past adaptations for flexed postures. Forelimb traits would be more likely to be retained in a transition to bipedalism involving considerable hindlimb modifications.

Terrestrial quadruped ancestor

The terrestrial quadruped hypothesis encompasses several more specific hypotheses. In its general form, this hypothesis simply argues that bipedalism evolved from an ancestor adapted to some form of terrestrial quadrupedal locomotion. The latter includes digitigrady, palmigrady, fist-walking, and knuckle-walking. What distinguishes these from one another is different usage of the hands. Digitigrade primates support their weight on their fingers and metacarpal heads, while palmigrade primates use the entire hand, including the digits and palm (Hunt et al., 1996). Fist-walking involves weight support in the backs of the proximal phalanges, and knuckle-walking entails weight support on the backs of the middle phalanges (see "Knuckle-walking ancestor," below, for more details).

Some recent advocates (Sarmiento, 1988, 1994; Gebo, 1992, 1996) present arguments that humans evolved from an ancestor adapted to some form of terrestrial quadrupedalism. These authors see evidence of terrestrial weight support in the skeleton of fossil hominins, and in the muscles, ligaments, and skeletons of extant African apes and humans. However, these researchers believe that the evidence does not strongly support one mode of terrestrial quadrupedalism over another (although Gebo (1992, 1996) leans towards a knuckle-walking ancestor based on parsimony).

The general form of the terrestrial quadruped hypothesis predicts that hominins, especially early taxa, exhibit adaptations to pronograde weight support and stability in the hands and feet (and, to a lesser extent, other anatomical regions). Such adaptations include carpal and tarsal morphology that reduces the stresses of weight support by increasing joint areas over which forces act, or orienting joint surfaces to better resist proximodistally directed forces. The terrestrial quadruped hypothesis also predicts moderate to high phalangeal robusticity, and moderate to low levels of phalangeal curvature.

Of the hypotheses on specific forms of terrestrial quadrupedalism, the knuckle-walking hypothesis has received the most attention and support, even from those (e.g., Gebo, 1996) who more cautiously argue for a "terrestrial quadrupedal" ancestor. The knuckle-walking hypothesis is considered separately below. Other terrestrial possibilities include digitigrade and palmigrade terrestriality (Delmas, 1972; Hotton et al., 1984; Sarmiento, 1988). These forms of locomotion are very similar to arboreal pronogrady in that the limbs move in parasagittal planes about a long, narrow, and deep trunk, and the hip, shoulder, and wrist joints are designed for stability and permit relatively restricted ranges of movement, especially in abduction (ulnar deviation is restricted in the wrist). However, digitigrade terrestrial quadrupeds differ from their arboreal cousins in having longer limbs, with elongation especially pronounced in the distal long bones. However, the limbs undergo smaller excursions during stride (Schmitt, 1994). The long bone shafts have distinctive shapes, such as pronounced anterior humeral curvature (Pilbeam et al., 1990), and the forelimb joints have many adaptations for stability, often at the expense of mobility. The metacarpals and metatarsals are elongated, but the fingers and toes are short and straight. There is little mechanical restric-

tion on body mass, but few terrestrial quadrupeds are small.

Predictions of a terrestrial palmigrade or digitigrade hypothesis, then, include an ancestor that has many of the traits outlined above. The hypothesis would be supported if the earliest bipeds displayed some of these characteristic traits, such as anteriorly convex humeri, elbow joints designed for stability, especially against forces acting medially on the hands (Schmitt, 1994), and wrist and pedal adaptations to terrestrial weight support (Sarmiento, 1994, 1998, 2000; Gebo, 1996). Sarmiento (1988) leaves open the possibility that the African ape and human LCA could have been (or recently evolved from) a digitigrade, palmigrade, or fist-walking quadruped that had an otherwise great-apelike skeleton. A fist-walking hypothesis would be very difficult to test, as there are no known adaptations to this behavior, although it is practiced regularly only by extant orangutans, probably as a means of terrestrial travel with very long, curved fingers. In any digitigrade or palmigrade hypothesis, the most critical support would be short, straight fingers and toes, and adaptations for metacarpophalangeal hyperextension, in the ancestor of the first bipeds and its early descendents.

Hylobatian ancestor

The hylobatian model is not quite what its name implies, because the model posits that the ancestor of the first bipeds practiced very little brachiation (arm-swinging), the most common locomotor behavior of modern hylobatids (Fleagle, 1976). Although Morton (1926) first advocated a hylobatian model, the main architect of its current formulation is Tuttle (1974, 1975, 1981). In his hylobatian model (Tuttle, 1974, 1975, 1981), the ancestor of bipeds was a small-bodied (9–13.5 kg) climber and arboreal biped with the following characteristics: relatively long, extensible hindlimbs like those of lesser apes; intermediate lumbar spine length (not reduced like those of great apes) that enabled lateral flexion of the back; a relatively low center of gravity; broad, coronally oriented iliac blades; broad thorax with laterally facing scapulae; mobile shoulder and wrist joints; long forelimbs, but not as long as those of extant hylobatids; long, curved fingers; and well-developed thumbs and first toes. Arboreal bipedalism, in the form of bipedal postures during foraging and bouts of bipedal travel, is viewed as a transition from which terrestrial bipedalism evolved. The ability to laterally flex the lower spine and low center of gravity are viewed as important features that enabled early terrestrial bipeds to walk with more extended hip and knee joints (relative to their hypothetical arboreal ancestors).

The hylobatian model is, in many ways, like the climbing model (see below). The hylobatian model is distinct in predicting a relatively small body mass and long hindlimbs, a longer lumbar region, and an emphasis on arboreal bipedalism.

Climbing (antipronograde) ancestor

The climbing hypothesis argues that bipedalism evolved from an ancestor that was primarily adapted for arboreal locomotion that involves considerable fore- and hindlimb mobility, suspensory postures, and use of multiple supports and, often, vertical supports. The climbing hypothesis explicitly argues that there was no significant terrestrial component, including knuckle-walking, to the locomotor repertoire of the ancestor of the earliest hominin bipeds (Napier, 1964; Tuttle, 1975; Stern, 1975; Prost, 1980; Hunt, 1996). In this hypothesis, arboreal locomotion is contrasted against forms of terrestrial quadrupedalism, and the more stereotypical limb movements of pronograde above-branch quadrupedalism that are commonly practiced by many monkeys. Thus, the term "antipronograde" was coined (Stern, 1975) in an attempt to better describe the body posture, often >45° from horizontal, used by great apes (especially the orangutan) while moving in trees. The less cumbersome term "climbing" will be used here to indicate these kinds of vertical climbing and orthograde clambering behaviors, described in more detail in Hunt et al. (1996).

During vertical climbing and suspension, all four limbs are used to grasp supports. Many of the major joints, including the hip, knee, ankle, shoulder, and wrist, are highly mobile to permit a wide range of cheiridial and limb positions (Stern, 1975; Hunt, 1991). Therefore, the climbing hypothesis is supported if the earliest bipeds its ancestor, and, to a lesser extent, modern humans retain characteristics associated with climbing behaviors, including high intermembral and brachial proportions, elongated and curved fingers and toes, and traits associated with mobility in the wrist, shoulder, and hindlimb joints. It also predicts a relatively large body mass (in the range of great apes), and features indicating any form of terrestrial quadrupedalism will be absent.

Knuckle-walking ancestor

The knuckle-walking hypothesis argues that knuckle-walking was a significant component of the locomotor repertoire of the ancestor of the first bipeds. The hypothesis predicts that the *Pan/Homo* LCA possessed adaptations to knuckle-walking. The retention of some vestiges of former knuckle-walking adaptations in hominins, especially in the earliest bipeds, would provide support for this hypothesis.

Anatomical adaptations for knuckle-walking are concentrated in the forelimb because of its unique locomotor role. During knuckle-walking, African apes bear their weight on the backs of their middle phalanges (middle segments of their fingers), which involves strongly flexed proximal interphalangeal joints, and extended metacarpophalangeal joints (Tuttle, 1967). Cineradiographic experiments (Jenkins and Fleagle, 1975) and preliminary data from ongoing kinematic experiments show that the wrist

maintains a slightly extended posture throughout the late support phase of knuckle-walking. The elbow also generally remains extended (Tuttle and Basmajian, 1974). Therefore, the knuckle-walking hypothesis would be supported by the presence in humans, and especially in the *Pan/Homo* LCA and its early bipedal descendents, of features related to stereotypical compressive weight-bearing, and stability in extended elbow, wrist, and metacarpophalangeal postures. It also predicts an ancestor with a body mass similar to that of extant African apes, limb proportions that are not as specialized as those of Asian apes, an apelike trunk (broad thorax with a laterally facing scapula), and manual digits intermediate in length between those of Asian apes and digitigrade cercopithecoids.

It is important to note that proponents of the knuckle-walking hypothesis do not argue that knuckle-walking was the only locomotor behavior practiced by this ancestor. Knuckle-walking is seen by many as a compromise adaptation that allows an arboreal ape to travel terrestrially while retaining features advantageous for climbing (Tuttle, 1974). The knuckle-walking hypothesis predicts that the locomotor behavior of the ancestor of the first bipeds would be best characterized as a repertoire consisting of terrestrial knuckle-walking, arboreal climbing, and occasional suspensory activities. Thus, the possession of climbing traits in the LCA, and the retention of climbing features in early hominins, would be fully consistent with the knuckle-walking hypothesis.

IMPLICATIONS OF PHYLOGENY

Phylogeny has played, and continues to play, an important role in reconstructions of the evolutionary history of human locomotion. The relations between humans and our closest relatives allow us to define possible scenarios about the origins of knuckle-walking and bipedalism, and to determine whether some scenarios are more likely than others. Most researchers today consider one of three phylogenetic hypotheses to correctly describe relations among African apes and humans. Humans and chimps are either most closely related to one another (Fig. 2A), or chimps, humans, and gorillas all derive from a trichotomous branching event at the base of the African ape and human clade (Fig. 2B), or else chimpanzees and gorillas form a clade with humans as the sister taxon (Fig. 2C). Although morphological studies (e.g., Martin, 1985, 1986; Andrews and Martin, 1987) have traditionally favored an African ape clade (Fig. 2C), the majority of molecular analyses (Ruvolo, 1994, 1995; Begun, 1999; Satta et al., 2000), and more comprehensive morphological analyses (Groves, 1986; Begun, 1992, 1994; Shoshani et al., 1996; Gibbs et al., 2000), favor a chimpanzee-human clade (Fig. 2A). Fossil hominoid anatomy is consistent with this hypothesis (Begun, 1992; White et al., 1994; Richmond and Strait, 2000; Wood and Richmond, 2000; Senut et al., 2001; Haile-Selassie,
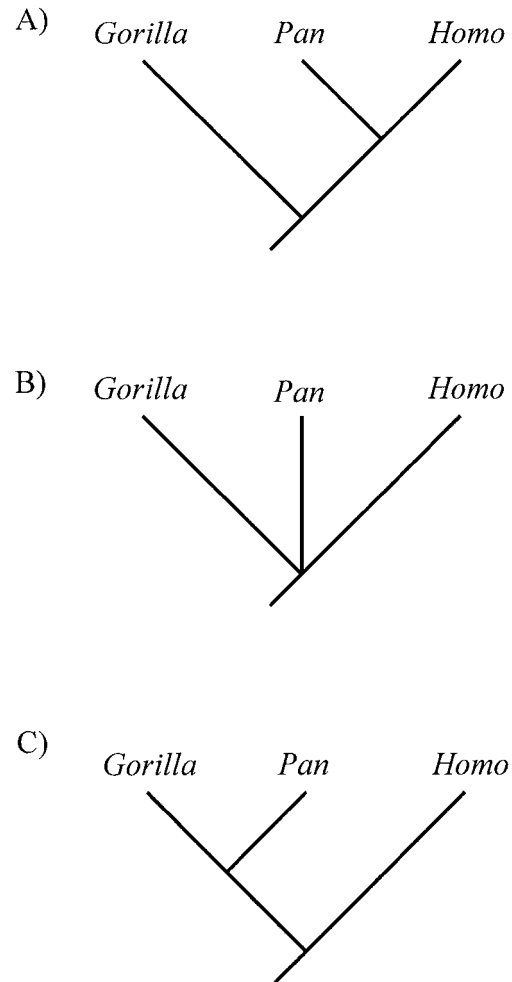

Fig. 2. Among African apes and humans, chimpanzees are either most closely related to (**A**) humans, to (**C**) gorillas, or (**B**) equally to both. Most studies, particularly those based on molecular data, favor a *Pan/Homo* clade (A) or a trichotomy (B).

2001). From a molecular perspective, the strongest opposing arguments to the *Pan/Homo* clade have been those favoring a trichotomy (Fig. 2B), in which the bifurcations are too close to resolve with any certainty (Marks, 1995; Rogers and Commuzzie, 1995; Green and Djian, 1995). This alternative holds essentially the same predictions as a *Pan/Homo* clade for the origins of bipedalism and knuckle-walking. Therefore, for the purposes of this paper, the *Pan/Homo* clade (Fig. 2A) will be treated as the working hypothesis.

The significance of phylogeny to the debate over the origin of bipedalism is based on the use of parsimony to reconstruct the pattern of character evolution implied by each phylogenetic hypothesis. Although parsimony is most often used to reconstruct phylogeny, it can be used to reconstruct characteristics present in the internal nodes of any given cladogram (Maddison and Maddison, 1992; Lockwood and Fleagle, 1999). The implications of phylogeny for reconstructing the ancestral mode of locomotion depend, in this case, upon whether knuckle-
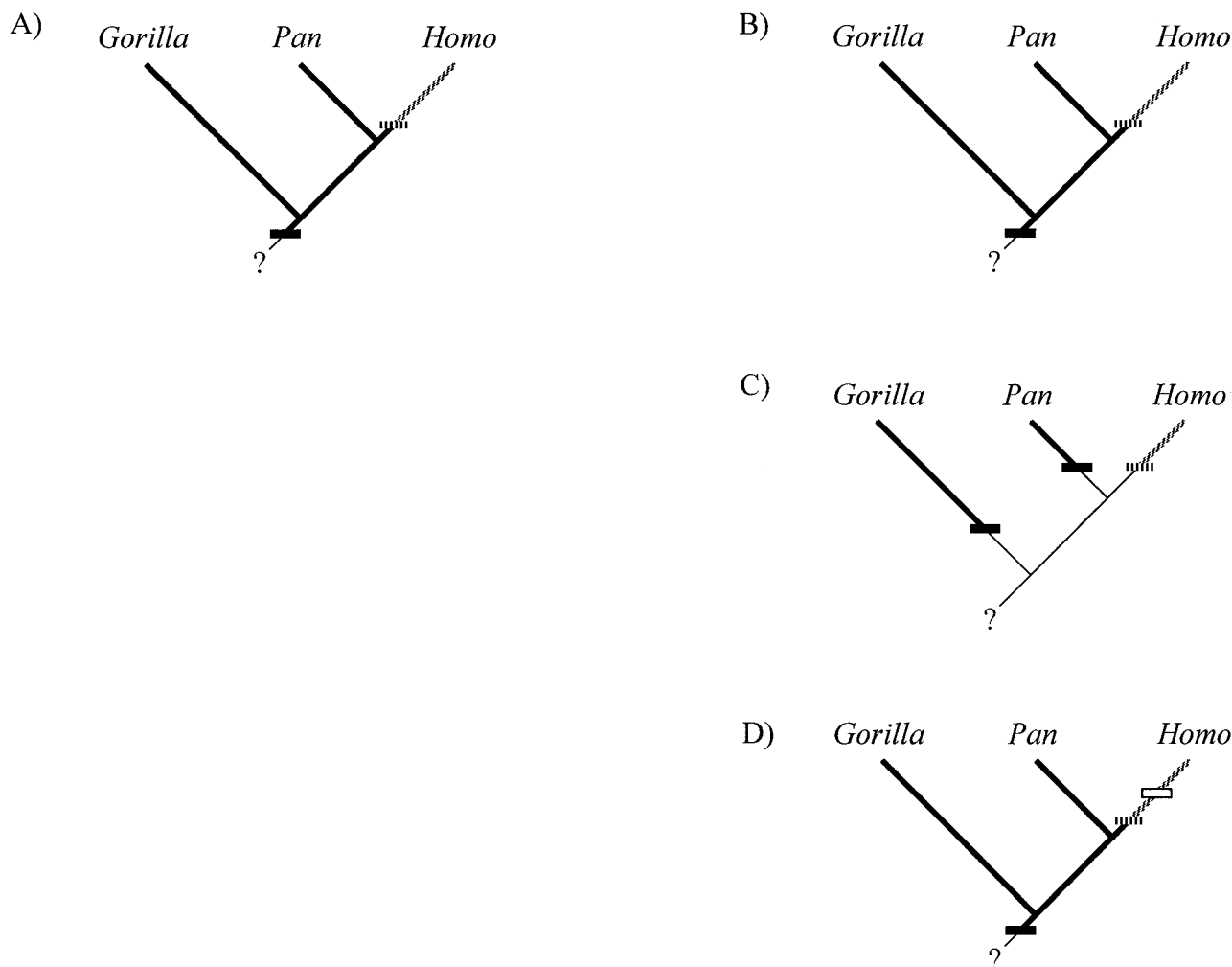
Behavior as character   Anatomical trait as character

Fig. 3. Character evolution of knuckle-walking and bipedalism in the African ape and human (AAH) phylogeny most widely regarded as correct. **A:** If locomotor behavior is treated as a character, then the most parsimonious solution is one in which knuckle-walking as a behavior (bold) evolved once at the base of the AAH clade, and bipedalism as a behavior (hatched) evolved from a knuckle-walking ancestor. **B–D:** Anatomical traits related to knuckle-walking (bold) and bipedalism (hatched) are shown. If any knuckle-walking anatomical traits (bold) are retained in members of the hominin clade, then the most parsimonious scenario (B) involves two steps. In this scenario (B), knuckle-walking traits evolved at the base of the AAH clade from an unknown mode of locomotion (simple line), and bipedal traits (hatched line) evolved at the base of the hominin clade. If no knuckle-walking traits are retained in members of the hominin clade, then two alternatives (C and D) are equally parsimonious, each involving three steps. In scenario C, knuckle-walking traits evolved 1) once in the gorilla lineage and 2) independently in the chimpanzee lineage, and 3) bipedal traits evolved in the hominin clade. In scenario D, 1) knuckle-walking traits evolved at the base of the AAH clade, 2) bipedalism evolved in hominins, and 3) knuckle-walking traits were lost (open bar). Therefore, a key question is whether or not knuckle-walking characteristics are present in hominins. Note that the most likely alternative phylogeny, that of an unresolved trichotomy, holds essentially the same predictions for character evolution as is the case for a *Pan/Homo* clade.

walking is treated at the level of behavior, or at the level of anatomical character states. For example, if one treats locomotor behavior itself as a character (Fig. 3A), in which knuckle-walking and bipedalism are character states, then it is most parsimonious for knuckle-walking to have evolved once at the base of the African ape and human clade. This relies on the important assumption that adaptations to these two behaviors are mutually exclusive, i.e., that loss of knuckle-walking and gain of bipedalism represent

the same evolutionary step. This may be a reasonable assumption, given that both are modes of terrestrial locomotion. Although extant knuckle-walkers can and do use bipedal postures and, on occasion, move bipedally (Doran, 1993; Hunt, 1994), they are not committed to bipedality to the extent that they have anatomical adaptations specific to this behavior. A hominin with bipedal specializations would be poorly suited for significant levels of knuckle-walking as a means of terrestrial travel. Therefore, the

taxon at a particular node might reasonably be considered as adapted to one or the other.

However, cladistic analyses in human evolution are based on anatomical characteristics (Fig. 3B–D). The implications of phylogeny with respect to the origin of bipedalism depend critically on the distribution of knuckle-walking features across taxa. Any feature that is shared by chimpanzees, gorillas, and humans is inferred to have been present in the last common ancestor of all three taxa (e.g., Gebo, 1996). Thus, if members of the hominin clade retain any knuckle-walking characteristics (Fig. 3B), parsimony strongly favors a scenario in which bipedalism evolved from a knuckle-walking ancestor.

