

Chapter 9

The Running-Fighting Dichotomy and the Evolution of Aggression in Hominids

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Abstract. A suite of functional tradeoffs involving specialization for fighting versus locomotor economy is hypothesized to have influenced the evolutionary pathways of hominids. Characters such as pronounced forelimb strength, robust distal limbs, short stature, wide hips, robust head and neck, and fully bipedal stance and gait gave australopithecines a body configuration that is consistent with specialization for fighting with the forelimbs. This, plus a high level of sexual dimorphism in body and forelimb size suggest that australopithecines were specialized for male-male aggression. Nevertheless, traits that made australopithecines effective fighters would also have made them inefficient runners by modern human standards. Given the evidence of specialization for male-male aggression in australopithecines, the evolution of high locomotor stamina in *Homo* represents a dramatic change in evolutionary trajectory. I suggest that the evolution of improved locomotor stamina in *Homo* was made possible by the invention of new weapon technology that reduced functional conflicts between specialization for economical transport and specialization for male-male fighting. Invention of the first effective weapons would have shifted selection for male-male aggression from favoring greater physical strength and agility to favoring creative innovation, allowing independent evolution of cursorial specialization. In this scenario, the emergence of *Homo* 1) is dependent on the invention of new weapons, and 2) represents both greatly improved distance transport and increased lethality in a lineage already highly specialized for fighting.

INTRODUCTION

The demands of survival and reproduction often require compromises in the design of organisms (Gans, 1988; Lauder, 1991; Maynard Smith et al., 1985). One category of functional tradeoff that may be particularly important in the evolution of vertebrate diversity is the set of compromises entailed by the requirements of locomotion versus the requirements of fighting. Both locomotion and fighting are critical to survival and reproductive fitness in many species. Yet, characters that make an individual good at fighting may, in many cases, limit locomotor performance and vice versa (Hamilton, 1979; Pasi and Carrier, 2003). For example, among apes, sexual dimorphism in body size and male-male fighting are most



Figure 1. Individuals of the two breeds of domestic dogs, pit bulls and greyhounds, which are used to illustrate functional conflicts between specialization for running versus specialization for fighting. Both individuals in this photograph are adult males with a body mass of 33 kg. Modified from Chase et al. (2002).

dramatic in gorillas (Nowak and Paradiso, 1983). Large body size allows dominant male gorillas to defend multi-female groups against lone males intent on killing the infants and attracting the females (Fossey, 1983, 1984; Watts, 1989). Large size, however, severely limits the ability of male gorillas to climb trees (Schaller, 1963). In contrast, both male and female gibbons brachiate with spectacular grace and agility. Gibbons exhibit little or no sexual dimorphism in body size and mate in monogamous pairs (MacKinnon and MacKinnon, 1984; Nowak and Paradiso, 1983). Both male and female gibbons participate in defense of territory and aggressive encounters rarely involve physical contact (Mitani, 1987; Preuschoft et al., 1984). This comparison illustrates what may be a general trend; locomotor performance is constrained in fighting specialists whereas fighting ability is limited in locomotor specialists.

The ideas presented in this chapter emerged from an investigation of functional trade-offs in the musculoskeletal system of two breeds of domestic dogs selected as examples of specialization for fighting versus specialization for running performance: pit bulls and greyhounds (Fig. 1; Pasi and Carrier, 2003). The more we learned about the anatomy of these two breeds, the more I began to see them as a possible analogy for many of the structural differences between australopithecines and *Homo*. For example, the short stature and broad stance of pit bulls is similar to that of australopithecines, whereas the longer limbed and more gracile body of greyhounds is comparable to the build of *Homo*. In the case of the

two dog breeds, we can be confident of the evolutionary basis of the anatomical differences; intense artificial selection for fighting ability in pit bulls versus intense artificial selection for economical, high speed running in greyhounds. Could functional tradeoffs associated with locomotor and fighting ability also have played a role in the evolution of hominids?

The origin of *Homo* has been argued to be associated with locomotor adaptations that improved economical transport and increased locomotor stamina (Bramble, 1990, 2000; Carrier, 1984; Jungers, 1991; McHenry, 1994; Porter, 1993; Ruff, 1991; Wolpoff, 1999). Much of the anatomy of australopithecines, in contrast, appears to be related to specialization for arboreal climbing (Stern and Susman, 1983; Susman, et al., 1984). It is clear, however, that australopithecines were highly specialized for terrestrial bipedality (Dart, 1925; Heglund and Schepens, 2002; Kramer, 1999; Kramer and Eck, 2000; Latimer et al., 1987; Latimer and Lovejoy 1989, 1990a, b; Lovejoy, 1981; 1988; Lovejoy, et al., 1973; Wolpoff, 1999). Although australopithecines were likely to have been much better climbers than any lineage of *Homo*, their specialization for terrestrial locomotion clearly compromised their climbing performance relative to that of their more fully arboreal ancestors (Latimer et al., 1987; Latimer and Lovejoy 1989, 1990a, b; Lovejoy, 1978). Thus, as is the case with *Homo*, the evolutionary origin of *Australopithecus* is associated with adaptations for terrestrial bipedalism.

Here I propose that australopithecines can also be distinguished from their arboreal climbing ancestors and from the genus *Homo* by characters that are related to specialization for fighting. Specifically, I suggest that australopithecines were anatomically specialized for male-male aggression, and that the evolution of cursorial specialization in *Homo* was made possible by the invention of new weapon technology that greatly reduced functional conflicts between specialization for endurance locomotion and specialization for fighting.

WERE AUSTRALOPITHECINES SPECIALIZED FOR FIGHTING?

There are a number of musculoskeletal differences between australopithecines (including *Paranthropus*) and *Homo* that are consistent with fighting specialization in the australopithecines and adaptation for locomotor economy in *Homo* (Table 1). Much of what gave australopithecines a fighting physique, however, were characters that clearly represent a legacy from arboreal ancestors. Indeed, a component of the fighting hypothesis, presented here, is that adaptations for suspension climbing, forelimb hanging, and brachiation preadapt a lineage for fighting with the forelimbs in the manner of chimps, gorillas, and humans. Thus, the aspect of the fighting hypothesis that is hardest to evaluate is not whether physical combat among male australopithecines was common and evolutionarily important, or if australopithecines had more of a fighting physique than any group of *Homo*, but whether or not the genus *Australopithecus* was specialized for fighting relative to their more arboreal ancestors. In the discussion that follows, I attempt to distinguish plesiomorphic, arboreal characters of *Australopithecus* that would have conveyed high fighting ability, from those characters that would have enhanced fighting ability but would likely have interfered with climbing performance (Table 1). This latter set of characters represents the strongest argument for fighting specialization in australopithecines.

Proximal to Distal Distribution of Limb Mass

The mechanical work of locomotion can be divided into two components, the work required to accelerate and decelerate the mass of the animal during each step and the work

Table 1. Comparison of expected musculoskeletal differences in primates specialized for terrestrial bipedal locomotion, fighting with forelimbs, and arboreal suspension climbing and brachiation.

	Bipedal locomotion	Forelimb fighting	Suspension climbing
Distal limb segments	Gracile	Robust	Robust
Forelimb/hindlimb robustness*	Low	High	Moderate
Elastic storage	High	Low	Low
Hip width*	Narrow	Wide	Narrow
Hindlimb length*	Short or long	Short	Long
Forelimb length	Short	Long	Long
Cranio-scapular musculature*	Limited	Robust	Moderate
Body size sexual dimorphism*	Low	High	Low
Forelimb sexual dimorphism*	Low	High	Low
Skull buttressing*	Low	High	Low
Habitual bipedal posture*	Well developed	Well developed	Poorly developed

*Characters that have potential to distinguish fighting specialization from climbing specialization.

required to swing the limbs relative to the center of mass of the animal. This latter component is referred to as the internal work of locomotion. During high speed running or in animals with heavy limbs, such as hominids, the internal work can constitute a significant portion of the total mechanical work of running (Cavagna and Kaneko, 1977; Fedak et al., 1982; Willems et al., 1995). This leads to the expectation that animals specialized for economical running will have relatively less muscle mass in their distal limbs to reduce the rotational inertia of the oscillating limbs (Hildebrand and Hurley, 1985; Steudel, 1991). In contrast, the distal limbs of animals specialized for fighting can be expected to be well muscled to allow the production of large forces and high power for opponent manipulation and agile movement (Table 1). This distinction appears to hold among many species comparisons. Consider the comparison of apes given above, or the comparison of lions and cheetahs. The distinction also exists between pit bulls and greyhounds (Pasi and Carrier, 2003). Pit bulls have a greater percentage of their limb muscle mass distal to the elbow and knee joints than do greyhounds (Fig. 2A). Hence, the relative robustness of distal limbs may help distinguish fighting from locomotor specialists.