On the other hand, if humans or early hominins lack knuckle-walking features altogether, then there are two equally parsimonious interpretations of the evolution of knuckle-walking and bipedalism in a phylogeny with the *Pan/Homo* clade (Fig. 3B,C). Both scenarios involve three steps. In one scenario (Fig. 3C), knuckle-walking traits (e.g., dorsal ridge on metacarpal head) evolved independently in the 1) chimpanzee and 2) gorilla lineages, and 3) hominins evolve bipedal traits from a nonknuckle-walking ancestor. In the alternative scenario (Fig. 3D), 1) knuckle-walking features (e.g., dorsal ridge on metacarpal head) evolve once in the LCA of African apes and humans, 2) bipedal features evolve in the human lineage, and 3) knuckle-walking features (e.g., dorsal ridge on metacarpal head) are lost at some point in the human lineage. In this alternative scenario, hominins evolved from a knuckle-walking ancestor. One might argue that the loss of knuckle-walking anatomical traits is linked with the evolution of bipedalism. However, it is not likely that many knuckle-walking features (largely in the forelimb) are linked to bipedal features (largely in the hindlimb) in a manner that requires one to be lost for the other to be gained. Therefore, the loss of knuckle-walking features must be considered as a step separate from the evolution of bipedal features.[2]

A key question, therefore, is whether knuckle-walking features are present in hominins. Some researchers have claimed that features functionally related to knuckle walking are present in modern humans (Marzke, 1971; Corruccini, 1978; Begun, 1993b, 1994, in press) and some fossil hominins (Richmond and Strait, 2000, 2001c,d; Corruccini and McHenry, 2001). If true, then according to parsimony, those features would be present in the LCA of African apes and humans, as well as the LCA of chimps and humans (Fig. 3B). Such a result would represent strong evidence that humans evolved from knuckle-walking ancestors. Obviously, less parsimonious interpretations are possible, but they require considerable qualifications. For example, if knuckle-walking features are present in chimps, gorillas, and at least some members of the human lineage, then a hypothesis in which hominins are *not* descended from knuckle-walkers would require that knuckle-walking features evolved once in gorillas, again in chimpanzees, and yet a third time in a nonknuckle-walking ape that was evolving or had evolved features related to bipedalism. The latter scenario would be extremely unlikely.

Some researchers, however, remain skeptical that knuckle-walking features are present in humans or fossil hominins (e.g., Stern and Susman, 1983; Ward et al., 1999a; Dainton, 2001; Lovejoy et al., 2001; Senut, 2001; Tuttle, 2001). Most of the disagreement stems from a lack of consensus over what characteristics are knuckle-walking adaptations. Therefore, it is critical that we fully understand how knuckle-walking works, and the osteological and other anatomical adaptations to this form of locomotion. In "Knuckle-walking ancestor," below, we consider anatomical features hypothesized to be related to knuckle-walking, and discuss the extent to which these anatomical regions in humans and fossil hominins are consistent with a knuckle-walking heritage.

Just as parsimony can reconstruct the pattern by which knuckle-walking features evolved, so too can it be applied to any aspect of ape locomotor anatomy. In this way, it might be possible to infer whether the LCA of chimpanzees and humans possessed anatomical features related to arboreal quadrupedalism, terrestrial palmigrady or digitigrady, climbing, or suspension. The fossil and comparative anatomical evidence for these locomotor modes is examined below.

CURRENT EVIDENCE

Five major hypotheses are evaluated below in the context of current evidence from comparative primate anatomy, biomechanics, and fossil hominin anatomy. The functional anatomy of fossil hominins is important to this debate, because most researchers expect that the earliest hominins retain some evidence of recent ancestral adaptations (see "Major Hypotheses," above).

Arboreal quadruped ancestor

The arboreal quadruped hypothesis was best articulated by Straus (1949), but does not enjoy wide support today. Much of its support came from comparative functional anatomy in the context of a phylogenetic hypothesis in which humans and apes diverged very early from each other, out of a generalized anthropoid stock. The strongest evidence of Straus (1949) came from the anatomical

---

[2]Knuckle-walking features that have been noted as absent in *Australopithecus* (e.g., dorsal ridge on metacarpal head), and thus might be considered "lost" in this scenario, are not suitable characters for cladistic analyses for a variety of reasons. Metacarpal head knuckle-walking features are often not present in African apes (Susman and Creel, 1979; Shea and Inouye, 1993; Inouye, 1994b), and their expression may be influenced by body mass and epigenetic factors during growth (Inouye, 1994b; Richmond and Strait, 2000; Lovejoy et al., 2001).

similarities in the hands of modern humans and arboreal quadrupeds (e.g., macaques). They both have finger lengths that are short compared with those of apes, combined with relatively long thumbs. Moreover, Straus (1949) saw what he considered to be possible evidence in early human ontogeny of the expression of ancestral locomotion in the form of palmigrade crawling. He noted that African apes cannot fully extend their fingers and wrists. However, like human infants, young African apes must learn how to walk like adults. Infant chimpanzees walk on palmigrade hands before learning to knuckle-walk in their first years of postnatal life (Doran, 1997).

Probably the strongest evidence for an arboreal pronograde ancestor is the fact that most fossil hominoids were adapted for some form of arboreal quadrupedalism, although often combined with evidence of climbing behaviors in a repertoire not quite like that of any living primate (Rose, 1983). Jenkins and Fleagle (1975) noted that many of the quadrupedal weight-support adaptations in African ape wrist structure (see "Knuckle-walking ancestor," below) could be primitive retentions from a pronograde ancestor rather than secondarily derived from a more antipronograde ancestor. Few would disagree with the notion that arboreal pronograde locomotion was the predominant mode of locomotion in some (earlier hominoid or anthropoid) part of human ancestry (Rose, 1993).

The morphology of early hominins offers little support for the hypothesis that bipedalism evolved from an ancestor adapted to arboreal (pronograde) quadrupedalism. Early hominin body mass is fairly large compared to the expectations of the hypothesis. Upper limb length is also long relative to expectations. Modern human and fossil hominin hand proportions are somewhat consistent with this hypothesis, but many other anatomical characteristics are not, including the mobile shoulder joint, broad thorax, deeply set vertebral column, aspects of the elbow, and many aspects of the wrist, such as the reduced ulnar styloid (Sarmiento, 1988).

Terrestrial quadruped ancestor

Gebo (1992, 1996) and Sarmiento (1988, 1994) most recently argued that African apes (especially gorillas), humans, and fossil hominins share homologous pedal features indicative of a common terrestrial ancestor. These terrestrial features do not discriminate, however, between the various forms of terrestrial locomotion. These terrestrial traits include potential adaptations to heel-strike plantigrady present in extant African apes and humans, such as a laterally rotated calcaneus, dorsally elevated distal calcaneus with a broad proximal heel, elevated navicular position with a large plantar ligamentous region, and a reorientation of subtalar and transverse tarsal joints (Gebo, 1992, 1996). However, orangutans also exhibits a "heel-strike" at the end of swing phase, and hylobatids and some

atelines contact the substrate with their heels, but lack the purported "heel-strike" adaptations (Meldrum, 1993; Schmitt and Larson, 1995). Gebo (1992, 1996) argued that heel-strike should be considered different from heel contact, and believes that the "heel-strike" of orangutans is functionally different (e.g., employing more inverted foot postures) from that observed in African apes and humans. The functional significance and morphology of heel-strike in anthropoids deserve more attention, but if the pedal morphology of African apes and humans is homologous and related to heel-strike, then these features provide support for a terrestrial phase in the LCA of African apes and humans. Other terrestrial features shared by African apes and hominins include a flat talar body, short talar neck, an origin of the flexor digitorum brevis from a well-developed plantar aponeurosis, a well-developed transverse head of adductor hallucis, and shorter, less curved phalanges and metatarsals (Sarmiento, 1994; Gebo, 1996).

Many of the forelimb features (including those of the elbow, and some of those of the wrist and metacarpals; see "Knuckle-walking ancestor," below) related to pronograde weight support are also consistent with other forms of terrestriality, including palmigrade and digitigrade terrestriality. Semidigitigrade adaptations have been described in the fossil hominoid *Equatorius* (*Kenyapithecus*) from Maboko Island (McCrossin and Benefit, 1997). Although it has also been suggested that this hominoid possesses knuckle-walking adaptations (McCrossin et al., 1998), the evidence from the metacarpal head and fragmentary distal radius so far presented is distinct from that in African apes. It would be unlikely that the knuckle-walking morphology observed in African apes could have evolved from an otherwise quite cercopithecoid-like semiterrestrial skeleton (McCrossin and Benefit, 1997). It is far more likely that knuckle-walking evolved from an arboreal ancestor as a solution for terrestrial travel while maintaining functional competence in climbing (Tuttle, 1975). *Equatorius* (*Kenyapithecus*) appears to be too distantly related to African apes, and its skeleton is too primitive, to make a very good model for the LCA of African apes and humans (McCrossin and Benefit, 1997; Begun et al., 1997; Ward et al., 1999b; but see McCrossin et al., 1998).

Hypotheses of a digitigrade or palmigrade terrestrial ancestor gain little support from the functional anatomy of fossil hominins. Metacarpal proportions do not match the expectations of the hypothesis (e.g., hominin metacarpals are short relative to predictions). Early fossil hominin finger proportions and thumb length are compatible with a recent digitigrade or palmigrade ancestor, but early hominin manual and pedal phalanges display a level of curvature suggesting that these hominins, and their recent ancestors, used their hands and feet in arboreal settings (Tuttle, 1981; Susman et al., 1984). The early hominin trunk is broad and shallow, with an

anteriorly placed vertebral column, and the shoulder joint faces laterally and displays considerable mobility (e.g., globular humeral head projecting superiorly above the tubercles), all features that contrast with the morphology and mechanical expectations of modern digitigrade and palmigrade quadrupeds.

Hylobatian ancestor

One of the strengths of the hylobatian hypothesis is the straightforward mechanism for a transition to bipedality. In the rendition by Tuttle (1974, 1975, 1981), arboreal bipedal postures and locomotion were important components of the hylobatian ancestor's positional repertoire, and therefore already had some adaptations for bipedality, thus making for an easy transition to terrestrial bipedality.

However, the hylobatian model is not well-supported by current evidence from the earliest hominins. Most of the evidence in support of the hylobatian model involves early hominin features related to climbing that also support the climbing model, such as a broad thorax, curved fingers, and mobile should and wrist joints (see "Climbing ancestor," below). Apart from features related to climbing, few traits present in early hominins can be argued to support the hylobatian model. These include relatively long hindlimbs and lumbar regions in *Australopithecus* compared to those of great apes (Robinson, 1972; Jungers, 1982). However, these bipedal adaptations are to be expected in early bipeds such as *Australopithecus* (Aiello and Dean, 1990), whether or not the ancestor of bipeds fits the hylobatian model. The presence of bipedal features in bipedal hominins tells us little about the ancestor of bipeds.

The hylobatian model, as distinct from the climbing model, is most strongly weakened by the body sizes of early hominins, all of which are well above 9–13.5 kg (Jungers, 1988; McHenry, 1992; White et al., 1994; Senut et al., 2001; Haile-Selassie, 2001). It is very unlikely that the ancestor of the earliest bipeds was considerably smaller (9–13.5 kg) than the apparent body masses of early hominins. This would require dramatic and very rapid body mass increases. Furthermore, in a phylogeny with a *Pan/Homo* clade (or a trichotomy), such a small body mass in the LCA would require independent and substantial body mass increases in all three African ape/human lineages. With a body mass closer to that of extant *Pan*, far fewer arboreal supports would be available to the ancestor of bipeds for arboreal postures and, especially, locomotion. At present, there is little evidence to support the hylobatian model in ways making it distinct from a climbing model.

Climbing (antipronograde) ancestor

Arguably the most popular hypothesis during the last several decades has been the climbing hypothesis. Its broad acceptance derives from three main sources of evidence: climbing/suspensory features retained in modern humans and shared with great apes, a variety of biomechanical similarities between human bipedalism and vertical climbing in great apes, and numerous climbing features retained in early hominin fossils.

There is little doubt that many aspects of modern human skeletal form, particularly in the trunk and upper limb, are products of an climbing arboreal heritage. For example, humans share with great apes a vertebral column that is ventrally situated to move it closer to the center of gravity in upright postures (Schultz, 1961). The broad, shallow shape of the rib cage positions the scapula on the back of the rib cage so that the shoulder faces laterally, thereby allowing greater mobility of the shoulder (Schultz, 1961). Humans also share with great apes a globular humeral head that projects above the tubercles, again enhancing mobility. Although humans make use of shoulder mobility in a wide variety of contexts, it is unlikely that humans evolved these characteristics in parallel with African apes, especially given their presence in early hominins (see below; there is, however, debate over whether these traits were present in the LCA of great apes; Pilbeam et al., 1990; Ward, 1997; Larson, 1998; Richmond and Whalen, 2001). Rather, these traits and many others (Schultz, 1936; Aiello and Dean, 1990) are the remains of an orthograde climbing heritage.

A second, powerful argument for climbing as an important part of the LCA's locomotor repertoire comes from the biomechanical similarities between vertical climbing and bipedalism (Prost, 1980; Fleagle et al., 1981; Stern and Susman, 1981; Ishida et al., 1985; Senut, 1988). For example, during vertical climbing, chimpanzees extend and medially rotate the thigh in ways comparable to those observed in human bipedalism (Fleagle et al., 1981). Electromyographic experiments in nonhuman primates have shown that bipedal walking and vertical climbing involve muscle recruitment patterns more similar to each other, and to human bipedality, than to quadrupedal behaviors. When species adapted to climbing, such as chimpanzees and orangutans, walk bipedally, they use a ground force pattern more similar to that of humans than to the bipedalism of other nonhuman primates. When walking bipedally, they also use some muscles, such as the gluteus medius, for the same functional role as when the muscles are used in human walking (Stern and Susman, 1981). This and other evidence suggest that vertical climbing adaptations may be "preadaptive" to bipedalism.

Advocates of the climbing hypothesis find considerable support in the early hominin skeleton, which exhibits many apelike arboreal climbing characteristics, and many others that are "intermediate" in form between a great ape and modern human condition. Of the many apelike arboreal traits of the early hominin skeleton (reviewed in McHenry, 1991;

Stern, 2000), some of the more widely discussed features include curved fingers and toes, pronounced ridges for the insertion of forearm flexor muscles (e.g., flexor digitorum superficialis), upper limbs with well-developed muscle scars, and aspects of the shapes of the metatarsal heads related to mobility.

Similarly, many aspects of the early hominin skeleton are "intermediate" in form between the modern human condition and that of some or all of the great apes, such as relative lengths of the femur, pisiform, hamulus, and fingers and toes, and the relative sizes of the femoral head, lumbar and sacral centra, and sacro-iliac joints (Jungers, 1982; Stern and Susman, 1983; Latimer, 1991; McHenry, 1991; Ruff, 1998). "Intermediate" traits such as these are widely interpreted to be the adaptive mark of bipedality recently evolved from an ancestor adapted for arboreal climbing (e.g., Stern and Susman, 1983; Latimer, 1991). Whether or not these characteristics are evidence of "current use" in arboreal settings (e.g., Tuttle, 1981; Jungers, 1982; Stern and Susman, 1983; Latimer and Lovejoy, 1990; Duncan et al., 1994; Hunt, 1998; Ward et al., 1999a; Richmond, 1999), most researchers agree that they are primitive features retained from an ancestor adapted to climbing and suspensory postures.

Not all researchers agree, however, on whether a purely arboreal climbing mode of locomotion characterized the immediate ancestor of bipeds, or occurred in an earlier ancestor (e.g., Gebo, 1996). For example, knuckle-walking is often viewed as a "compromise" adaptation for terrestriality that allows for the retention of important climbing features, such as long, curved fingers (Tuttle, 1974); in this scenario, knuckle-walking is thought to have evolved from an ancestor adapted to climbing and suspensory behaviors. Most of the climbing and "intermediate" adaptations, including those discussed above, are fully compatible with some terrestrial adaptations, such as knuckle-walking or fist-walking, as practiced by modern great apes when traveling on the ground. Therefore, much of the evidence for an antipronograde climbing ancestor, including the evidence suggesting that vertical climbing is preadaptive for bipedalism, does not refute a terrestrial fist- or knuckle-walking component to the ancestral locomotor repertoire.

A few sources of evidence have been used both to support a climbing hypothesis and argue against a knuckle-walking (or other terrestrial) hypothesis. This evidence generally involves cases in which early hominins lack purported knuckle-walking features and more closely resemble the orangutan condition. For example, many advocates of the climbing hypothesis have not favored a knuckle-walking ancestor in large part because of the absence of knuckle-walking characteristics in the metacarpals of *A. afarensis* (Bush et al., 1982; Tuttle, 1981; Stern and Susman, 1983; Ward et al., 1999a), *A. africanus* (Ricklan, 1988), and *H. (A.) habilis* (Susman and Stern, 1979). However, it is generally acknowledged that the absence of the metacarpal features in hominins does not rule out a knuckle-walking ancestry, because these features are often not present in extant knuckle-walkers (Susman and Creel, 1979; Shea and Inouye, 1993; Inouye, 1994b), and because these taxa postdate the origins of bipedalism by a substantial period of time in which traces of ancestral adaptations may disappear (Stern and Susman, 1983). The presence of the metacarpal head traits may be size-related, as they are best expressed in gorillas, but are quite variable in common chimpanzees and bonobos. The possibility also remains that, in addition to size-related influences, this metacarpophalangeal joint morphology may be epigenetically influenced by activity during growth (Richmond and Strait, 2000; Lovejoy et al., 2001). Throughout ontogeny and adulthood, chimpanzees and bonobos are more active in arboreal environments and spend less time knuckle-walking than do gorillas (Doran, 1997). The difference in magnitude and frequency of loading may influence the expression of metacarpophalangeal knuckle-walking features. This hypothesis has not yet been tested, but if supported, it would indicate that the absence of these features in early hominins only means that these hominin individuals did not knuckle-walk during growth (Richmond and Strait, 2000).

Evidence from humeral shaft shape has also been cited in support of a climbing hypothesis and against a knuckle-walking ancestor. Compared to pronograde monkeys, apes have a humeral head that is rotated medially relative to the distal end. A medially facing humeral head is associated with a laterally facing glenoid fossa positioned on the back of a broad, shallow rib cage (Larson, 1996). The medial orientation of the humeral head in hominoids and *Ateles* gives the shaft a "twisted" shape that is known as humeral "torsion," in a strictly morphological sense (i.e., not referring to a strain pattern). In contrast, the humerus in most nonhuman primates faces posteriorly, to articulate with a ventrally facing scapula on the side of a deep, narrow thorax (Larson, 1996). African apes have unusually high levels of humeral torsion, because the forelimb must be used in a parasagittal plane and articulate with a laterally facing scapula (Larson, 1988). Humans have African-apelike levels of humeral torsion that, in themselves, would suggest a knuckle-walking heritage (Begun, in press). However, Larson (1996) finds a knuckle-walking ancestor unlikely based on torsion estimates from fragmentary fossil hominin humeri that more closely resemble orangutan humeri. Larson (1996) argues that the high levels of torsion in modern humans more likely evolved independently in association with forelimb use in manipulation and tool-related behaviors.

Unfortunately, the known early hominin humeri are fragmentary, and questions remain as to the accuracy with which torsion can be determined from the preserved morphology (Begun, in press). For example, multiple regressions predict very similar

torsion values for African ape and orangutan humeri, despite the fact that the actual values for African ape humeri are much higher than those of orangutan humeri (Larson, 1996). Therefore, the fossil hominin humeri may be more African-apelike, or more orangutan-like, than their torsion estimates suggest. In addition, 2 of the 3 specimens have suffered damage that could influence the estimates. As Larson (1996) notes, discoveries of more complete early hominin humeri will address these problems.

Even if lower torsion in early hominins is confirmed, evidence suggesting that torsion may be sensitive to use during growth further complicates the significance of early hominin humeral torsion. Captive, predominately quadrupedal orangutans have substantially higher torsion than their wild counterparts, a difference attributable to locomotor behavioral differences during growth (Sarmiento, 1985). Thus, lower torsion in early hominins may be consistent with the hypothesis that hominins evolved from a knuckle-walking ancestor, in that high torsion would not develop in early bipeds that no longer used their limbs in knuckle-walking postures and probably used their upper limbs for climbing.

Fossil evidence of the distal radial joint surface proportions has also called into question the homology of a trait shared between humans and African apes (Heinrich et al., 1993). African ape and human radii, like the radii of nonhominoid monkeys, have large scaphoid joint surfaces relative to lunate joint surfaces, a feature related to pronograde weight support (Jenkins and Fleagle, 1975). In contrast, Asian apes have relatively large lunate joint surfaces, arguably an adaptation for stress across the wrist joint when the wrist is held in adducted (ulnar-deviated) postures like those often used in climbing (Heinrich et al., 1993). Early hominin radii attributed to *A. anamensis* and *A. afarensis* have relatively wide lunate joint surfaces like those of orangutans (Heinrich et al., 1993), offering some support for the climbing hypothesis.