The distal segments of both the fore- and hindlimbs of australopithecines appear to have been robust and massive compared to those of *Homo* (Fig. 3). Mid-shaft diameters of the radius and ulna suggest that the forearms of australopithecines were often exceptionally robust (Hartwig-Scherer, 1993; McHenry, 1986). Evidence of relatively massive forearms, compared to *Homo*, also emerges from analysis of the articular surfaces of the elbow joint (McHenry, 1978, 1992; McHenry and Berger, 1998). Forearms of australopithecines also appear to have been very long relative to humeral length (reviewed by McHenry and Coffing, 2000). Similarly, australopithecines are known to have had relatively larger hands and feet (Stern and Susman, 1983) and larger peroneal muscles (Stern and Susman, 1983; Tuttle, 1981) than *Homo*. Additionally, the structure of the metacarpals and wrist bones of australopithecines suggest that the muscles of the forearm associated with wrist and finger flexion were relatively large (Stern and Susman, 1983).

Certainly, a component of the relatively enlarged distal forelimbs of australopithecines may be explained as a legacy from their arboreal ancestors as well as specialization for forelimb dominated climbing given that they no longer possessed a significant capacity for grasping with their feet (Latimer and Lovejoy, 1990a, b; Wolpoff, 1999; Table 1).

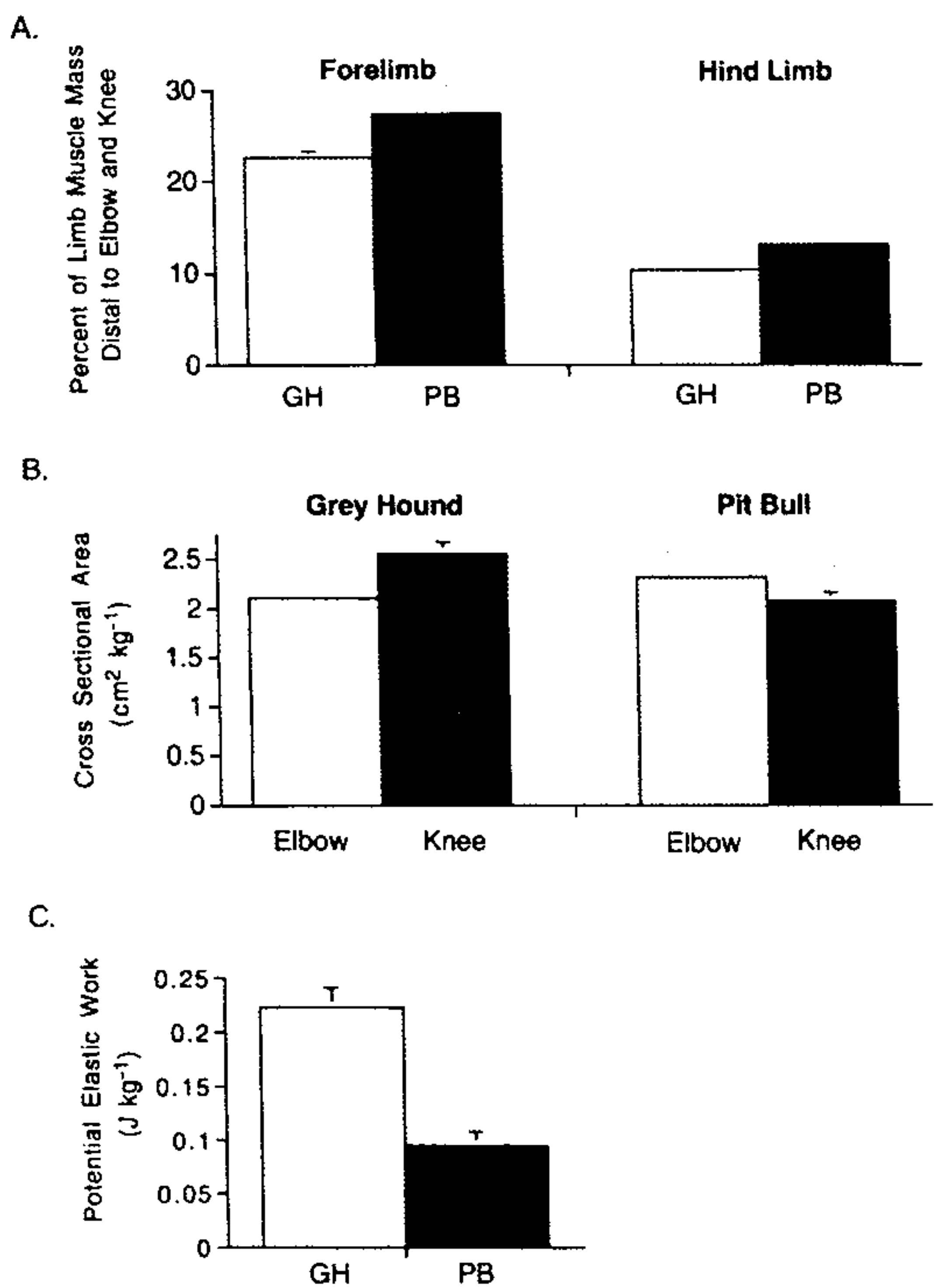