In summary, the climbing hypothesis is strongly supported by the biomechanical similarities between vertical climbing and human bipedalism, the retention in humans and early hominins of a long list of primitive arboreal features, and traits "intermediate" between great ape and human conditions. Although a few early hominin features (such as the lack of metacarpal head tori, possibly lower humeral torsion, and Asian-apelike radiocarpal joint proportions) argue (albeit not strongly) against a knuckle-walking hypothesis, the vast majority of the features supporting a climbing hypothesis are also consistent with the knuckle-walking hypothesis. Indeed, most researchers believe that knuckle-walking evolved from a climbing ancestor as a means for an ape to travel terrestrially while maintaining climbing adaptations (Tuttle, 1974).

Knuckle-walking ancestor

One of the few points of agreement among researchers is that the retention of knuckle-walking features in modern humans or early hominins would provide strong evidence of a knuckle-walking ancestor (see "Major Hypotheses," above) (e.g., Corruccini, 1978; Corruccini and McHenry, 2001; Tuttle, 1981; Stern and Susman, 1983; McHenry, 1984; Begun, 1993a; Shea and Inouye, 1993; Ward et al., 1999a; Richmond and Strait, 2000). Some researchers have argued that knuckle-walking retentions do exist in the forelimbs of humans and fossil hominins (Corruccini, 1978; Corruccini and McHenry, 2001; Begun, 1993a; Richmond and Strait, 2000).

Indeed, African apes and hominins share many forelimb characteristics that may be functionally related to knuckle-walking, and yet are retained in humans because they are compatible with bipedalism and the functions required of a hominin upper limb. Most of these features are functionally related to each other and involve two functional goals. The first involves stabilizing the wrist both transversely and in a slightly extended posture (by close-packing in extended positions and by reducing the potential for joint translation through bone fusion, the development of more complex joint surfaces, and the presence of more strongly developed wrist flexor power arms). The second involves reducing stress from vertically directed compressive loads (through enlarged and repositioned articular surfaces and more robust bones).

The terrestrial traits (see "Terrestrial quadrupedal ancestor," above) of the feet shared by African apes and humans also add support to the knuckle-walking hypothesis (Sarmiento, 1988, 1994; Gebo, 1992, 1996). Although these traits cannot be linked specifically with knuckle-walking, they provide evidence of either a shared terrestrial ancestry or independent evolution of terrestriality in all three lineages (Figs. 3C). If the terrestrial traits are homologous, it is far more parsimonious to reconstruct the LCA as a knuckle-walker than as a fist-walker, or as a digitigrade or palmigrade quadruped (Gebo, 1996).

Shoulder. As discussed above, humeral torsion is greater in African apes than in other anthropoids, owing to parasagittal use of the forelimbs during knuckle-walking in combination with a trunk designed to support a laterally facing scapula (Larson, 1988). Modern humans also have a high degree of humeral torsion, but this feature may not be homologous in African apes and humans (Larson, 1996). If it is homologous, and early hominins have a degree of humeral torsion greater than that seen in the Asian apes, humeral torsion would provide good evidence of a shared terrestrial, probably knuckle-walking (given phylogeny), ancestor of African apes and humans (Begun, in press).

Other humeral features observed in fossil hominins, such as a globular humeral head that projects above the tubercles, and a relatively straight shaft, are associated with climbing and suspension. However, the presence of these traits in African apes indicates that they are fully consistent with a knuckle-walking ancestor.

Elbow. Tuttle and Basmajian (1974) noted that the elbow is typically extended during knuckle-walking. They suggest that stability in extended postures may be particularly important to resist torque (Tuttle and Basmajian, 1974). Although it is not as well-developed as in terrestrial cercopithecoids, African ape distal humeri have steep lateral margins of the olecranon fossa with proximally extended joint surfaces. Schmitt (1994) showed that, when walking on the ground, the anthropoid forelimb experiences a medially oriented ground reaction force that would result in medial bending of the ulna about the elbow joint. Strain experiments on the macaque ulna confirm a medially compressive bending regime (Demes et al., 1998). Medial bending engages the lateral wall of the olecranon process with the lateral wall of the olecranon fossa. The development of these joint surfaces is especially pronounced in terrestrially adapted cercopithecoids (Ciochon, 1993; Richmond et al., 1998). The lateral margin of the olecranon fossa in humans is not as steep in the humeri of African apes. All of the known early hominin humeri lack steep lateral margins. However, some humeri (e.g., TM 1517) have features related to strong elbow extension, such as extension of the distal margin of the capitulum onto the posterior aspect of the humerus (Aiello and Dean, 1990).

Radiocarpal joints. The wrist is also adapted for stability in weight support, particularly in a slightly extended wrist posture. Passive manipulation of wrist joints in anesthetized and cadaver anthropoids indicates that gorilla and chimpanzee wrists have restricted ranges of extension compared to wrists of *Pongo*, *Hylobates*, *Papio*, *Erythrocebus*, and *Cebus* (Tuttle, 1969b, unpublished data). Several osteological mechanisms contribute to the limitation of wrist extension. In African apes, the dorsal margin of the distal radius projects distally (Fig. 4), buttressing the scaphoid as it rotates during extension (Tuttle, 1967; Jenkins and Fleagle, 1975; Corruccini, 1978; Richmond and Strait, 2000). When the rotating proximo-dorsal surface of the scaphoid contacts the distal radial joint surface, and when other joints, such as the scaphoid-capitate joint, achieve a "close-packed" position, little to no further extension is possible (Fig. 4) (Jenkins and Fleagle, 1975).

The scaphoid notch along the dorsal ridge of the radius is relatively large, possibly to reduce stress by increasing the area over which weight-bearing forces are distributed (Richmond and Strait, 2000). The scaphoid notch is also oriented dorsally relative to a somewhat more radial orientation in Asian apes. The shape of the scaphoid bone also reflects this extension-limiting mechanism (Jenkins and Fleagle, 1975). In African apes, the scaphoid has a relatively pronounced concavity on the dorsal surface that contacts the scaphoid notch on the distal radius (Tuttle, 1967). Obviously, the midcarpal joint, as well as ligaments and perhaps muscle tension, must also be involved in order to successfully limit wrist extension (Lovejoy et al., 2001; Richmond and Strait, 2001a). The contributions of these structures do not diminish the importance of carpal joint structure in providing stability (Hamrick, 1996). As noted by Jenkins and Fleagle (1975, p. 221), "There is little reason to assume that only one morphological feature is principally responsible; rather, this limited excursion is probably reflected in many aspects of wrist morphology." Thus, African ape distal radii have distally projecting dorsal margins, a broad and dorsally oriented scaphoid notch, and relatively coplanar scapho-lunate joint surfaces (Tuttle, 1967; Jenkins and Fleagle, 1975; Corruccini, 1978; Richmond and Strait, 2000).

Nonhominoid anthropoid terrestrial quadrupeds (e.g., *Papio*, *Erythrocebus*) have similar mechanisms that limit radiocarpal joint extension, but these mechanisms differ from those in African apes in permitting a much greater range of extension before reaching a close-packed position. The radii of baboons and patas monkeys exhibit projecting dorsal processes, along with very large and deep scaphoid notches (Fig. 5). Thus, in these terrestrial anthropoids, the scaphoid rotates much farther before the concave portion of the dorsal surface contacts the deep scaphoid notch on the dorsal radius and prevents further mobility (Whitehead, 1993). This morphology is consistent with observations on positional behavior. During terrestrial locomotion, patas monkeys extend their wrists to a greater extent than is observed in African apes (Richmond, 1998). Although baboons maintain a neutral wrist position throughout the support phase of terrestrial locomotion, they use more extended wrist postures while traveling on arboreal supports (Schmitt, 1994). In contrast to the morphology in these anthropoids and in African apes, the radii of Asian apes are generally characterized by a dorsal ridge that does not project as far distally (Fig. 5), a more acute relationship between the scaphoid and lunate articular surfaces, and a relatively small scaphoid notch. Human radii are derived in having very weakly projecting dorsal ridges (Fig. 5) and greater mobility in wrist extension (Heinrich et al., 1993).

Richmond and Strait (2000) observed this knuckle-walking morphology in distal radii attributed to two of the earliest hominins. Like *Pan troglodytes* and *Gorilla gorilla*, the radii of these early hominin species exhibited distally projecting dorsal ridges, relatively coplanar scaphoid and lunate articular surfaces, and large, dorsally oriented scaphoid notches (Fig. 5). When these features are measured, and the
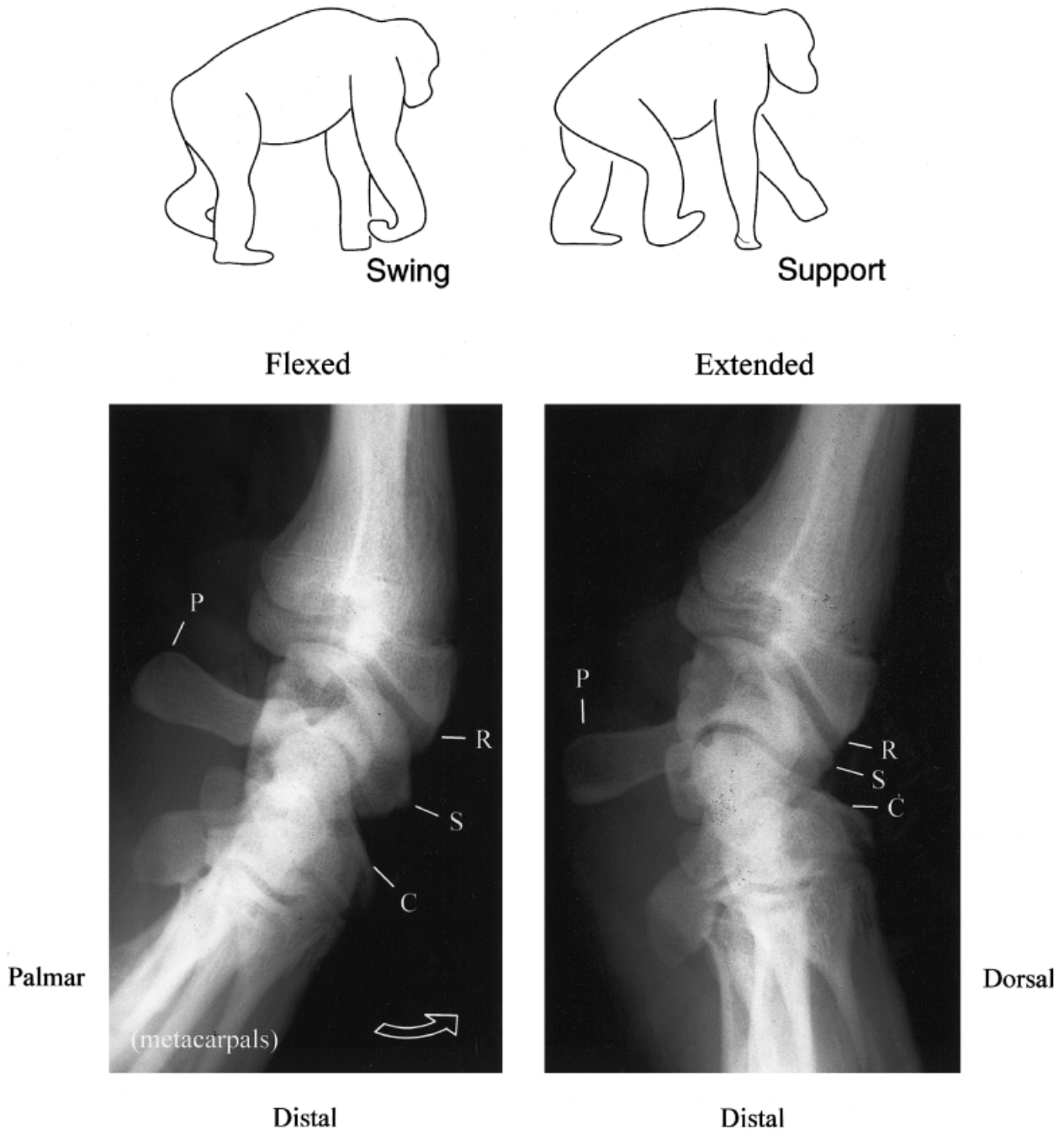
Fig. 4. Radiograph of cadaver chimpanzee wrist, in flexed (left) and fully extended (right) postures, as would be used during the swing (left) and support (right) phases of knuckle-walking. In the extended wrist, the dorsal surface of the scaphoid achieves a close-packed position of stability with the projecting dorsal margin of the distal radius. Similarly, the capitate and hamate rotate relative to the proximal carpal row until a close-packed position is reached, after which further movement is not possible without disengaging the articular surfaces. R, distal end of dorsal radius; S, scaphoid, dorsal margin; C, capitate, dorsal margin; P, pisiform.

linear metrics size-standardized by maximum radial breadth, a canonical variates analysis (CVA) of these features shows considerable, albeit not complete, discrimination of African apes from other taxa (Richmond and Strait, 2000). The CVA and Mahalanobis D^2 distances and approximate significance from respective F-tests (Richmond and Strait, 2000, 2001c) show that the radii attributed to *A. anamensis* and *A. afarensis* resemble African apes more

closely than other taxa in these knuckle-walking traits.

One could argue that there are appropriates measures of distal radius size other than the maximum radial breadth used in Richmond and Strait (2000). The analysis was performed again here, using radiocarpal articular area as a measure of distal radius size (Fig. 6). Projected area was measured by digitizing the outline of the combined scaphoid-lunate
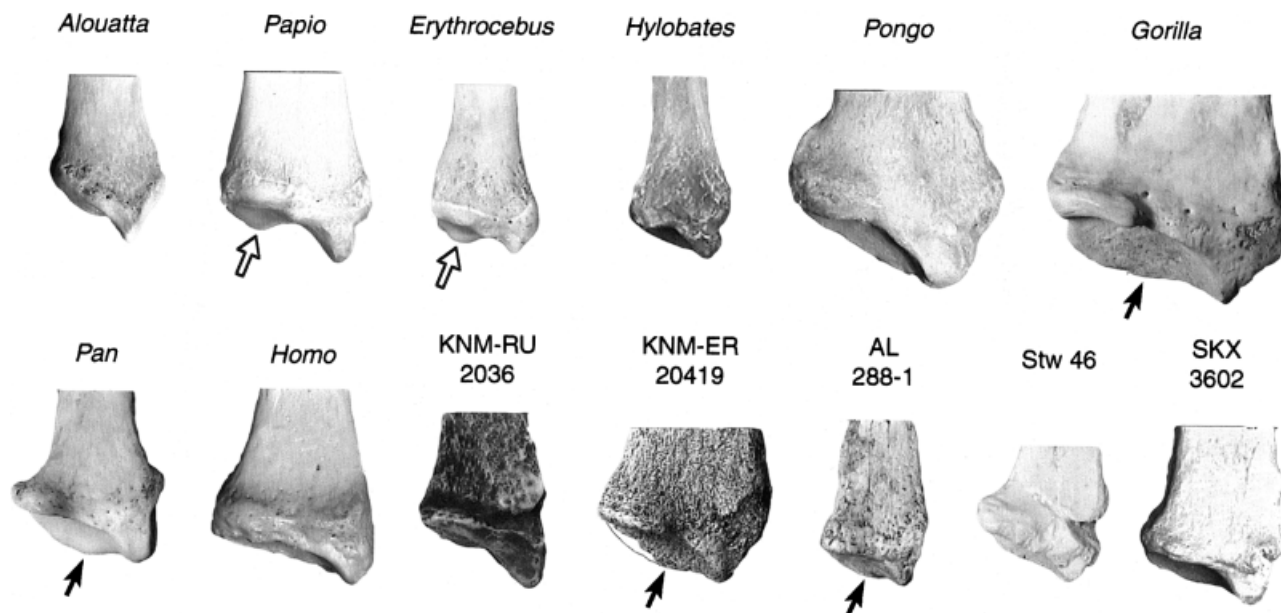
Fig. 5. Anthropoid distal radii in palmar view, as illustrated by Tuttle (1967), who first identified knuckle-walking specializations in the radiocarpal joints. Note the distal projection (arrows) of the dorsal margin in *Gorilla*, *Pan*, and the radii attributed to *A. anamensis* (KNM-ER 20419) and *A. afarensis* (AL288-1). These taxa also have a scaphoid notch size and scaphoid-lunate facet angle (SLA; reflecting the degree to which the radiocarpal surface is a flat plane or scaphoid and lunate surfaces are angled relative to each other) that is intermediate between the conditions in pronograde quadrupedal anthropoids (large notch and SLA) and the suspensory Asian apes (small notch and SLA). The digitigrade terrestrial quadrupeds (*Papio* and *Erythrocebus*) have distally projecting dorsal processes (open arrows) that are invaded by very large scaphoid notches that permit a greater degree of wrist extension before achieving a very stable configuration. Note the more humanlike morphology of the more recent hominin radii SKX 3602 (*P. robustus*) and especially Stw 46 (*A. africanus*).

articular surfaces from a view perpendicular to the distal joint surface. Radiocarpal areas were collected from the same calibrated distal-view video images in which the scaphoid notch angle (SNA) measurements were collected (Richmond and Strait, 2000).

The results from this CVA (Fig. 6) are not very different from the original CVA (Richmond and Strait, 2000). This CVA (Fig. 6), and the respective Mahalanobis D^2 distances (Table 1) and F-test approximate significance values between group centroids (Table 2), show that fossil radii attributed to *A. anamensis* (KNM-ER 20419) and *A. afarensis* (AL 288-1) most closely resemble the African apes in morphology functionally related to knuckle-walking. These hominin radii are significantly different from all extant taxa except *Pan* and *Gorilla* (Table 2). Later hominins, however, appear more humanlike in their wrist morphology. The radius of the robust australopithecine *Paranthropus robustus* (SKX 3602) appears more humanlike (e.g., it is not significantly different from *Homo*; Table 2), but is somewhat intermediate (Fig. 6). The radius attributed to *A. africanus* (Stw 46) closely resembles those of humans in these features. Therefore, it appears these later hominins, especially *A. africanus*, may have exhibited a more humanlike (greater) range of wrist extension. It is not clear why greater wrist extension appears in later hominins (including modern humans), but it may arguably be related to tool use (Ambrose, 2001), such as throwing and hammering activities (Marzke, 1971).

Other features of the radioulnar and radiocarpal joints shared by African apes and humans include a large ulnar head and a well-formed articular disc (Sarmiento, 1988). Both of these features are related to the use of the forelimb to transmit compressive stress from the ulna to the ulnar carpal row (triquetrum) while preventing the ulnar styloid process from articulating directly with the triquetrum and pisiform, as it does in most primates other than great apes and humans (Beard et al., 1986; Sarmiento, 1988). This arrangement allows for effective weight-bearing, while retaining a wide range of pronation and supination, and mobility in wrist adduction.

The elongated pisiform of nonhuman primates increases the moment arm for the flexor carpi ulnaris muscle (Lewis, 1989). Although the latter is almost certainly important during climbing, the fact that African apes have more elongated pisiforms than those of orangutans (Sarmiento, 1985) suggests that it plays a role in forelimb propulsion, and perhaps limiting wrist extension, in African apes during knuckle-walking, especially at high speeds. Terrestrial functionality is further supported by the observation that some captive orangutans (likely to have practiced much more terrestriality) have more elongated and palmarly directed pisiforms like those of African apes (Sarmiento, 1985).