Figure 2. A) Percent of total limb muscle mass distal to the elbow and knee joints in four greyhounds and five pit bulls. In each comparison, the percent of muscle mass in the distal limb is significantly greater in the pit bulls. B) Comparison of the average cross-sectional area of the extensor muscles of the elbow and knee joints in four greyhounds and five pit bulls. The greyhounds have stronger muscles in their hindlimbs, whereas the pit bulls have stronger muscles in their forelimbs. C) Comparison of the average potential for storage and recovery of elastic strain energy in the tendons of the extensor muscles of the ankle joint in four greyhounds and five pit bulls. (Pasi and Carrier, in press).

Nevertheless, the exceptional sexual dimorphism in distal limb size and robustness observed among australopithecines (McHenry, 1991a, 1996, discussed below) is more consistent with specialization for male-male aggression than with an arboreal lifestyle. In contrast, the relative reduction in distal limb mass that characterizes *Homo* is consistent with improved locomotor economy (Hildebrand and Hurley, 1985; Steudel, 1991).

Relative Muscular Strength of Fore- and Hindlimbs

The contractile physiology of muscle leads to the expectation that the relative strength of fore and hindlimb muscles will be different in quadrupedal runners and fighters. Because active skeletal muscle generates much greater force when it is stretched than when it shortens (Katz, 1939) we expect quadrupedal animals specialized for running to have less muscle