Dainton and Macho (1999) recently documented differences in the later stages of ontogeny of the ulnar carpal region, and interpret these develop-
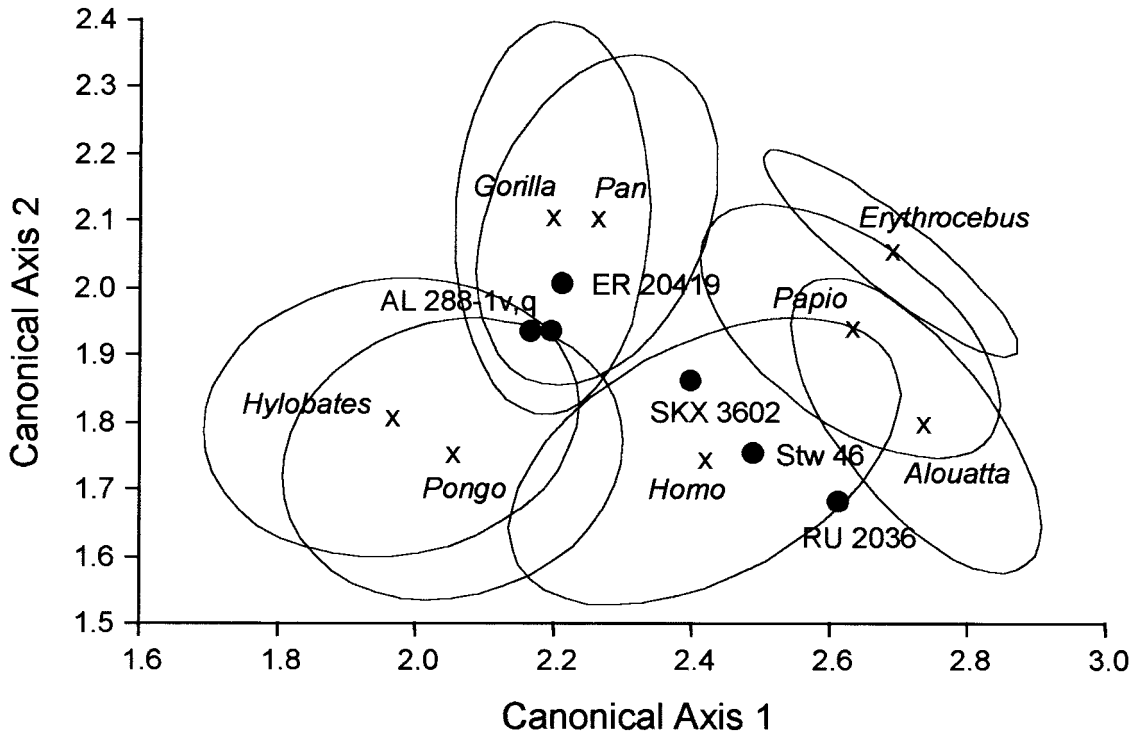
Fig. 6. Bivariate plot of group canonical score means (x) and 95% density ellipses. The analysis is based on the same methods and variables used in Richmond and Strait (2000), with the exception that radiocarpal articular area, rather than maximum radial breadth (MRB), was used to standardize for size (the ulnarmost portion of the dorsal articular margin of KNM-ER 20419 was reconstructed as passing through the center of the slight erosion; minimum and maximum possible areas resulted in very similar measurements, as when compensating for missing (if any) articular margin from the lateral edge of the scaphoid surface). The earliest hominin taxa *A. anamensis* (KNM-ER 20419) and *A. afarensis* (AL 288-1) exhibit the knuckle-walking morphology, whereas *Paranthropus robustus* (SKX 3602) and especially *A. africanus* (Stw 46) resemble modern humans.

TABLE 1. Mahalanobis D^2 distances between group centroids

Taxon	A. anamensis	A. afarensis	A. africanus	P. robustus	Pan	Gorilla	Homo	Pongo	Hylobates	P. heseloni	Alouatta	Papio
A. afarensis	1.13	0.00										
A. africanus	19.35	17.38	0.00									
P. robustus	7.82	7.05	2.84	0.00								
Pan	2.29	5.88	24.70	11.24	0.00							
Gorilla	1.51	3.78	28.02	13.25	1.88	0.00						
Homo	15.96	12.99	.96	2.08	21.75	24.50	0.00					
Pongo	16.17	11.83	30.54	21.95	24.10	24.75	21.95	0.00				
Hylobates	18.65	11.38	41.02	28.61	30.23	22.00	31.52	13.56	0.00			
P. heseloni	42.95	38.19	7.76	15.45	50.17	51.54	10.49	59.85	59.29	0.00		
Alouatta	42.29	43.20	8.19	15.46	42.40	50.94	13.20	64.80	82.52	9.82	0.00	
Papio	27.10	28.71	9.22	9.44	24.91	30.50	12.19	56.75	63.47	11.83	5.48	0.00
Erythrocebus	37.92	43.36	25.37	22.57	28.31	39.52	28.17	70.85	88.54	34.27	14.42	6.80

mental differences as evidence that knuckle-walking is not homologous in the two African-ape genera. However, there is no reason to expect every aspect of forelimb morphology and ontogeny to be identical in *Pan* and *Gorilla* for knuckle-walking to be homologous. Brachiation and suspension are almost certainly homologous in siamangs and lar gibbons, and yet the relative growth of their locomotor skeletons are substantially different (Jungers and Cole, 1992). Australopithecines and modern humans have fundamental differences in adult lower limb design, and grew very differently, in terms of rate, duration, and pattern within the skeleton (Bromage, 1987; Dean et al., 1993; Tardieu, 1999). Does this mean that bipedalism is not homologous in australopithecines and modern humans? Most importantly, even when

adult structures in different species are identical, and phylogenetically homologous (i.e., present in their LCA), developmental differences can exist (Raff, 1996). Natural selection can act on early stages of growth without apparent changes in the adult structures (Raff, 1996).

More likely causes of the differences in African-ape carpal development include general growth difference in body mass (Leigh and Shea, 1996) and the kinematic differences in knuckle-walking between the African apes (Inouye, 1994a; Dainton and Macho, 1999). Kinematic differences in knuckle-walking may be related to specialization in gorillas for knuckle-walking at large body size as adults and/or, as Inouye (1994b) notes, differences in locomotor repertoire such as a greater emphasis on arboreality

TABLE 2. P-*values based on F-tests indicating approximate significance of Mahalanobis D^2 distances between centroids*

Taxon	Pan	Gorilla	Homo	Pongo	Hylobates	Alouatta	Papio	Erythrocebus
A. anamensis	0.73	0.85	0.01**	0.01**	0.00**	0.00**	0.00**	0.00**
A. afarensis	0.26	0.49	0.02*	0.03*	0.04*	0.00**	0.00**	0.00**
A. africanus	0.00**	0.00**	0.93	0.00**	0.00**	0.12	0.08	0.00**
P. robustus	0.04*	0.02*	0.75	0.00**	0.00**	0.01*	0.08	0.01**
Pan		0.02*	0.00**	0.00**	0.00**	0.00**	0.00**	0.00**
Gorilla	0.02*		0.00**	0.00**	0.00**	0.00**	0.00**	0.00**
Homo	0.00**	0.00**		0.00**	0.00**	0.00**	0.00**	0.00**
Pongo	0.00**	0.00**	0.00**		0.00**	0.00**	0.00**	0.00**
Hylobates	0.00**	0.00**	0.00**	0.00**		0.00**	0.00**	0.00**
P. heseloni	0.00**	0.00**	0.05	0.00**	0.00**	0.07	0.03*	0.00**
Alouatta	0.00**	0.00**	0.00**	0.00**	0.00**		0.00**	0.00**
Papio	0.00**	0.00**	0.00**	0.00**	0.00**	0.00**		0.02*

* $P < 0.05$.
** $P < 0.01$.

in chimpanzees. Finally, differences in carpal growth need not be a consequence of carpal function: many of the differences could be a product of the complex interactions of timing and rate of limb and body mass growth in the two genera.

Midcarpal joints. Like the radiocarpal joint, the midcarpal joint of African apes is designed to limit wrist extension beyond a certain range of movement. As the distal carpal row rotates during extension, the proximo-dorsal joint surfaces of the capitate and hamate achieve a close-packed position with the scaphoid, lunate, and triquetrum (Fig. 4). In African apes, the morphology of the midcarpal joint surfaces provides stability in slightly extended postures, and is well-suited to withstand the relatively stereotypical compressive stresses of quadrupedal weight support (Tuttle, 1967; Jenkins and Fleagle, 1975; Sarmiento, 1988; Begun, in press). Features related to the resistance of compressive stresses in African apes are similar in many ways to the morphology of pronograde cercopithecoid wrists (Jenkins and Fleagle, 1975). African apes have a relatively broad midcarpal joint. The midcarpal joint surfaces of the capitate and hamate are broad, and include large, proximally oriented surfaces that articulate with the scaphoid, lunate, and triquetrum (Fig. 7). In contrast, Asian-ape midcarpal joints are better described as "ball and socket" joints (Jenkins and Fleagle, 1975), in which the capitate and hamate are mediolaterally narrow and have extensive joint surfaces facing radially and ulnarly, respectively (Fig. 7). The dorsal joint surfaces of African-ape capitates and hamates are concavo-convex, often with pronounced ridges along the dorsal margins that act, along with other structures, to limit further movement of the proximal carpal row during extension. In this manner, the flat to concave shapes of the dorsal surfaces of the capitate are analogous to the extension-limiting mechanisms of the metacarpal heads (see below). Preliminary attempts at quantifying these features suggest that African-ape capitates are short and broad, have broad articular heads and concave scaphoid facets, and are morphometrically distinct relative to other anthropoids (Richmond and Strait, 2001b).

These data are consistent with earlier work demonstrating the morphometric differences between African apes and humans on the one hand, and Asian apes and macaques on the other (Corruccini, 1978; Corruccini and McHenry, 2001). Importantly, Corruccini (1978) found that extant humans most closely resemble African apes in these respects, thereby providing support for the knuckle-walking hypothesis. Some of the more influential features in his analysis include a long (proximodistal) ridge on the capitate head separating the lunate and scaphoid facets, a sharp angle between the medial and distal surfaces of the lunate, a short triquetral facet, a relatively short (proximodistal) distal ulnar facet on the radius that is obtusely angled relative to the distal carpal surface, and a fused os centrale (Corruccini, 1978). Corruccini (1978) contends that all of these traits have been functionally related to knuckle-walking. The functional significance of some of these features (e.g., long lunate-scaphoid ridge on the capitate head) is not entirely clear, but others (e.g., fused os centrale) have received more attention and are arguably adaptations for weight transmission or close-packing carpal geometry (Tuttle, 1967; Jenkins and Fleagle, 1975).

The capitate facet of the scaphoid (centrale portion) dominates the midcarpal joint in African apes and humans, whereas the centrale, lunate, and triquetrum contribute more equally to the socket of the midcarpal joint in other anthropoids. The difference is due mostly to proximal expansion of the scaphoid's capitate facet in African apes and humans. The centrale portion of the scaphoid in African apes and humans also wedges itself between the tightly bound trapezoid and capitate in extension, offering stability to the wrist in this position (Figs. 7, 8).
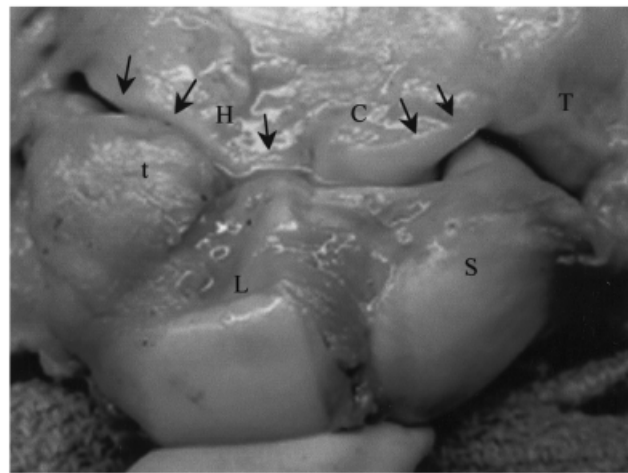
Of all the wrist bone similarities between African apes and humans, the fusion of the os centrale to the scaphoid has received the most commentary (e.g., Weinert, 1932; Schultz, 1936; Marzke, 1971; Jenkins and Fleagle, 1975; Lewis, 1974, 1985; Sar-

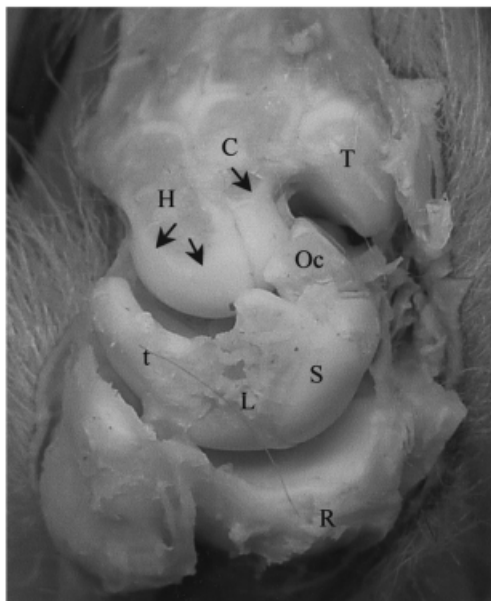## *Pan*

Flexed
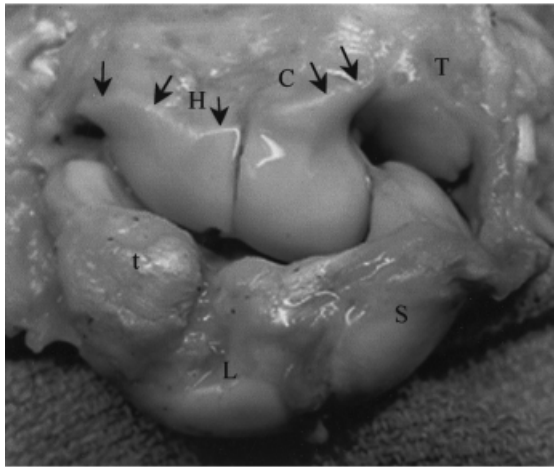
Extended

Hylobates
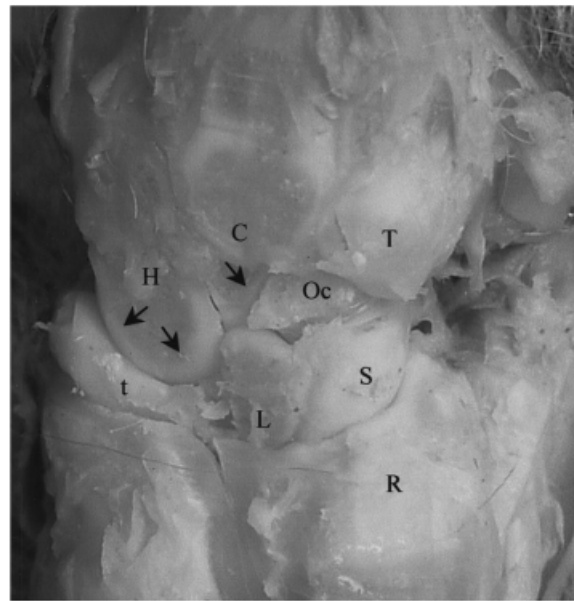
Flexed

Neutral

Fig. 7. Dorsal views of wrists of chimpanzee (top) and gibbon (bottom) cadavers. Note breadth of the chimpanzee midcarpal joint compared to the narrower, ball-and-socket shape in the gibbon. African apes, as seen in the chimpanzee here, have flat to concave dorsal joint surfaces of the capitate and hamate (dorsal margins indicated by arrows), often with pronounced ridges that help limit further extension (see extended wrist posture, right). In gibbons, the dorsal portions of the capitate and hamate joint surfaces are more rounded, and lack these buttressing structures (arrows, flexed and neutral wrist postures, left and right, respectively). R, distal end of radius; S, scaphoid; L, lunate; t, triquetrum; Oc, os centrale; T, trapezoid; C, capitate; H, hamate.

miento, 1988; Begun, 1992, 1994; Tuttle, 1992; Gebo, 1996; Schwartz and Yamada, 1998; Richmond and Strait, 2000). The os centrale or the centrale portion of the scaphoid in anthropoids articulates distally principally with the capitate disto-medially and 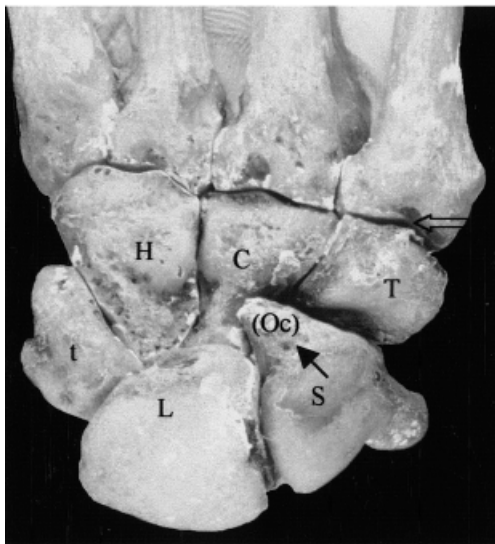the trapezoid disto-laterally (Fig. 7, 8). In most *Pongo*, *Hylobates*, and cercopithecids, the scaphoid is excluded from articulation with the capitate, and therefore does not contribute to the midcarpal joint (Fig. 7, 8). In these taxa, the os centrale articulates with the capitate medially and supports the trapezoid disto-laterally.
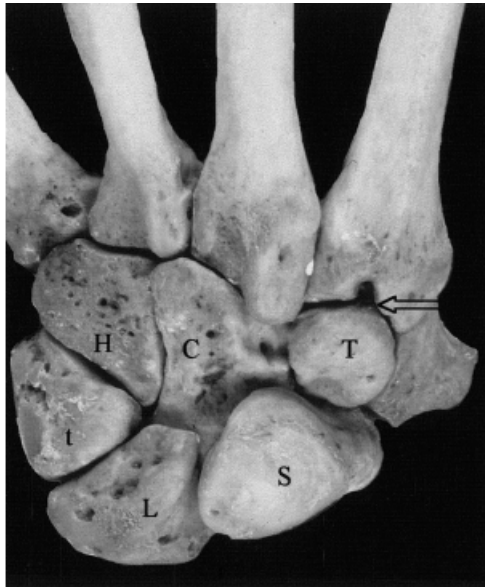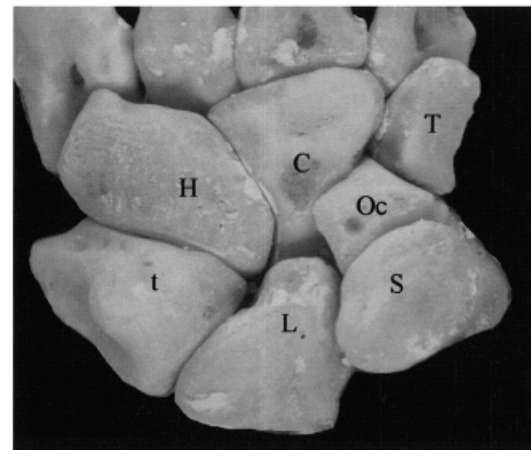
Homo
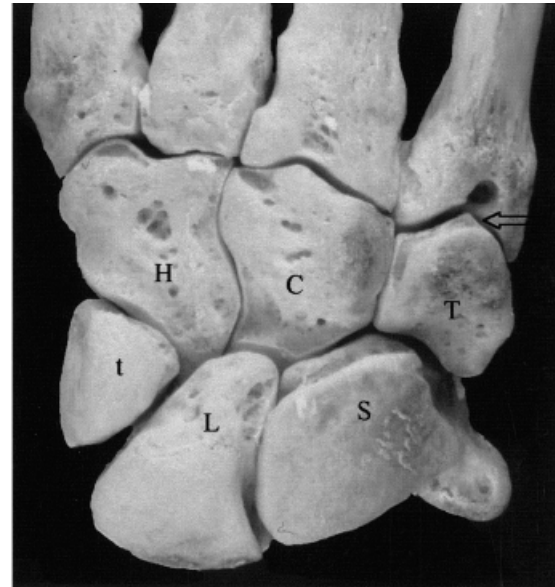
Pan

Pongo

Papio

Fig. 8. Dorsal views of some catarrhine left wrists in extended midcarpal postures, scaled to maximum carpal breadth. Top row from left, *Homo* and *Pan*. Bottom row from left, *Pongo* and *Papio*. Note dorsal beak (arrow) on the *Pongo* scaphoid, representing a fused os centrale in this individual. Os centrale fusion in *Pan* and *Homo* does not produce such a beak, instead reinforcing the joints between the scaphoid, and the capitate and trapezoid distally. Note also the irregular joint surfaces of the carpo-metacarpal joints (especially the joint between the trapezoid and second metacarpal, indicated by open arrow) in *Homo* and *Pan* and their more continuous contours in *Pongo*. See Figure 7 for abbreviations and text for discussion.

The trapezoid, which supports the second metacarpal, is firmly attached to the trapezium, which supports the first metacarpal. Therefore, the os centrale is essentially functionally wedged between the first and second metacarpals laterally and the third metacarpal medially, and transmits forces coming from both these directions, i.e., grips and other loads between the thumb and the ring-middle fingers. Strong ligaments are sufficient to respond to shear stress at the scaphoid-centrale joint in most pri-

mates, which have unfused scaphoids and centrales. However, in African apes and humans it appears as if shear across the scaphoid-centrale joint due to loading, especially along the third and second metacarpals, has selected for fusion of these bones. With the fusion of the centrale to the scaphoid there is a solid bony wedge directly connecting the radius to the second and third metacarpals via the incisure of the capitate, into which the centrale portion of the scaphoid fits, and the second metacarpal, via the trapezoid.