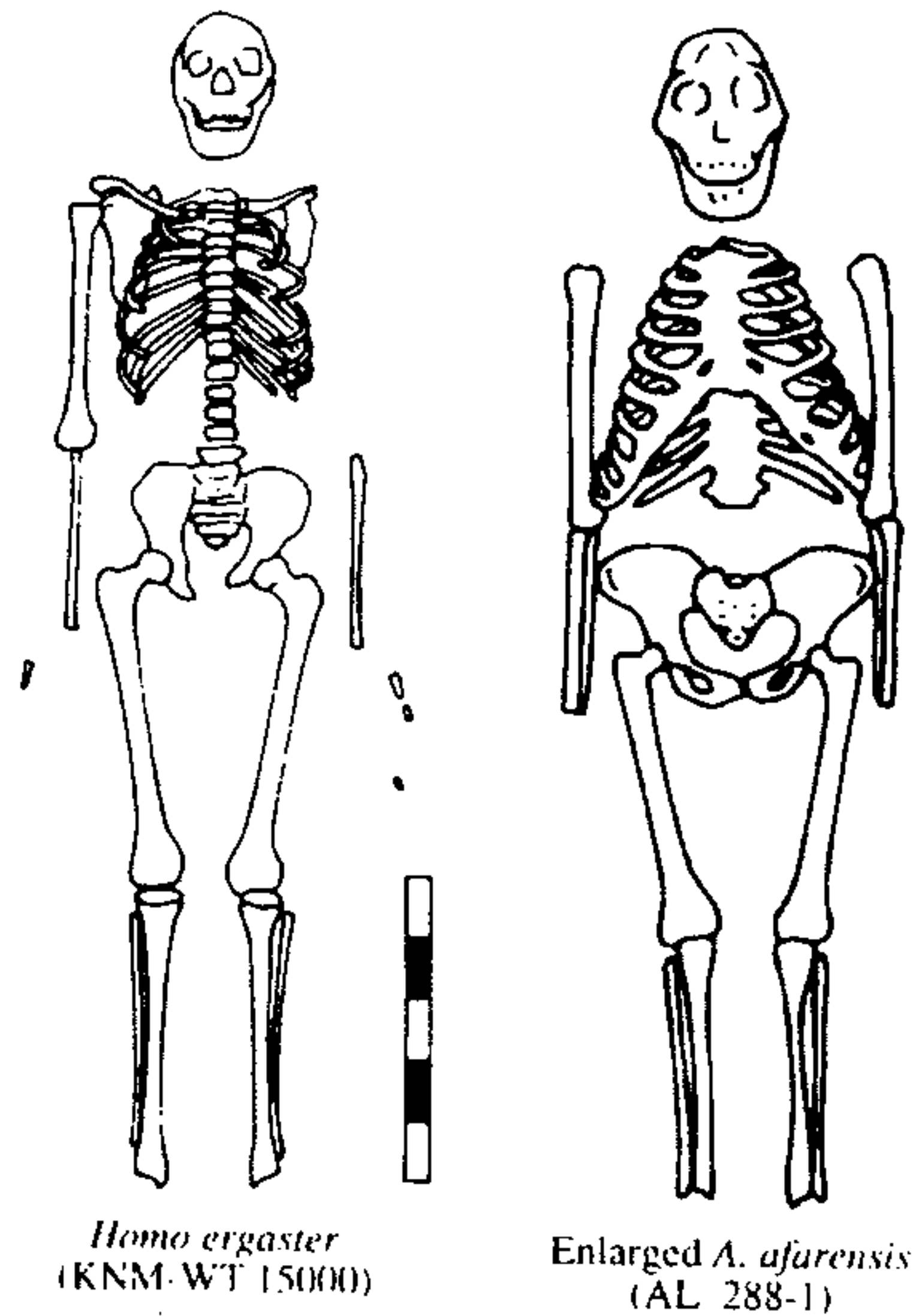


Figure 3. Illustrations of the skeletal anatomy of *Homo ergaster* and *Australopithecus afarensis*. The drawing of *A. afarensis* has been scaled up to the same height as *H. ergaster* to better illustrate the differences in proportions. Modified from Klein (1999).

strength in their forelimbs than in their hindlimbs (Pasi and Carrier, 2003). This hypothesis emerges from the observed division of labor in the limbs in which the forelimbs of running animals play a greater role in deceleration and hindlimbs play a greater role in acceleration (Blickhan and Full, 1987; Cavagna et al., 1977; Cruse, 1976; Full et al., 1991; Heglund et al., 1982; Jayes and Alexander, 1978). Because the extensor muscles of the limbs must actively stretch to absorb energy during deceleration, but must actively shorten to produce acceleration, less muscle strength will be required in the forelimbs than the hind limbs. In contrast, the extensor muscles of the forelimbs of animals specialized for fighting can be expected to be as large or larger than those of the hindlimbs because forelimbs are often used to initiate rapid turns as well as to strike and manipulate an opponent during fighting.

Here also comparison of closely related species seems to support this expectation. The hindlimbs of cheetahs appear to have more muscle mass than the forelimbs, whereas the muscle mass of the forelimbs of lions appears to be greater than that of their hindlimbs. Similarly, our comparison of the relative strength (i.e., cross sectional area) of the extensor muscles in the forelimb and hindlimb of dogs shows that greyhounds have stronger extensor muscles in their hindlimbs than in their forelimbs, whereas the pattern is reversed in pit bulls, who have greater or equal strength in the extensor muscles in their forelimbs than in their hindlimbs (Fig. 2B; Pasi and Carrier, 2003).