Knuckle-walkers load their hands and wrists in compression, and experience compressive and shear stresses between the bones of their wrists as their intermediate phalanges strike the ground, first with their fourth digits, and then rolling onto their third and second digits. The trapezoid facet of the scaphoid in African apes and humans (the centrale portion) is oriented normal to the long axis of the second metacarpal, suggesting a reorientation in response to compression along the axis of this bone (Fig. 8). The trapezoid, to which the second metacarpal primarily attaches, is also highly modified in African apes and humans compared to Asian apes (see below). During knuckle-walking, African apes often contact the ground first with their fourth or fifth middle phalanges (Wunderlich and Jungers, 1998). As weight is transferred from the ulnar digits to the radial digits, compression along the metacarpals would lead to shear stresses between the carpals in the distal row. Shear stress between these carpals, and between the carpals and the metacarpals, in knuckle-walkers may account for other changes in the joints between these bones that are discussed below. With regard to the proximal carpals, fusion of the os centrale to the scaphoid in knuckle-walkers is probably related to shear across the joint in an extended wrist loaded in compression with rolling from the fourth to the second ray.

Schultz (1936) and others noted that hylobatids and *Pongo* occasionally fuse their os centrales to their scaphoids but only relatively late in ontogeny, well after normal loading in adult locomotion (Fig. 8). In contrast, African apes and humans nearly always fuse these bones before they are loaded, in most cases in utero or perinatally. Fusion of these bones in African apes and humans is therefore an aspect of their developmental programming, and is not an epigenetic response to loading. Instances of nonfusion are in fact rare. While Schultz (1936) was correct in noting the significance of the difference in timing of fusion of the centrale and scaphoid in African apes vs. humans, this difference (humans tend to fuse the bones earlier) is probably less important than the fact that other hominoids do not fuse these bones until they load them, and then only rarely. The fact that Asian hominoids occasionally fuse these bones under different circumstances is not an indication that early fusion of these bones in African apes and humans is not homologous.
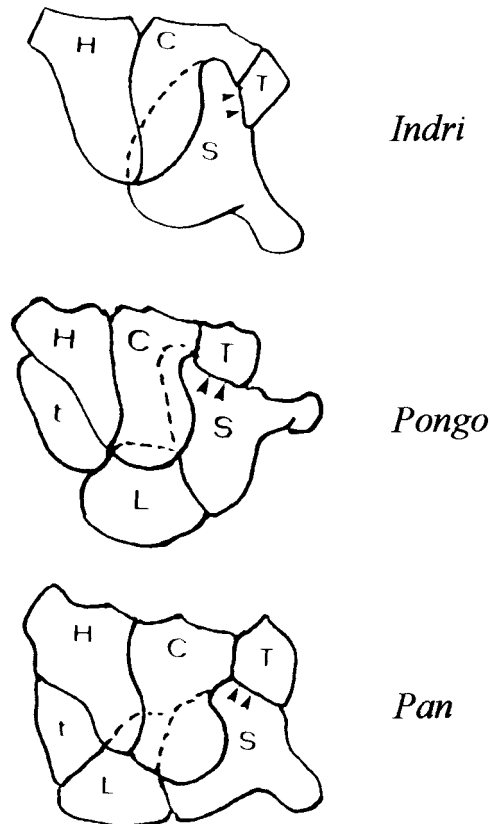

Fig. 9. Schematic drawings of dorsal views of left wrists of an indriid (*Indri*), *Pongo* (with a fused os centrale), and *Pan*, drawn to comparable carpal breadths. Dotted lines represent dorsal superpositioning of bones. Arrows point to joint surface between the scaphoid and the trapezoid. See Figure 7 for abbreviations and text for discussion.

Some indriids have also fused the os centrale to the scaphoid (Schwartz and Yamada, 1998; Hamrick et al., 2000) (Fig. 9). These authors note that because the fusion of the os centrale is not universal in indriids, and even varies within one indriid taxon (2 of 9 *Paleopropithecus* described by Hamrick et al. (2000) did not fuse these bones), the early fusion of the os centrale has no clear functional significance or locomotor distribution. However, it is unlikely that fusion of these bones simply occurs randomly in primates. If that were the case, one would expect it to have a broader distribution than in only two clades of primates, indriids, and the African ape and human clade. *Paleopropithecus* is unusual in having a relatively high frequency of each condition (fused and unfused), although the small sample size makes the significance of this finding unclear. All other primates that commonly fuse the centrale rarely have this element unfused (*Avahi*, *Indri*, *Lepilemur*, *Babakotia*, *Pan*, *Gorilla*, and *Homo*). While Schwartz and Yamada (1998) dismissed the difference in timing of fusion between African and Asian apes, and implied that there is no real difference in frequency, fusion is much more rare in Asian apes and confined to older individuals (Schultz, 1936, and personal observations). In most indriids, os centrale
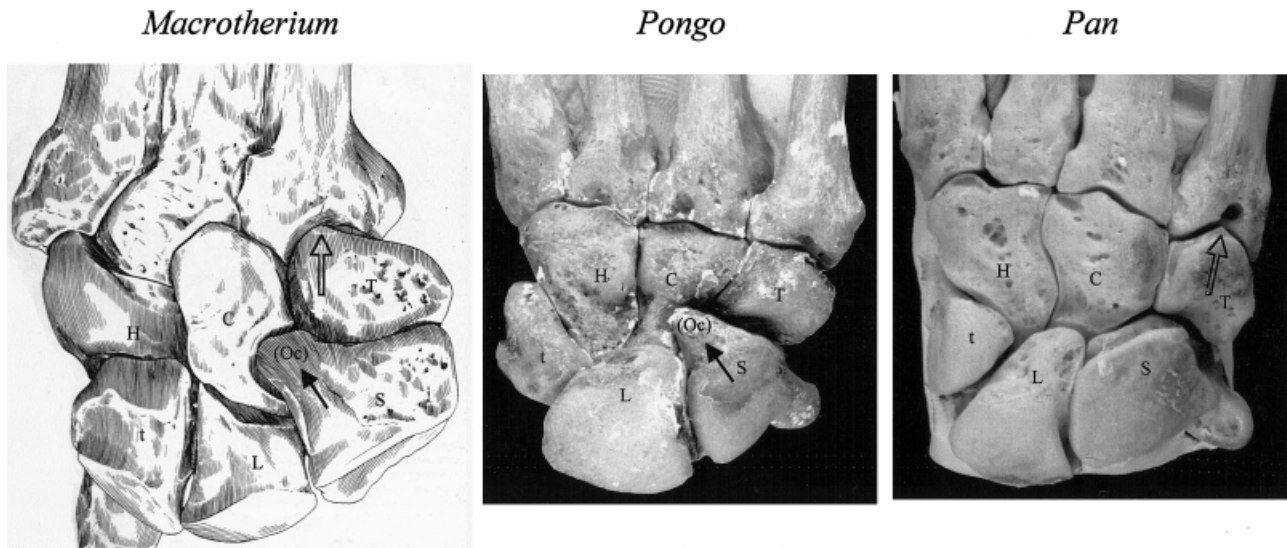
Fig. 10. Dorsal views of left wrists of *Macrotherium*, *Pongo*, and *Pan*, showing a number of convergent features. Arrows indicate fused os centrale, and open arrows denote the trapezoid keel. See Figure 7 for abbreviations and text for discussion. View of *Macrotherium* modified from Zapfe (1979).

fusion to the scaphoid is associated with a radial orientation of the facet for the trapezoid, which may be a response to compression along the long axis of the first metacarpal, which is large in these vertical climbers and leapers (Fig. 9). It is not known, to our knowledge, at what point in ontogeny this fusion occurs, but the fact that it is not reported to vary in the indriids that have this condition suggests that it is probably a feature that appears early. It may well be a similar response to that seen in African apes and humans, in which the fused os centrale stabilizes the trapezoid along the long axis of the second metacarpal. In indriids, the fused os centrale reorients the trapezoid facet radially, probably in response to transverse shear, such as might be generated by a powerful, strongly divergent pollex opposing the other metacarpals in a powerful grasp. *Paleopropithecus* may sometimes lack this feature because the articular surface for the trapezoid is small (Hamrick et al., 2000). This in turn may relate to the presence of a number of wrist and hand specializations associated with the development of hook-like hands in these primates, and the possible reduced relative importance of pollical grips.

Therefore, stabilization of the radial-side carpals in order to maintain a very powerful grip generated by a large and highly divergent pollex, as seen in some indriids, may be another reason to fuse the os centrale to the scaphoid in primates. In fact, it has been argued that fusion of the os centrale to the scaphoid serves this function in humans (Marzke, 1971). However, the absence of other indriid forelimb characters in African apes and humans, and the absence of a large pollex in African apes, suggests that the indriid model does not effectively account for the suite of features seen in African apes, just as the absence of African ape and human characters in indriids suggests that a knuckle-walking

ancestry is not a good explanation for indriid forelimb morphology.

There are reasonable explanations for fusion of the os centrale in primates that generate high levels of shear stress between the scaphoid and the centrale, whether proximo-distally (African apes and humans) or transversely (most indriids), but the more interesting questions may concern why it is variable in *Paleopropithecus* and why it does not occur in indriids (e.g., *Propithecus*) that otherwise have similar hands to those that have a fused os centrale. We also do not know why the os centrale on occasion fuses in *Pongo* and *Hylobates* with age (but see below). These questions and others that relate to the ontogeny of the carpus in indriids require further study. However, the premise that fusion of adjacent carpal bones related to elevated shear is to be expected in mammals is illustrated below in the example of a nonprimate that has converged on the African ape pattern anatomically, functionally, and behaviorally.

The example of convergence is another mammal that retains most of the primitive elements of mammalian forelimbs, and has a hand that is modified into a hook-like appendage with features for terrestrial quadrupedalism. It is found in the morphology of chalicotheres, an unusual family of extinct perissodactyls. Zapfe (1979), in his exceptional monograph on *Chalicotherium grande* (now attributed by many to *Macrotherium grande*), illustrates the complete carpus, articulated manus, and articulated skeleton. The parallels to the skeletal morphology of African apes and humans are striking (Fig. 10).

There are, of course, many dramatic differences between the hands of chalicotheres and hominoids related to differences in evolutionary history and functional anatomy. Like other "hook-handed" mammals (e.g., South American tree sloths, order

Xenartha), *Macrotherium* has long metacarpals, very short proximal phalanges, and greatly enlarged and elongated terminal phalanges. Xenartha are superficially similar to African apes and distinct from *Macrotherium* in having elongated intermediate phalanges, but in the case of the South American taxa, unlike hominoids, the intermediate phalanges are as long as or longer than the metacarpals. In both nonprimate groups, it is the terminal phalanges that bear the bulk of body mass, in contrast to African apes in which it is the proximal and especially the intermediate phalanges. Other critical differences from African apes include the fact that *Macrotherium* had only three hand digits (rays 2–4), as in *Bradypus* (the three-toed sloth; *Choloepus*, the two-toed sloth has also lost the fourth ray), and a further reduction or fusion of carpal bones (*Macrotherium* lacks a trapezium, and in *Choloepus* it is fused to the first metacarpal; Mendel, 1985). However, *Macrotherium*, which appears to have loaded its forelimb in a flexed digitigrade posture similar to that of African apes (Zapfe, 1979), has a number of surprising similarities to African apes not found in the highly suspensory sloths.

The wrist of *Macrotherium* retains the same bones with roughly similar morphology as found in African apes and humans (except the trapezium, not surprising given that chalicotheres had no thumbs). Among the more detailed similarities to African apes and humans are the comparatively large scaphoid, the distally projected and robust hamate hamulus, the distal orientation of the facets of the proximal carpals for the distal carpals, and the irregular morphology of the facets of the distal carpals for the metacarpals (Fig. 10). In dorsal view, a deep facet on the capitate articulates dorso-laterally with the centrale portion of the scaphoid, a mechanism very similar to that seen in African apes and humans to restrict excessive extension at the midcarpal joint. The "jagged" morphology of the carpo-metacarpal joint is also obvious in dorsal view, including such detailed similarities to African apes and humans as the strongly keeled trapezoid deeply notched second metacarpal and the strongly divergent facets for the third metacarpal on the capitate (see below). The hamate receives the base of the third and fourth metacarpal in this perissodactyl that lacks the fifth digit, but is otherwise functionally similar to the African ape and human hamate, with divergent facets for the fourth and fifth metacarpals. The capitate is not waisted mediolaterally as in African apes and fossil humans. African apes and fossil humans have transversely very broad capitate heads, probably to maintain joint congruence in wide ranges of pronation and supination. *Macrotherium* had much less mobility in the wrist, as is typical of ungulates, and lacked a transversely broad capitate, but achieved the same stabilizing effect with proximodistal waisting (the capitate of *Macrotherium* has deep notches proximally and distally providing a structural link between the lunate and third metacarpal; Zapfe,

1979). Perhaps the most striking convergence between African ape/human wrists and those of chalicotheres is the fusion of the os centrale to the scaphoid, represented by a prominent dorsal process (Fig. 10). Interestingly, when *Pongo* fuses the os centrale to the scaphoid, a very similar morphology results, with a prominent, pointed process positioned dorsally over the capitate (Fig. 10). Other basic similarities to hominoids in the skeleton of *Macrotherium* include a semierect vertebral column, reduced number of lumbar vertebrae, broad ilium, long forelimbs, short hindlimbs (intermembral index = 141), reduced brachial index (83), increased range of elbow extension, supination set at the wrist, and short, stout metacarpals (compared to forelimb long bones, but not compared to the phalanges) (Zapfe, 1979).

The distal carpals have also undergone considerable changes related to knuckle-walking in the common ancestor of African apes and humans. The capitate is the most obviously modified bone, with a broad, short head, strongly developed waisting between the head and distal portion of the bone, and a complex joint surface for the third metacarpal. Dorsally, the nonarticular surface of the capitate in African apes and humans is expanded, such that the lunate cannot rotate dorsally on the capitate to the same extent as is possible in Asian apes or even in digitigrade monkeys like baboons, which also must place a premium on limiting extension at the midcarpal joint (Fig. 8). The head of the capitate, which forms most of the ball of the ball-and-socket midcarpal joint in African apes and humans, is broad transversely and, in African apes and fossil humans, separated from the distal portion by a deep notch, contributing to a waisted morphology (Bush et al., 1982; McHenry, 1983; Ward et al., 1999a) (Fig. 8). The centrale portion of the scaphoid fits into the embrasure formed by the capitate notch medially and the trapezoid laterally, and is close-packed in dorsiflexion (extension) (Lewis, 1989). This configuration contributes to limiting extension at the midcarpal joint in African apes and humans. As with the hamate and the trapezoid, the capitate's metacarpal articular surface is more complex than in Asian apes and other catarrhines (see below). McHenry (1983) stresses the chimpanzee-like morphology of australopithecine capitates, and this is supported by newer material described in Ward et al. (1999a,b). McHenry (1983) interprets australopithecine chimpanzee-like capitate characters to be retained primitive characters, and at least one of these features, a waisted capitate neck, is functionally consistent with knuckle-walking. Ward et al. (1999a,b) also describe a "keel" on the capitate head that may correspond to the lengthy lunate-scaphoid ridge that Corruccini (1978) considered to be a knuckle-walking adaptation.

Carpometacarpal joints. African ape and human distal carpal bones have modified distal articular surfaces for the bases of the metacarpals. The

trapezoid is a relatively large bone in African apes and humans (Sarmiento, 1985). In addition to having a proximally oriented proximal surface for the centrale portion of the scaphoid, the trapezoid in African apes and humans has a strongly keeled distal articular surface that fits tightly into a deep notch on the base of the second metacarpal (Fig. 8). This notch-keel morphology is further reinforced by the facet on the trapezium that articulates medially with the enlarged lateral tubercle of the second metacarpal. *Pongo* has a flatter distal trapezoid joint surface that is continuous with a relatively large, concave facet for the second metacarpal on the trapezium, which together match the broad, transversely convex joint surface of the orangutan second metacarpal (Fig. 8). While hylobatids and other anthropoids have a more restrictive trapezoidal-second metacarpal joint than orangs, none have the complex keel-notch pattern seen in African apes and humans.

This theme is continued medially. The large facet for the third metacarpal on the capitate is keeled along the dorsal half of the joint surface in African apes and fossil humans, while it is broadly rounded in *Pongo* and other anthropoids (Fig. 8). McHenry (1983) described a distal cupping morphology of this surface, which is probably related to the keeling described here, and he attributed this morphology to a mechanism to stabilize the wrist in knuckle-walking postures (see below). He also noted that "cupping" does not occur in the australopithecines he examined (*A. afarensis* and *A. africanus*), though it does appear to have been present in other specimens of *Australopithecus* (Ward et al., 1999a,b). While there are other important differences in the capitate distal articular surfaces between fossil humans and African apes (Bush et al., 1982; Marzke, 1983; McHenry, 1983; Marzke et al., 1992; Ward et al., 1999a), they all share this keeled morphology, which is lost in later humans. The distal articular surface of the hamate is also keeled in African apes and fossil humans, separating to some degree the facets for the fourth and fifth metacarpal bases, which are thus somewhat divergent (Bush et al., 1982; Marzke, 1983; Ward et al., 1999a). *Pongo* and other anthropoids have more smoothly concave joint surfaces, with less or no distinction between the metacarpal joint surfaces (Fig. 8).

A keeled articular surface for the metacarpal bases in African apes and fossil humans, and a corresponding series of notches on the metacarpals, contribute to a transversely "jagged" carpo-metacarpal joint that is probably related to resistance to movement at these joints, such as would be generated during the stance phase of knuckle-walking as body mass transfers across the carpo-metacarpal joints (Marzke, 1983; Marzke et al., 1994; McHenry, 1983). The high incidence in African apes and humans of type III fourth carpometacarpal joints, in which the fourth metacarpal lacks contact with the capitate and the third and fourth metacarpal bases

are offset relative to one another, contributes to the irregularity of the carpometacarpal articulations (Marzke et al., 1994).

Metacarpophalangeal joints. Some of the clearest adaptations for knuckle-walking appear in the metacarpophalangeal joints (Tuttle, 1967; Jenkins and Fleagle, 1975; Susman, 1979). The metacarpal head is expanded dorsally to permit extension of the proximal phalanx until the phalanx contacts a dorsal ridge that prevents further extension and thus stabilizes the joint (Fig. 11). The metacarpal head is also wider dorsally than palmarly, a mechanism that acts to tighten collateral ligaments during extension (Susman, 1979). Recent research reports another probable character in this metacarpal head complex. In knuckle-walkers, the dorsal half of the metacarpal head has a larger radius of curvature (i.e., is flatter) than the ventral half (Zylstra, 1998, 1999), indicating that the dorsal half is adapted for stability relative to the palmar half (Hamrick, 1996). Together, these features show that the African ape metacarpal head is functionally differentiated into regions emphasizing mobility during flexed finger postures, and stability in hyperextended postures.

Although it has been noted by many researchers that early hominin metacarpals lack some of these features (Bush et al., 1982; Tuttle, 1981; Stern and Susman, 1983; Ricklan, 1988; Susman and Stern, 1979; Ward et al., 1999a), these authors acknowledge that the absence of these features does not refute the knuckle-walking hypothesis, because these features are often not present in extant knuckle-walkers (Susman, 1979, #109; Shea and Inouye, 1993, #2244; Inouye, 1994a,b, #8140). Furthermore, early hominins were not knuckle-walking, so it is not surprising that they lack some of the features of their knuckle-walking ancestors (Begun, 1993a).

Although less frequently discussed, most metacarpophalangeal features are also problematic because they are not specific to knuckle-walking anthropoids (McCrossin and Benefit, 1997). Some metacarpal characteristics also occur in terrestrial digitigrade anthropoids, such as large individuals of *Mandrillus* and *Papio* (Fig. 11). The dorsal ridge, the expanded and flattened dorsal articular surface, and the dorsally widened metacarpal head are adaptations for stability in extended metacarpophalangeal joints, a posture employed both by knuckle-walkers and digitigrade terrestrial anthropoids such as baboons and patas monkeys. Therefore, if these features are found in early hominins, they would provide evidence of a terrestrial ancestor, but these traits alone would not resolve digitigrady from knuckle-walking. In fact, many of the features related to compressive weight-bearing and the limitation of metacarpophalangeal and wrist extension could, theoretically, be useful adaptations in a digitigrade quadruped (Sarmiento, 1988). The recent report of African-apelike features of the metacarpal head and radius of *Equatorius* (*Kenyapithecus*) from Maboko Island (Mc-
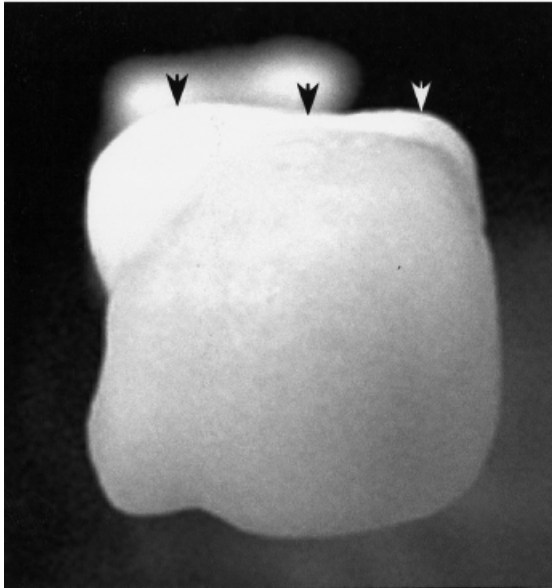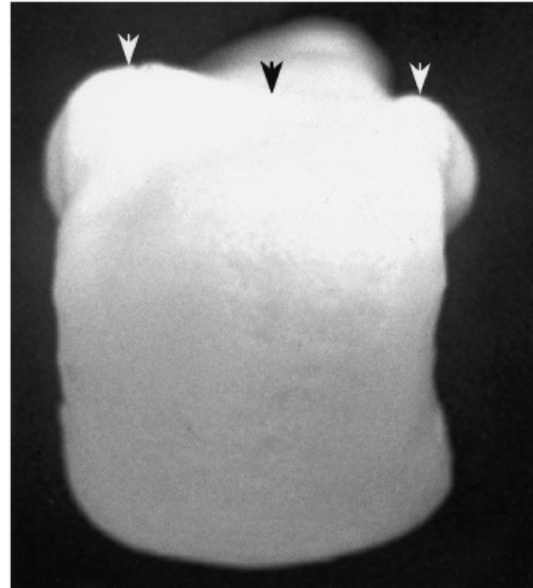
Papio   *Gorilla*

Fig. 11. Distal views of fourth metacarpal heads of *Papio* (left) and *Gorilla* (right). Note dorsal ridge (top) on both specimens. The dorsal ridge (arrows) helps to limit further extension of the metacarpophalangeal joint, and to transmit stresses in an extended joint posture.

Crossin et al., 1998), in an otherwise cercopithecoid-like semiterrestrial skeleton (McCrossin and Benefit, 1997), supports this idea. However, the African-apelike affinities of these postcranial fossils have yet to be established. Furthermore, there is little evidence to suggest that the LCA of African apes and humans evolved from a digitigrade terrestrial ancestor (see above). If the extension-limiting and dorsal stability features are found in future hominin metacarpals, or their immediate ancestors, phylogenetic context would make knuckle-walking a far more likely interpretation. The total morphological pattern can clearly distinguish knuckle-walking from other forms of terrestriality.

Middle phalanx and proximal interphalangeal joints. By definition, "knuckle-walking" involves a unique role of the middle and proximal phalanges in weight support. It is a surprise, then, that no clear knuckle-walking adaptations are known in these bones. One potential adaptation in this region is middle phalanx elongation to provide a large area of support both to increase stability and reduce the stresses placed on the middle phalanges (Begun, 1993a, 1994). African apes and humans have long middle phalanges, relative to proximal phalanx length, as compared to orangutans (Begun, 1994), but it is possible that orangutans are the specialized ones in having long proximal phalanges. One would also expect the dorsal surface of the middle phalanx shaft to be fairly straight, to distribute weight-bearing forces evenly across the bone surface. To our

knowledge, no analyses have been undertaken to examine these features.

The middle phalanges are more strongly flexed during knuckle-walking than during other forms of hand use. The range of flexion is potentially limited by joint capsular structures, tension along the extensor hood, and the point at which the base of the middle phalanx contacts the palmar surface of the proximal phalangeal shaft just proximal to the trochlea. The trochleae of chimpanzee and gorilla proximal phalanges tend to be very deep palmodorsally relative to shaft depth, and this is consistent with a high degree of flexion at the proximal interphalangeal joints. This morphology could be useful in discriminating knuckle-walking from other forms of hand use, but requires confirmation with kinematic data on hand use, comparative data on joint ranges of motion, and morphometric data on a broad sample of anthropoid phalanges.

Summary and recent fossil evidence

In summary, the comparative anatomy of extant anthropoids and fossil hominins suggests that humans evolved from a knuckle-walking ancestor. Pedal features suggest a terrestrial ancestor. Upper limb and trunk features are consistent with some form of climbing, whereas other upper limb features are consistent with terrestriality and, in a variety of ways, knuckle-walking (Table 3). The terrestrial features are inconsistent with a purely arboreal ancestor, either a quadruped or climber (including a hy-

TABLE 3. *Anatomical traits thought to be functionally related to terrestriality, or specifically to knuckle-walking, in African apes, and distribution of these traits in hominins*[1]

Traits	Description	Presence in hominins
Shoulder and arm		
T	High humeral head torsion	MH (not EH?)
T	Extension of distal margin of capitulum onto posterior aspect of humerus	EH
Wrist		
KW	Distal projection of dorsal radius (related to "volar slant")	EH
T	Coplanar scaphoid-lunate surfaces	EH
KW*	Intermediate to large, dorsally oriented scaphoid notch	All
T	Large ulnar head	All
T	Well-formed triangular articular disc	MH (all?)
T	Elongate, rod-like (and palmarly oriented) pisiform	EH
KW*	Fused os centrale	All
KW	Enlarged trapezoid	MH (all?)
KW	Trapezoid facet of scaphoid oriented normal to second metacarpal long axis	MH (all?)
T	Broad proximal- and midcarpal joints	MH (all?)
KW	Dorsal ridges on capitate, hamate	None?
KW	Waisted capitate neck	EH
KW?, T?	Long proximodistal ridge on capitate head separating lunate and scaphoid facets	MH (all?)
KW	Large hamate spiral facet	MH (all?)
KW	"Keeled" metacarpophalangeal joints (e.g., with trapezoid)	MH/variable
KW	Type III fourth carpometacarpal joint	MH/variable
Metacarpals and phalanges		
T	Dorsal ridge on metacarpal head	None
T	Dorsal expansion of metacarpal head	None
T?, KW?	Metacarpal head wider dorsally than palmarly	None
KW?	Relatively long middle phalanges	MH (all?)

[1] T, terrestrial trait; KW, knuckle-walking trait; KW*, KW in context of other traits; MH, modern humans; EH, early hominins; all, all hominins. "All?" indicates that fossil evidence is absent or poorly known.

lobatian climber). The climbing features are inconsistent with a palmigrade or digitigrade terrestrial ancestor. Collectively, virtually all features are consistent with a knuckle-walking ancestor. Knuckle-walkers retain obvious anatomical specializations related to suspensory positional behavior in both their forelimbs and hindlimbs, and all knuckle-walkers are adept climbers as well. Compelling evidence from biomechanical studies as to the pre-adaptive nature of vertical climbing to bipedal walking (Prost, 1980; Stern and Susman, 1981; Fleagle et al., 1981; Senut, 1988) is fully consistent with an African-apelike ancestor that both knuckle-walked terrestrially and climbed trees.

Recent fossil discoveries from the late Miocene and earliest Pliocene promise to help test these hypotheses. White et al. (1994) mention a few characteristics (e.g., foramen magnum position) that might indicate bipedalism in *Ardipithecus*, but they acknowledge that more conclusive evidence requires the discovery and analysis of relevant postcranial remains. Likewise, the recently described fossils attributed to a newly erected subspecies of *Ardipithecus*, *Ar. ramidus kadabba* (Haile-Selassie, 2001), are not conclusive on the topic of bipedalism. The 5.5–5.77-My-old fragmentary fossils appear to belong to early hominins, based primarily on canine morphology. Although the 5.2-My-old proximal foot phalanx (AME-VP-1/71) is reported to have a dorsally canted proximal joint surface similar to that in Hadar specimens (Haile-Selassie, 2001), many Hadar specimens are not distinguishable from extant chimpanzees and gorillas in this feature (Duncan et al., 1994). Therefore, in the absence of quantitative comparisons or other fossil evidence, evidence for bipedality is not conclusive.

Published details of the forelimb remains of *Ardipithecus*, including a well-developed lateral trochlear ridge on the distal humerus and a chimpanzee-like strong angulation of the distal radius (White et al., 1994), are consistent with the knuckle-walking hypothesis. The lack of suspensory/climbing specializations more extreme than those of African apes (e.g., like those of Asian apes) does not support a hypothesis of a suspensory/climbing LCA that did not also practice terrestrial behaviors. For example, curvature of the manual and pedal phalanges of *Ardipithecus* most closely resembles the condition in some *A. afarensis* and chimpanzee individuals (Haile-Selassie, 2001).

Relevant forelimb remains from which to discern knuckle-walking adaptations are also lacking for the earliest putative hominin, *Orrorin tugenensis* (Senut et al., 2001). Therefore, *Orrorin* is currently silent on the locomotor mode of the *Pan/Homo* LCA. However, the available information regarding the *Orrorin* femora does not provide indisputable evidence of bipedalism. The femoral morphology (e.g., head breadth relative to shaft breadth) is consistent with both *Australopithecus* and *Pan*. The "intertrochanteric groove" apparently refers to the groove for the tendon of the obturator externus muscle. If so,

this groove, or similar smoothed areas, are found in primates with short ischia that extend their hips, which includes obligate bipeds, as well as other primates for which bipedalism is a relatively minor component of the locomotor repertoire (Stern and Susman, 1991). Nothing about the morphology of *Orrorin* rules out knuckle-walking, climbing, or bipedalism.

IMPLICATIONS FOR SCENARIOS ON THE ORIGIN OF BIPEDALISM

The most fundamental implication of having a knuckle-walking ancestor is that hypotheses purporting to explain the origin of bipedalism must explain why it would be advantageous for an already terrestrial ancestor to stand upright on two legs. Thus, hypotheses in which bipedalism was simply a consequence of a shift from arboreal to terrestrial travel would not hold. Instead, the selective agents for bipedalism must offered significant advantages over knuckle-walking.

Below, we consider existing scenarios on the origins of bipedalism in light of current information. Based on current paleoenvironmental evidence, what we know about the earliest hominins, and reconstructions of the LCA, some scenarios can be rejected while others remain tenable.

Reconstruction of the last common ancestor of *Pan* and *Homo*

Current evidence suggests that the body mass of the LCA of chimpanzees and humans more closely resembled that of *Pan* than those of hylobatids or gorillas. The high (near gorilla) levels of sexual dimorphism in all early hominins for which sufficient data are available, including *Australopithecus* (McHenry, 1986; Lockwood et al., 1996; Lockwood, 1999; Ward et al., 2001) and *Paranthropus* (Silverman et al., 2001), imply that strong sexual dimorphism in body size characterized the LCA. However, these taxa appeared millions of years after the LCA, so the reconstruction of the LCA as highly sexually dimorphic must await confirmation from earlier taxa. There is not yet enough information to determine whether or not canine dimorphism was as pronounced, but the reduced size of all hominin canines and all the moderate dimorphism of *Pan* and *Astralopithecus* canines suggests that it may have been somewhere in the range between *Pan* and *Australopithecus*. If the inference of strong body size dimorphism in the LCA is correct, then social groups were likely to have been polygynous, with high levels of male-male competition. The molar morphology of the earliest hominins resembles that of *Pan* in many respects, implying a similar, fairly frugivorous diet. A gorilla-like emphasis on folivory is unlikely. Aside from not having enamel as thick as the "hyperthick" enamel of *Paranthropus*, the degree of enamel thickness in the LCA remains a topic of debate (White et al., 1994; Senut et al., 2001; Haile-Selassie, 2001).

These characteristics would have been combined with a locomotor skeleton adapted for climbing, suspension, and knuckle-walking. Early hominins (especially those older than 4.2 Ma) are found in wooded habitats (Pickford and Senut, 2001; WoldeGabriel et al., 2001), suggesting that the LCA inhabited similar environments as well. There is no evidence that the LCA had tool-making and -using capabilities that were any greater than those seen in extant great apes.

Paleoenvironments

Most hypotheses of bipedal origins involve scenarios in which bipedalism is seen as an adaptation, at least in part, to environmental conditions. The rate and extent to which a global cooling and drying event occurred in the late Miocene are a matter of debate (Kingston et al., 1994; Cerling et al., 1997). However, there is evidence (e.g., in airborne dust records) of substantially cooler and drier intervals in eastern Africa between 5–7 Ma (deMenocal and Bloemendal, 1995). Such climatic intervals would involve expansion of open environments. In near-equatorial areas of Africa, forests would fragment during these intervals, producing mosaics of dense forest, closed and open woodlands, and grasslands. It is during these times that populations of the *Pan/Homo* LCA are most likely to have become fragmented and isolated, conditions favorable to niche diversification and speciation (Brain, 1981).

Between 3.5–8 My, sites in eastern and southern Africa were home to environments that ranged from relatively closed forests (e.g., Tugen Hills, Kanam, Middle Awash, and Sterkfontein) to savanna mosaic habitats (e.g., Lothogam, Kanapoi, and Laetoli). The range of environments recorded during the late Miocene in eastern Africa leaves open a wide range of potential habitats for the earliest hominins. The key questions concern what habitats were favored by the LCA, and by the earliest bipeds. Answers to these questions will require that paleoenvironmental data correspond precisely with hominin fossils, especially in light of environmental variability over time in eastern Africa (Potts, 1998).

Current paleoenvironmental evidence suggests that the earliest bipeds, and perhaps the LCA, are typically found in habitats that were wooded to at least some degree. Data over the past couple of decades show that *Australopithecus* fossils are found in a variety of paleoenvironments, making it unlikely that a move to open grassland habitats was critical to the origin of bipedal gait (Hill, 1987; Kingston et al., 1994; Potts, 1998, and references therein). The strongest support for the idea that bipedalism originated in wooded environments comes from the paleoenvironmental data accompanying recent fossil discoveries of *Orrorin*, *Ardipithecus* at 4.4 Ma, and what has been attributed to an early form of *Ardipithecus* over 5 My old (WoldeGabriel et al., 1994, 2001; Pickford and Senut, 2001). However, at present, these discoveries offer only a few data

points, and evidence for bipedality is not conclusive, precluding any broad conclusions about the paleoenvironments preferred by the earliest bipeds.

Although the phylogenetic status of *Orrorin tugenensis* is not yet certain, its anatomy suggests that it lies close to the LCA (Senut et al., 2001). Depending on whether it is an early member of the hominin clade, panin clade, a sister taxon to the LCA, or the LCA itself, the fact that it is found in a context with signs of open woodland and more densely wooded areas may support the idea that wooded environments were important in early human origins.

Additional evidence of the importance of woodland habitats to very early hominins comes from the western margin of the Middle Awash, where hominins are found in wooded environments, and are scarce in otherwise fossiliferous sediments from more open environments (WoldeGabriel et al., 2001). The precise relevance of the paleoenvironmental information depends on whether or not this hominin is in fact adapted to bipedalism. The earliest undisputed biped, *A. anamensis* (Leakey et al., 1995; Ward et al., 2001), is found in a wider range of habitats. Micro- and macrofauna at Kanapoi indicate dry, possibly open, bushland or woodland conditions, although gallery forests at Kanapoi and Allia Bay would have accompanied the rivers responsible for the deposits (Leakey et al., 1995; Wynn, 2000). Thus, early members of the genus *Australopithecus* typically inhabited environments with or near tree cover, but were not restricted to woodlands, as may have been the case for *Ardipithecus* (WoldeGabriel et al., 2001).

Scenarios that can be rejected

Evidence that bipedalism evolved from a knuckle-walking ancestor allows us to reject scenarios that rely on a strictly arboreal ancestor. These include scenarios in which bipedalism arose from an ancestor with forelimbs that were poorly suited to bear compressive weight support (Reynolds, 1985), and models in which terrestrial bipedality was the terrestrial elaboration of arboreal bipedality (Tuttle, 1975, 1981). A knuckle-walking ancestor, along with other data, allow us to reject the hypothesis that bipedality evolved as an adaptation to ambush predation in arboreal environments (Eickhoff, 1988). Essentially, a knuckle-walking ancestor precludes all hypotheses that posit a purely arboreal ancestor (Napier, 1964; Tuttle, 1975; Stern, 1975; Prost, 1980; Hunt, 1996).

The fact that the earliest hominins are not typically found in open grassland environments contradicts long-standing "savanna" hypotheses that place the agents of selection for bipedality on open grasslands (these hypotheses have been questioned by researchers, such as Washburn (1967), since at least the late 1960s). There are many savanna-based hypotheses on the origin of bipedalism (Rose, 1991). Those that rely on the earliest hominins primarily inhabiting or feeding in grasslands may be rejected

if the current patterns of finding early hominins in more wooded paleoenvironments are confirmed. For example, the available paleoenvironmental data contradict the hypothesis that bipedality arose as an adaptation to long-distance travel to scavenge from migrating ungulate populations (Sinclair et al., 1986). Other hypotheses involving foraging in open, grassy environments are similarly weakened or are no longer tenable (e.g., Jolly, 1970). If the earliest hominins were not often in very open habitats, then sun exposure also could not have been the major selective factor for the origin of bipedalism (Wheeler, 1991).

However, not all "savanna" hypotheses can be rejected. In a regional context in which open areas were spreading, bipedalism may have been an effective means of moving through patches of open terrain while maintaining a forest or woodland life (Rodman and McHenry, 1980; Isbell and Young, 1996). Similarly, one could argue that a locomotor repertoire of bipedalism and climbing provided a versatile locomotor strategy that accommodated settings with many or very few trees; such a strategy would be useful in times of environmental variability (Potts, 1998). These hypotheses, however, should now also explain the advantage of bipedalism over knuckle-walking in achieving these goals. Rodman and McHenry (1980) pointed out that human bipedality is more efficient than chimpanzee knuckle-walking, but further research is needed to assess whether or not the earliest bipeds would have enjoyed energetic efficiency or economy over knuckle-walking (Steudel, 1996).

Of course, the paleoenvironmental data associated with the earliest hominins do not preclude open habitats from playing an important role in the later evolution of bipedalism. *Australopithecus* fossils are often found in paleoenvironmental contexts that are more open (if not savanna) than those so far described for *Ardipithecus* and *Orrorin*. Indeed, it is likely that the process of increasing commitment to bipedality involved an extended and complex opening of habitats, rather than a single, abrupt transition from dense forest to open savanna (Rose, 1991). If the earliest hominins exhibit more primitive forms of bipedalism than that of *Australopithecus*, then the differences in paleoenvironments favored by these taxa may have played a role in bipedal refinements of *Australopithecus*. Much later, early members of the genus *Homo* became associated with open grasslands. By 1.5 Ma, the Nariokotome skeleton provides clear evidence that *H. ergaster* was adapted to a hot, arid climate and long-distance bipedal travel (Ruff and Walker, 1993). Thermoregulatory advantages and locomotor efficiency, for example, may not have been key to the origin of bipedality, but bipedality, along with slender body form and larger body mass, may have offered these advantages in later periods of human evolution (Carrier, 1984; Wheeler, 1993).

Levels of sexual dimorphism in early hominins also bear on a number of bipedal origin scenarios. Although fossil evidence of the earliest hominins is still sparse, the fact that high levels of size dimorphism characterize *Australopithecus*, *Paranthropus*, and early *Homo* is not consistent with monogamy in these hominins. It also suggests that the earliest bipeds did not have monogamous social groups (Foley and Lee, 1989), contradicting an important foundation for some hypotheses, such as the well-known and elaborate male provisioning hypothesis of Lovejoy (1981).

Tenable scenarios

Most existing scenarios explaining the origin of bipedalism cannot be rejected in light of the anatomical, social, and paleoenvironmental conditions discussed above. Indeed, many scenarios are difficult or impossible to test. While untestable hypotheses are not particularly useful, we are left with the unsatisfying possibility that one or more of them may actually be correct. It is beyond the scope of this discussion to review the multitude of remaining hypotheses, many of which are outlined in Rose (1991). Instead, we will discuss how the origin of bipedalism might be understood in the context of the diversification of African apes and humans from their common ancestors.

Modern primates live in complex environments, with considerable spatial and temporal variability. The same was almost certainly true for the earliest hominins. Indeed, paleoenvironmental data point to varied, but generally wooded habitats for the earliest hominins and their close relatives. The woodlands of the Middle Awash hominin fossil sites show that trees were spaced apart widely enough to allow sufficient sunlight through for grass to grow under the canopy. Isotope data indicate that grass constituted 20–45% of the biomass at hominin sites (WoldeGabriel et al., 2001). A large-bodied primate in an environment with discontinuous canopy cover would have no choice but to travel at least part of the time on the ground, especially in light of the larger day ranges of large-bodied primates.

Temporal variability in environments and habitat fragmentation associated with periods of cooling and drying produce mosaics of dense forest, woodlands, and grasslands (Potts, 1996, 1998). These factors are favorable to niche diversification in isolated populations. Within this ecological context, some apes maintained a forest-oriented adaptation, while others may have begun to exploit forest margins and grassy woodlands. Some unique aspects of gorilla and chimpanzee morphology and behavior may be related to the use of fall-back resources, which they can exploit during times of the year when other preferred resources are in low supply (Terborgh, 1983). Gorillas have a folivorous dentition and gastrointestinal tract, coupled with large body mass, even though many of them (especially lowland gorillas) consume up to as much fruit, and as many fruit species, as do chimpanzees (Remis, 1997). These folivorous adaptations allow them to subsist entirely on pith, herbaceous plants, and fibrous fruits when the preferred fleshy fruits are in low supply (Remis, 1997, and references therein). Although chimpanzees also use these fibrous foods, they rely more heavily on fruit as part of their diet. In times of fruit scarcity, chimpanzee groups fragment into smaller foraging parties to decrease daily travel distance (and its associated costs) and minimize intragroup competition for food resources (Tutin et al., 1991). In light of their reliance on fruits, it is possible that the long premaxillae and broad upper lateral incisors of chimpanzees (synapomorphies shared with hominins) are related to effectiveness in food processing (Ungar, 1994).

Hominin bipedalism is also likely to be an adaptation to some aspect of food acquisition, a point made by Jolly (1970) in his landmark paper on the "seed-eater" model. Eighty percent of chimpanzee bipedalism (the majority of which is postural) occurs during feeding (Hunt, 1994). Food acquisition is also the context in which baboons most frequently practice bipedalism (again, mostly postural) (Rose, 1976; Wrangham, 1980). Chimpanzees are most often bipedal when feeding on small fruits from small, open-forest trees (Hunt, 1994, 1996). The habitats reconstructed for the earliest hominins are consistent with the hypothesis of Hunt (1994, 1996). The advantages of bipedal standing to chimpanzees include a higher reach into short trees, thereby bringing more fruit within reach, and the ability to continuously gather fruit with both hands (Hunt, 1994). Since gathering, not consuming, is typically the slowest step, using both hands to gather food confers a real advantage to having free hands during bipedal posture.

Fossil and paleoenvironmental evidence shows that frugivory and relatively open woodlands were important components of early hominin paleobiology. A greater emphasis on foraging in these contexts, or heavy reliance on these food sources during low resource availability, may have led to increased postural and/or locomotor bipedality within the locomotor repertoire (Rose, 1991). This, in turn, could have led to bipedal adaptations in the earliest hominins (Wrangham, 1980; Rose, 1984, 1991; Hunt, 1994, 1996).

Carrying hypotheses also have some merit, but there must be clear advantages associated with carrying. Carrying infants (Etkin, 1954; Iwamoto, 1985) is unlikely to have been important, since there is no indication of infant altriciality in the earliest hominins, and their infants probably clung to their mother's hair, as is the case for most other primates (although African-ape mothers assist their infants in the first month or two). Most food items are not worth carrying because gathering is more time-consuming that ingestion (Hunt, 1994). Furthermore, for most food items (e.g., small fruits), it is difficult to manually transport more than a few at a time.

Foods worth carrying are those that are very energy-rich or fulfill a particular nutritional need, and that could be carried in large quantities (e.g., nuts or fruits attached to a stalk, meat) (Hewes, 1961; Garber, personal communication). If such a food source occurs in widely spaced patches, then it may become beneficial to carry the food while foraging in other locations, rather than returning the source in the near future. Provisioning could also play a role in this scenario, which would have social and reproductive advantages for the provisioning individual (Lovejoy, 1981). Foods that require extensive processing (e.g., some nuts) may also be worth transporting to a processing location. Conversely, processing tools (e.g., rocks) may be carried to food sources (Washburn, 1967; Boesch-Aschermann and Boesch, 1994). Hypotheses invoking hand use in tool-related activities (e.g., digging, throwing) also remain viable (Marzke et al., 1988).

Many food acquisition and carrying hypotheses remain tenable in light of current evidence. They offer advantages to bipedalism in an ape already adapted to terrestriality. Note that for these hypotheses to be tenable, they must demonstrate that the benefits of bipedal food acquisition or carrying must outweigh the costs of adopting a novel locomotor mode. Importantly, because knuckle-walking is an inefficient form of terrestrial locomotion (Taylor and Rowntree, 1973), the transition from knuckle-walking to bipedalism as a more dominant part of a locomotor repertoire would be less costly than it would be from other forms of locomotion.

AREAS OF FUTURE RESEARCH

New fossil discoveries of the earliest hominins, the LCA, and the detailed environmental contexts in which they occur are the only means to ultimately test the knuckle-walking and climbing hypotheses, given that the LCA undoubtedly continued to exploit arboreal environments. Even after the recovery of these fossils, major hurdles will remain in reliably identifying the LCA and basal panins and hominins (see, for example, the conflicting interpretations of Senut et al., 2001, and Haile-Selassie, 2001). Fossil taxa near the base of the African ape and human clade may differ by only a few subtle anatomical characteristics (Wood and Richmond, 2000).

Paleoenvironmental data of the LCA and the earliest bipeds will be crucial in testing hypotheses on the selective agents for the origin of bipedalism. It is particularly important that paleoenvironmental data be precisely linked with the loci in which the hominin fossils were buried. A paleolandscape approach will be most informative, by providing an indication of the spatial and temporal variability of paleoenvironments, where hominins occur within this context (and where they do not occur), and how hominin habitat preferences changed over time.

Just as detailed data on the paleoenvironmental contexts of the LCA and the earliest bipeds will be critical for testing hypotheses on the potential selective agents favoring bipedalism, data on extant primates in diverse ecological settings are needed to provide a framework within which to interpret the fossil record. Information on how African ape locomotor, feeding, social grouping, and other behaviors respond to various ecological conditions (e.g., relatively closed vs. open habitats, variation in seasonal availability of resources) will be particularly useful in this respect.

It is also critical that we understand the biomechanics and functional anatomy involved in knuckle-walking, climbing, bipedalism, and other forms of locomotion so that reliable interpretations of fossils are possible. Researchers do not fully understand how the anthropoid hand and wrist are used (e.g., in terms of kinematics or muscle activity) during locomotion, and how anthropoid skeletal anatomy relates to in vivo function. Existing studies do not agree with each other on interpretations of hand and wrist function and morphology (e.g., Tuttle, 1967; Jenkins and Fleagle, 1975; Lewis, 1989), and many hypotheses about functional anatomy remain untested. Integrating studies of morphology with those of in vivo function, following the early study by Jenkins and Fleagle (1975), promise to greatly improve our understanding of carpal functional anatomy and its significance in human evolutionary history.

Further research is also warranted on the biomechanics of bipedal postures and locomotion in the African apes. Given the generally apelike skeleton of the earliest hominins (McHenry, 1984; White et al., 1994), research into the commonalities of bipedal biomechanics among great apes will provide insight into the benefits, costs, and mechanics of bipedalism in the earliest hominin bipeds. Understanding the biomechanical bases underlying the *differences* in bipedality between the great apes will also be valuable in refining our abilities to make predictions from skeletal form.

Lastly, more research is needed on the genetic and epigenetic bases of skeletal morphology. Researchers disagree on how they expect ancestral morphology to be expressed in descendent taxa and, when primitive retentions occur, how best to interpret them. For example, *Australopithecus* metacarpals lack knuckle-walking features, but the variability in these features in African apes may be influenced by activity during growth. If so, one would not expect these traits to persist in nonknuckle-walking descendents. A better understanding of the influence of activity on morphology during development will provide a stronger basis from which to make predictions about morphological change in human evolution.

CONCLUSIONS

The weight of current evidence suggests that humans evolved from an ancestor adapted to knuckle-walking and climbing. This evidence includes terrestrial features in the hands and feet, climbing features throughout the skeleton, and knuckle-

walking features in the wrist and hand that are shared by African apes and humans, or by African apes and some early hominins. This allows us to narrow the list of possible evolutionary scenarios on the origins of bipedalism, because knuckle-walking is inconsistent with scenarios positing a purely arboreal ancestor. Evidence from the paleobiology and paleoenvironments of the earliest known hominins, and their close relatives, suggests that other hypotheses may be rejected, including those based on a monogamous social structure and those in which the selective agents for the origin of bipedalism occurred in open savanna environments. Food acquisition and carrying hypotheses deserve more attention, and would benefit from the construction of tests for these hypotheses. More research should be directed towards finding fossils of the *Pan/Homo* last common ancestor, and the earliest hominin bipeds, collecting carefully associated information on their paleoenvironments, and more closely examining the functional anatomy involved in extant anthropoid positional behaviors (especially climbing, knuckle-walking, and bipedalism).

ACKNOWLEDGMENTS

LITERATURE CITED

Aiello L, Dean C. 1990. An introduction to human evolutionary anatomy. London: Academic Press.

Ambrose SH. 2001. Paleolithic technology and human evolution. Science 291:1748–1753.

Andrews PJ, Martin LB. 1987. Cladistic relationships of extant and fossil hominoids. J Hum Evol 16:101–118.

Beard KC, Teaford MF, Walker A. 1986. New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. Folia Primatol (Basel) 47:97–118.

Begun DR. 1992. Miocene fossil hominids and the chimp-human clade. Science 257:1929–1933.

Begun DR. 1993a. Knuckle-walking ancestors. Science 259:294.

Begun DR. 1993b. New catarrhine phalanges from Rudabanya (Northeastern Hungary) and the problem of parallelism and convergence in the hominoid postcranial morphology. J Hum Evol 24:373–402.

Begun DR. 1994. Relations among the great apes and humans: new interpretations based on the fossil great ape *Dryopithecus*. Yrbk Phys Anthropol 37:11–63.

Begun DR. 1999. Hominid family values: morphological and molecular data on relations among the great apes and humans. In: Parker ST, Mitchell RW, Miles HL, editors. The mentalities of gorillas and orangutans: comparative perspectives. Cambridge: Cambridge University Press. p 3–42.

Begun DR (in press). Knuckle-walking and the origin of human bipedalism. In: Meldrum J, Hilton C, editors. The emergence of modern human walking, running, and resource transport. New York: Kluwer.

Begun DR, Ward CV, Rose MD. 1997. Events in hominoid evolution. In: Begun DR, Wand CV, Rose MD, editors. Function,

phylogeny, and fossils: Miocene hominoid evolution and adaptations. New York: Plenum Press. p 389–415.

Boesch-Aschermann H, Boesch C. 1994. Hominization in the rainforest: the chimpanzee's piece of the puzzle. Evol Anthropol 3:9–16.

Boule M. 1912. L'homme fossil de la Chapelle-aux-Saints. Ann Paleontol 7:3–192.

Brain CK. 1981. The evolution of man in Africa: Was it the result of Coinozoic cooling? Annex Trans Geol Soc S Afr J Sci 84:1–19.

Bromage TG. 1987. The biological and chronological maturation of early hominids. J Hum Evol 16:257–272.

Bush ME, Lovejoy CO, Johanson DC, Coppens Y. 1982. Hominid carpal, metacarpal, and phalangeal bones recovered from the Hadar Formation: 1974–1977 collections. Am J Phys Anthropol 57:651–677.

Carrier DR. 1984. The energetic paradox of human running and hominid evolution. Curr Anthropol 25:483–495.

Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehrlinger JR. 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389:153–158.

Ciochon RL. 1993. Evolution of the Cercopithecoid forelimb: phylogenetic and functional implications from morphometric analyses. Univ Calif Publ Geol Sci 138:1–251.

Corruccini RS. 1978. Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. J Hum Evol 7:307–321.

Corruccini RS, McHenry HM. 2001. Knuckle-walking hominid ancestors. J Hum Evol 40:507–511.

Dainton M. 2001. Did our human ancestors knuckle-walk? Nature 410:325.

Dainton M, Macho GA. 1999. Did knuckle walking evolve twice? J Hum Evol 36:171–194.

Dart RA. 1925. *Australopithecus africanus*: the man-ape of South Africa. Nature 115:235–236.

Darwin C. 1871. The descent of man and selection in relation to sex. New York: Random House, Inc.

Day MH. 1986. Bipedalism: pressures, origins and modes. In: Wood B, Martin L, Andrews P, editors. Major topics in human evolution. Cambridge: Cambridge University Press. p 188–202.

Dean MC, Benyon AD, Thackeray JF, Macho GA. 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. Am J Phys Anthropol 91:401–419.

Delmas A. 1972. L'homme devant l'hominisation. Quaderni Anat Pratica 28:22–56.

deMenocal PB, Bloemendal J. 1995. Plio-Pleistocene variability in subtropical Africa and the paleoenvironment of hominid evolution: a combined data-model approach. In: Vrba E, Denton G, Partridge T, Burckle L, editors. Paleoclimate and evolution, with emphasis n human origins. New Haven: Yale University Press. p 262–288.

Demes B, Stern JT, Hausman MR, Larson SG, McLeod KJ, Rubin CT. 1998. Patterns of strain in the macaque ulna during functional activity. Am J Phys Anthropol 106:87–100.

Doran DM. 1993. Sex differences in adult chimpanzee positional behavior: the influence of body size on locomotion and posture. Am J Phys Anthropol 91:99–115.

Doran DM. 1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. J Hum Evol 32:323–344.

Duncan AS, Kappelman J, and Shapiro L. 1994. Metatarsophalangeal joint function and positional behavior in *Australopithecus afarensis*. Am J Phys Anthropol 93:67–81.

Eickhoff R. 1988. Origin of bipedalism—when, why, how, and where? S Afr J Sci 84:486–488.

Etkin W. 1954. Social behavior and the evolution of man's faculties. Am Nat 88:129–142.

Fleagle JG. 1976. Locomotion and posture of the Malayan Siamang and implications for hominoid evolution. Folia Primatol (Basel) 26:245–269.

Fleagle JG. 1998. Primate adaptation and evolution. San Diego: Academic Press.

Fleagle JG, Stern JT, Jungers WL, Susman RL, Vangor AK, Wells JP. 1981. Climbing: a biomechanical link with brachiation and bipedalism. Symp Zool Soc London 48:359–373.

Foley R, Lee PC. 1989. Finite social space, evolutionary pathways, and reconstructing hominid behavior. Science 243:901–905.

Gebo DL. 1992. Plantigrady and foot adaptation in African apes: implications for Hominid origins. Am J Phys Anthropol 89:29–58.

Gebo DL. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. Am J Phys Anthropol 101:55–92.

Gibbs S, Collard M, Wood B. 2000. Soft-tissue characters in higher primate phylogenetics. Proc Natl Acad Sci USA 97:11130–11132.

Goodman M. 1963. Man's place in the phylogeny of primates as reflected in serum proteins. In: Washburn S, editor. Classification and human evolution. Chicago: Aldine Publishing Co. p 204–224.

Green H, Djian P. 1995. The involucrin gene and hominoid relationships. Am J Phys Anthropol 98:213–216.

Gregory WK. 1916. Studies on the evolution of the primates. Part II. Phylogeny of recent and extinct anthropoids with special reference to the origin of man. Bull Am Mus Nat Hist 35:258–355.

Gregory WK. 1927. Two views of the origin of man. Science 65:601–605.

Groves C. 1999. Nomenclature of African Plio-Pleistocene hominins. J Hum Evol 37:869–872.

Groves CP. 1986. Systematics of the great apes. In: Swindler D, Erwin J, editors. Comparative primate biology, volume 1: systematics, evolution, and anatomy. New York: Alan R. Liss. p 187–217.

Haeckel E. 1874. Anthropogenie oder Entwickelungsgeschichte des Menschen. Leipzig: Engelmann.

Haile-Selassie Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. Nature 412:178–181.

Hamrick MW. 1996. Articular size and curvature as determinants of carpal joint mobility and stability in Strepsirhine primates. J Morphol 230:113–127.

Hamrick MW, Simons EL, Jungers WL. 2000. New wrist bones of the Malagasy giant subfossil lemurs. J Hum Evol 38:635–650.

Heinrich RE, Rose MD, Leakey RE, Walker AC. 1993. Hominid radius from the Middle Pliocene of Lake Turkana, Kenya. Am J Phys Anthropol 92:139–148.

Hewes GW. 1961. Food transport and the origin of hominid bipedalism. Am Anthropol 63:687–710.

Hill AH. 1987. Causes of percieved faunal change in the later Neogene of East Africa. J Hum Evol 16:583–596.

Hotton F, Leguebe A, Louryan S. 1984. L'acquisition de la marche bipède, témoin de l'hominisation. Medica Physica 7:121–126.

Hunt KD. 1991. Mechanical implications of chimpanzee positional behavior. Am J Phys Anthropol 86:521–536.

Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. J Hum Evol 26:183–202.

Hunt KD. 1996. The postural feeding hypothesis: an ecological model for the origin of bipedalism. S Afr J Sci 9:77–90.

Hunt KD. 1998. Ecological morphology of *Australopithecus afarensis*: travelling terrestrially, eating arboreally. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. Primate locomotion. New York: Plenum Press. p 397–418.

Hunt KD, Cant JGH, Gebo DL, Rose MD, Walker SE, Youlatos D. 1996. Standardized descriptions of primate locomotor and postural modes. Primates 37:363–387.

Huxley TH. 1863. Evidence as to man's place in nature. London: Williams and Norgate.

Inouye S. 1994a. Ontogeny of knuckle-walking hand postures in African apes. J Hum Evol 26:459–485.

Inouye SE. 1994b. The ontogeny of knuckle-walking behavior and associated morphology in the African Apes. Ph.D. dissertation, Northwestern University.

Isbell LA, Young TP. 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. J Hum Evol 30:389–397.

Ishida H, Kumakura H, Kondo S. 1985. Primate bipedalism and quadrupedalism: comparative electromyography. In: Kondo S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p 59–79.

Iwamoto M. 1985. Bipedalism of Japanese monkeys and carrying models of hominization. In: Kondo S, editor. Primate morphophysiology, locomotor analyses and human bipedalism. Tokyo: University of Tokyo Press. p 251–260.

Jenkins FAJ, Fleagle JG. 1975. Knuckle-walking and the functional anatomy of the wrists in living apes. In: Tuttle R, editor. Primate functional morphology and evolution. The Hague: Mouton. p 213–231.

Jolly CJ. 1970. The seed-eaters: a new model of hominid differentiation based on a baboon analogy. Man 5:5–26.

Jungers WL. 1982. Lucy's limbs: skeletal allometry and locomotion in *Australopithecus afarensis*. Nature 297:676–678.

Jungers WL. 1985. Body size and scaling of limb proportions in primates. In: Jungers W, editor. Size and scaling in primate biology. New York: Plenum. p 345–381.

Jungers WL. 1988. New estimates of body size in australopithecines. In: Grine F, editor. Evolutionary history of the "robust" australopithecines. New York: Aldine de Gruyter. p 115–121.

Jungers WL, Cole MS. 1992. Relative growth and shape of the locomotor skeleton in lesser apes. J Hum Evol 23:93–105.

Keith A. 1903. The extent to which the posterior segments of the body have been transmuted and suppressed in the evolution of man and allied primates. J Anat Physiol 37:18–40.

Keith A. 1923. Man's posture: its evolution and disorders. Br Med J 1:451–454, 499–502, 545–548, 587–590, 624–626, 669–672.

Keith A. 1940. Fifty years ago. Am J Phys Anthropol 26:251–267.

Kingston JD, Marino BD, Hill A. 1994. Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley. Science 264:955–959.

Larson SG. 1988. Subscapularis function in gibbons and chimpanzees: implications for interpretation of humeral head torsion in hominoids. Am J Phys Anthropol 76:449–461.

Larson SG. 1996. Estimating humeral torsion on incomplete fossil anthropoid humeri. J Hum Evol 31:239–257.

Larson SG. 1998. Parallel evolution in the hominoid trunk and forelimb. Evol Anthropol 6:87–99.

Latimer BM. 1991. Locomotor adaptations in *Australopithecus afarensis*: the issue of arboreality. In: Coppens Y, Senut B, editors. Origine(s) de la bipédie chez les Hominidés. Paris: Centre National de la Recherche Scientifique. p 169–176.

Latimer BM, Lovejoy CO. 1990. Hallucal tarsometatarsal joint in *Australopithecus afarensis*. Am J Phys Anthropol 82:125–133.

Le Gros Clark WE. 1940. Palaeontological evidence bearing on human evolution. Biol Rev 15:202–230.

Leakey MG, Feibel CS, McDougall I, Walker AC. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. Nature 376:565–571.

Leigh SR, Shea BT. 1996. Ontogeny of body size variation in African apes. Am J Phys Anthropol 99:43–66.

Lewis OJ. 1974. The wrist articulations of the Anthropoidea. In: Jenkins FA, editor. Primate locomotion. New York: Academic Press. p 143–169.

Lewis OJ. 1985. Derived morphology of the wrist articulations and theories of hominid evolution. Part I. The lorisine joints. J Anat 140:447–460.

Lewis OJ. 1989. Functional morphology of the evolving hand and foot. Oxford: Oxford University Press.

Lockwood CA. 1999. Sexual dimorphism in the face of *Australopithecus africanus*. Am J Phys Anthropol 108:97–127.

Lockwood CA, Fleagle JG. 1999. The recognition and evaluation of homoplasy in primate and human evolution. Yrbk Phys Anthropol 42:189–232.

Lockwood CA, Richmond BG, Jungers WL, Kimbel WH. 1996. Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. J Hum Evol 31:537–548.

Lovejoy CO. 1981. The origin of man. Science 211:341–350.

Lovejoy CO, Heiple KG, Meindl RS. 2001. Did our human ancestors knuckle-walk? Nature 410:325–326.

Maddison WP, Maddison DR. 1992. MacClade: analysis of phylogeny and character evolution. Version 3.0. Sunderland, MA: Sinauer Associates.

Marks J. 1995. Learning to live with a trichotomy. Am J Phys Anthropol 98:211–232.

Martin LB. 1985. Significance of enamel thickness in hominoid evolution. Nature 314:260–263.

Martin LB. 1986. Relationships among extant and extinct great apes and humans. In: Wood B, Martin L, Andrews PJ, editors. Major topics in primate and human evolution. Cambridge: Cambridge University Press. p 161–187.

Marzke MW. 1971. Origin of the human hand. Am J Phys Anthropol 34:61–84.

Marzke MW. 1983. Joint function and grips of the *Australopithecus afarensis* hand, with special reference to the region of the capitate. J Hum Evol 12:197–211.

Marzke MW, Longhill JM, Rasmussen SA. 1988. Gluteus maximus muscle function and the origin of hominid bipedality. Am J Phys Anthropol 77:519–528.

Marzke MW, Wullstein KL, Viegas SF. 1992. Evolution of the power ("squeeze") grip and its morphological correlates in hominids. Am J Phys Anthropol 89:283–298.

Marzke MW, Wullstein KL, Viegas SF. 1994. Variability at the carpometacarpal and midcarpal joints involving the fourth metacarpal, hamate, and lunate in catarrhini. Am J Phys Anthropol 93:229–240.

McCrossin ML, Benefit BR. 1997. On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the Middle Miocene of eastern Africa. In: Begun D, Ward C, Rose M, editors. Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations. New York: Plenum Press. p 241–267.

McCrossin ML, Benefit BR, Gitau SN, Palmer AK, Blue KT. 1998. Fossil evidence for the origins of terrestriality among Old World higher primates. In: Strasser E, Fleagle J, Rosenberger A, McHenry H, editors. Primate locomotion: recent advances. New York: Plenum Press. p 353–396.

McHenry HM. 1983. The capitate of *Australopithecus afarensis* and *A. africanus*. Am J Phys Anthropol 62:187–198.

McHenry HM. 1984. The common ancestor: a study of the postcranium of *Pan paniscus*, *Australopithecus* and other hominids. In: Susman R, editor. The pygmy chimpanzee. New York: Plenum Press. p 201–230.

McHenry HM. 1986. Size variation in the postcranium of *Australopithecus afarensis* and extant species of Hominoidea. Hum Evol 1:149–156.

McHenry HM. 1991. First steps? Analysis of the postcranium of early hominids. In: Coppens Y, Senut B, editors. Origine(s) de la bipĐdie chez les Hominidés. Paris: Centre National de la Recherche Scientifique. p 133–141.

McHenry HM. 1992. Body size and proportions in early hominids. Am J Phys Anthropol 87:407–431.

Meldrum DJ. 1993. On plantigrady and quadrupedalism. Am J Phys Anthropol 91:379–381.

Mendel FC. Adaptations for suspensory behavior in the limbs of two-toed sloths. In: Montgomery GG, editor. The evolution and ecology of armadillos, sloths, and vermilinguas. Washington, DC: Smithsonian Institution Press. p 151–162.

Morton DJ. 1926. Evolution of man's erect posture: preliminary report. J Morphol Physiol 43:147–149.

Napier JR. 1964. The evolution of bipedal walking in the hominids. Arch Biol (Liege) 75:673–708.

Osborn HF. 1927. Recent discoveries relating to the origin and antiquity of man. Science 65:481–488.

Pickford M, Senut B. 2001. The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya. C R Acad Sci [Iia] 332:145–152.

Pilbeam DR, Rose MD, Barry JC, Shah SMI. 1990. New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* and *Pongo*. Nature 348:237–239.

Potts R. 1996. Humanity's descent: the consequences of ecological instability. New York: William Morrow & Co.

Potts R. 1998. Environmental hypotheses of hominin evolution. Yrbk Phys Anthropol 41:93–136.

Prost JH. 1980. Origin of bipedalism. Am J Phys Anthropol 52:175–189.

Raff RA. 1996. The shape of life. Chicago: University of Chicago Press.

Remis MJ. 1997. Western lowland gorillas (*Gorilla gorilla gorilla*) as seasonal frugivores: use of a variable resource. Am J Primatol 43:87–109.

Reynolds TR. 1985. Stresses on the limbs of quadrupedal primates. Am J Phys Anthropol 67:351–362.

Richmond BG. 1998. Ontogeny and biomechanics of phalangeal form in primates. Ph.D. dissertation, State University of New York at Stony Brook, Stony Brook.

Richmond BG. 1999. Reconstructing locomotor behavior in early hominids: evidence from primate development. J Hum Evol 36:20.

Richmond BG, Strait DS. 2000. Evidence that humans evolved from a knuckle-walking ancestor. Nature 404:382–385.

Richmond BG, Strait DS. 2001a. Did our human ancestors knuckle-walk? Nature 410:326.

Richmond BG, Strait DS. 2001b. Knuckle-walking and the midcarpal joint. Am J Phys Anthropol [Suppl] 32:126.

Richmond BG, Strait DS. 2001c. Knuckle-walking hominid ancestor: a reply to Corruccini and McHenry. J Hum Evol 40:513–520.

Richmond BG, Strait DS. 2001d. Les hommes ont-ils eu un ancêtre "knuckle-walker"? Primatologie 3:555–570.

Richmond BG, Whalen M. 2001. Forelimb function, bone curvature, and phylogeny of *Sivapithecus*. In: de Bonis L, Koufos G, editors. Eurasian neogene hominoid phylogeny. Cambridge: Cambridge University Press. p 326–348.

Richmond BG, Fleagle JG, Kappelman J, Swisher CC III. 1998. First hominoid from the Miocene of Ethiopia and the evolution of the catarrhine elbow. Am J Phys Anthropol 105:257–277.

Ricklan DE. 1988. A functional and morphological study of the hand bones of early and recent South African hominids. Ph.D. dissertation, University of the Witwatersrand, Johannesburg.

Robinson JT. 1972. Early hominid posture and locomotion. Chicago: University of Chicago Press.

Rodman PS, McHenry H. 1980. Bioenergetics and the origin of hominoid bipedalism. Am J Phys Anthropol 52:103–106.

Rogers J, Commuzzie AG. 1995. When is ancient polymorphism a potential problem for molecular phylogenetics? Am J Phys Anthropol 98:216–218.

Rose MD. 1976. Bipedal behaviour of olive baboons *Papio anubis* and its relevance to understanding the evolution of human bipedalism. Am J Phys Anthropol 44:247–261.

Rose MD. 1983. Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both? In: Corruccini R, editor. New interpretations of ape and human ancestry. New York: Plenum Press. p 405–417.

Rose MD. 1984. Food acquisition and the evolution of positional behaviour: the case of bipedalism. In: Chivers DJ, Wood BA, Bilsborough B, editors. Food acquisition and processing in primates. New York: Plenum. p 509–524.

Rose MD. 1991. The process of bipedalization in hominids. In: Coppens Y, Senut B, editors. Origine(s) de la bipédie chez les Hominidés. Paris: Centre National de la Recherche Scientifique. p 37–48.

Rose MD. 1993. Locomotor anatomy of Miocene hominoids. In: Gebo DL, editor. Postcranial adaptation in nonhuman primates. DeKalb: Northern Illinois University Press. p 252–272.

Ruff CB. 1998. Evolution of the hominid hip. In: Strasser E, Fleagle JG, Rosenberger A, McHenry H, editors. Primate locomotion: recent advances. New York: Plenum Press. p 449–469.

Ruff CB, Walker AC. 1993. Body size and body shape. In: Walker A, Leakey R, editors. The Nariokotome *Homo erectus* skeleton. Cambridge, MA: Harvard University Press. p 234–265.

Ruvolo M. 1994. Molecular evolutionary processes and conflicting gene trees: the hominoid case. Am J Phys Anthropol 94:89–113.

Ruvolo M. 1995. Seeing the forest and the trees: replies to Marks; Rogers and Commuzzie; Green and Djian. Am J Phys Anthropol 98:218–232.

Sarich VM, Wilson AC. 1967. Immunological time scale for hominid evolution. Science 158:1200–1203.

Sarmiento EE. 1985. Functional differences in the skeleton of wild and captive orang-utans and their adaptive significance. Ph.D. thesis, New York University.

Sarmiento EE. 1988. Anatomy of the hominoid wrist joint: its evolutionary and functional implications. Int J Primatol 9:281–345.

Sarmiento EE. 1994. Terrestrial traits in the hands and feet of gorillas. Am Mus Nat Hist Novitates 3091:1–56.

Sarmiento EE. 1998. Generalized quadrupeds, committed bipeds and the shift to open habitats: an evolutionary model of hominid divergence. Am Mus Novitates 3250:1–78.

Sarmiento EE. 2000. The os navicular of humans, great apes, OH 8, Hadar, and *Oreopithecus*: function, phylogeny, and multivariate analyses. Am Mus Novitates 3288:1–38.

Satta Y, Klein J, Takahata N. 2000. DNA archives and our nearest relative: the trichotomy revisited. Mol Phylogenet Evol 14:259–275.

Schmitt D. 1994. Forelimb mechanics as a function of substrate type during quadrupedalism in two anthropoid primates. J Hum Evol 26:441–457.

Schmitt D, Larson SG. 1995. Heel contact as a function of substrate type and speed in primates. Am J Phys Anthropol 96:39–50.

Schultz AH. 1930. The skeleton of the trunk and limbs of higher primates. Hum Biol 2:303–438.

Schultz AH. 1936. Characters common to higher primates and characters specific to man. Q Rev Biol 11:259–283.

Schultz AH. 1961. Vertebral column and thorax. Primatologia 4:1–66.

Schwartz J, Yamada T. 1998. Carpal anatomy and primate relationships. Anthropol Sci 106:47–65.

Senut B. 1988. Climbing as a crucial preadaptation for human bipedalism. Int J Skeletal Res 14:35–44.

Senut B. 2001. Quand les caractères deviennent magiques. Primatologie 3:575–576.

Senut B, Tardieu C. 1985. Functional aspects of Plio-Pleistocene hominid limb bones: implications for taxonomy and phylogeny. In: Delson E, editor. Ancestors: the hard evidence. New York: Alan R. Liss. p 193–201.

Senut B, Pickford M, Gommery D, Mein P, Cheboi K, Coppens Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). C R Acad Sci [IIa] 332:137–144.

Shea BT, Inouye SE. 1993. Knuckle-walking ancestors. Science 259:293–294.

Shoshani J, Groves CP, Simons EL, Gunnell GF. 1996. Primate phylogeny: morphological vs. molecular results. Mol Phylogenet Evol 5:101–153.

Silverman NJ, Richmond BG, Wood BA. 2001. Testing the taxonomic integrity of *Paranthropus boisei sensu stricto*. Am J Phys Anthropol 115:167–178.

Sinclair ARE, Leakey MD, Norton-Griffiths M. 1986. Migration and hominid bipedalism. Nature 324:307–308.

Stern JT Jr. 1975. Before bipedality. Yrbk Phys Anthropol 19:59–68.

Stern JT Jr. 2000. Climbing to the top: a personal memoir of *Australopithecus afarensis*. Evol Anthropol 9:113–133.

Stern JT Jr, Susman RL. 1981. Electromyography of the gluteal muscles in *Hylobates*, *Pongo*, and *Pan*: implications for the evolution of hominid bipedality. Am J Phys Anthropol 55:153–166.

Stern JT Jr, Susman RL. 1983. The locomotor anatomy of *Australopithecus afarensis*. Am J Phys Anthropol 60:279–317.

Stern JT Jr, Susman RL. 1991. "Total morphological pattern" versus the "magic trait": conflicting approaches to the study of early hominid bipedalism. In: Coppens Y, Senut B, editors. Origine(s) de la bipédie chez les Hominidés. Paris: Cahiers de Paleoanthropologie, CNRS. p 99–112.

Steudel K. 1996. Limb morphology, bipedal gait, and the energetics of hominid locomotion. Am J Phys Anthropol 99:345–355.

Strait DS, Grine FE, Moniz MA. 1997. A reappraisal of early hominid phylogeny. J Hum Evol 32:17–82.

Straus WL. 1949. The riddle of man's ancestry. Q Rev Biol 24:200–223.

Susman RL. 1979. Comparative and functional morphology of hominoid fingers. Am J Phys Anthropol 50:215–235.

Susman RL, Creel N. 1979. Functional and morphological affinities of the subadult hand (OH 7) from Olduvai Gorge. Am J Phys Anthropol 51:311–331.

Susman RL, Stern JT Jr. 1979. Telemetered electromyography of flexor digitorum profundus and flexor digitorum superficialis in *Pan troglodytes* and implications for interpretation of the O.H. 7 hand. Am J Phys Anthropol 50:565–574.

Susman RL, Stern JT Jr, Jungers WL. 1984. Arboreality and bipedality in the Hadar hominids. Folia Primatol (Basel) 43:283–306.

Tardieu C. 1999. Ontogeny and phylogeny of femoro-tibial characters in humans and hominid fossils: functional influence and genetic determinism. Am J Phys Anthropol 110:365–377.

Taylor CR, Rowntree VJ. 1973. Running on two or four legs: which consumes more energy? Science 179:186–187.

Terborgh J. 1983. Five new world primates: a study in comparative ecology. Princeton, NJ: Princeton University Press.

Tutin CE, Fernandez M, Rogers ME, Williamson EA, McGrew WC. 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lope Reserve, Gabon. Philos Trans R Soc Lond [Biol] 334:179–186.

Tuttle RH. 1967. Knuckle-walking and the evolution of hominoid hands. Am J Phys Anthropol 26:171–206.

Tuttle RH. 1969a. Knuckle-walking and the problem of human origins. Science 166:953–961.

Tuttle RH. 1969b. Quantitative and functional studies on the hands of the anthropoidea: I. The Hominoidea. J Morphol 128:309–363.

Tuttle RH. 1974. Darwin's apes, dental apes, and the descent of man: normal science in evolutionary anthropology. Curr Anthropol 15:389–398.

Tuttle RH. 1975. Parallelism, brachiation, and hominoid phylogeny. In: Luckett WP, Szalay FS, editors. Phylogeny of the primates: a multidisciplinary approach. New York: Plenum Press. p 447–480.

Tuttle RH. 1981. Evolution of hominid bipedalism and prehensile capabilities. Philos Trans R Soc Lond [Biol] 292:89–94.

Tuttle RH. 1992. Hands from newt to napier. In: Matano S, Tuttle RH, Ishida H, Goodman M, editors. Topics in primatology, vol 3: Evolutionary biology, reproductive endocrinology and virology. Tokyo: University of Tokyo Press. p 3–20.

Tuttle RH. 2001. Le knuckle-walking revisité. Primatologie 3:571–573.

Tuttle RH, Basmajian JV. 1974. Electromyography of brachial muscles in *Pan gorilla* and hominoid evolution. Am J Phys Anthropol 41:71–90.

Ungar PS. 1994. Patterns of ingestive behavior and anterior tooth use differences in sympatric anthropoid primates. Am J Phys Anthropol 95:197–219.

Ward CV, Leakey MG, Walker A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. J Hum Evol 41:255–368.

Ward CV, Leakey MG, Brown B, Brown F, Harris J, Walker A. 1999a. South Turkwel: a new Pliocene hominid site in Kenya. J Hum Evol 36:69–95.

Ward SC. 1997. The taxonomy and phylogenetic relationships of Sivapithecus revisited. In: Begun D, Ward C, Rose M, editors. Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations. New York: Plenum Press. p 269–290.

Ward SC, Brown B, Hill A, Kelley J, Downs W. 1999b. *Equatorius*: a new hominoid genus from the Middle Miocene of Kenya. Science 285:1382–1386.

Washburn SL. 1967. Behavior and the origin of man. Proc R Anthropol Inst Gr Br Ire 3:21–27.

Weinert H. 1932. Ursprung der Menscheit. Ueber den engeren Anschluss des Menschengeschlechts an die Menschenaffen. Stuttgart: Ferdinand Enke Verlag.

Wheeler PE. 1991. The thermoregulatory advantages of hominid bipedalism in open equatorial environments: the contribution of increased convective heat loss and cutaneous evaporative cooling. J Hum Evol 21:107–115.

Wheeler PE. 1993. The influence of stature and body form on hominid energy and water budgets: a comparison of *Australopithecus* and early *Homo* physiques. J Hum Evol 24:13–28.

White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. Nature 371:306–312.

Whitehead PF. 1993. Aspects of the anthropoid wrist and hand. In: Gebo DL, editor. Postcranial adaptations in nonhuman primates. DeKalb: Northern Illinois University Press. p 96–120.

Williams GC. 1992. Natural selection: domains, levels, and challenges. New York: Oxford University Press.

WoldeGabriel G, White TD, Suwa G, Renne P, de Heinzelin J, Hart WK, Heiken G. 1994. Ecological and temporal placement of early hominids at Aramis, Ethiopia. Nature 371:330–333.

WoldeGabriel G, Haile-Selassie Y, Renne PR, Hart WK, Ambrose SH, Asfaw B, Heiken G, White TD. 2001. Geology and palaeontology of the Late Miocene Middle Awash valley, Afar rift, Ethiopia. Nature 412:175–178.

Wood BA, Richmond BG. 2000. Human evolution: taxonomy and paleobiology. J Anat 196:19–60.

Wood Jones F. 1916. Arboreal man. London: Edward Arnold.

Wood Jones F. 1929. Man's place among the mammals. New York: Longman Green.

Wood Jones F. 1964. Arboreal man. New York: Hafner Publishing Co.

Wrangham RW. 1980. Bipedal locomotion as a feeding adaptation in Gelada baboons and its implications for hominid evolution. J Hum Evol 9:329–331.

Wunderlich RE, Jungers WL. 1998. Force distribution on the digits during knuckle-walking. Am J Phys Anthropol, Suppl 26:236.

Wynn JG. 2000. Paleosals, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya. J Hum Evol 39:411–432.

Zapfe H. 1979. Chalicotherium grande aus der miozänen Spaltenfüllung von Neudorf an der March (Devinská Nová Ves), Tschechoslowakei. Vienna: Ferdinand Bergerr & Söhne.

Zylstra M. 1998. Metacarpophalangeal joint morphology in nonhuman primates. Am J Phys Anythropol [Suppl] 26:240.

Zylstra M. 1999. Functional morphology of the hominoid forelimb: implications for knuckle-walking and origin of hominid bipedalism. Ph.D. dissertation, University of Toronto, Toronto.