Although hominids walk and run bipedally the analogy for relative limb strength holds and is useful when comparing *Australopithecus* and *Homo*. Hominids specialized for fighting are expected to have relatively strong forelimbs for opponent manipulation (Table 1).

In contrast, those specialized for running are expected to have relatively weak forelimbs, to reduce body mass, and strong hindlimbs to generate the needed locomotor forces and power. Compared to *Homo*, australopithecines had relatively less robust hindlimbs and significantly more massive forelimbs (McHenry, 1992; Fig. 3). Relative to their hindlimbs and sacral vertebrae both *A. afarensis* and *A. africanus* have robust forelimbs (McHenry and Berger, 1998). In this case, as in the previous comparison of distal limb robustness, the difference between *Australopithecus* and *Homo* is likely due, at least in part, to specialization for forelimb dominated climbing in *Australopithecus* and to specialization for economical terrestrial transport in *Homo*. Nevertheless, the dramatic sexual dimorphism in the size and robustness of the forelimbs of australopithecines (discussed below) suggests that specialization for fighting maybe more important than specialization for climbing in explaining the robustness of the forelimbs.

Potential for Storage and Recovery of Elastic Strain Energy

Storage and recovery of elastic strain energy in the tendons of distal limb muscles is thought to greatly enhance the economy of transport during both low and high speed running (Alexander, 1984; Biewener, 1998; Cavagna et al., 1964; Dawson and Taylor, 1973; Roberts et al., 1997; Taylor, 1994). For this reason we expect animals specialized for distance and/or high speed running to have a high capacity for elastic storage, i.e., long stretchy tendons. In contrast, long stretchy tendons in series with extensor muscles would likely pose a handicap for any animal attempting to over-power an opponent during physical combat. Hence, we expect animals specialized for fighting to have relatively limited abilities to use elastic storage during running (Table 1). Breeds of domestic dogs selected for running and fighting appear to fit these expectations. Greyhounds have more than a two-fold greater capacity to store and recover elastic strain energy in the extensor muscles of their ankle than do pit bulls (Fig. 2C; Pasi and Carrier, 2003).

Analysis of modern humans suggests that storage and recovery of elastic strain energy is an effective and important mechanism of energy conservation in human runners (Alexander, 1988; Cavagna et al., 1964; Ker et al., 1987). The potential of australopithecines to use elastic storage is difficult to access, but it can be assumed to have been substantially less than that observed in modern humans (Bramble pers. com.). It is known that the major sites of elastic strain are the in-series tendons, likely including apponeroses, rather than the muscle tissue itself (Alexander, 1988). Furthermore, the amount of energy that can be stored in a tendon is a direct function of its length. Because tendon length is related to leg length, animals with relatively long legs tend to have longer tendons and a greater capacity for elastic storage than animals with relatively short legs. In our comparison of greyhounds and pit bulls, tendon length played the greatest role in determining the estimated two-fold difference in potential for elastic storage (Pasi and Carrier, 2003). Hence, the relatively short hindlimbs of australopithecines relative to humans (Jungers, 1982; Ruff, 1988; Wolpoff, 1983, 1999; Fig. 3) lead to the suggestion that the potential for elastic storage was probably much lower in australopithecines than in modern humans.

Stature and Girdle Breadth

Although the two dogs shown in Figure 1 both weighed 330 N at the time the photograph was taken, they differ dramatically in shape. The greyhound is long limbed and narrow in the thoracic girdle. In contrast, the pit bull is shorter in stature, much broader in the thoracic

girdle, and has a circular thorax. Narrow girdles and deep chests are common in animals specialized for running (Hildebrand and Goslow, 2001). Narrow girdles allow the limbs to swing in a parasagittal plane and reduce lateral moments at the limb joints and on the trunk. Hence, narrow girdles are thought to reduce the cost of transport. Long limbs also decrease the cost of transport by increasing stride length, thereby reducing the number of times the locomotor muscles must turn on and off to cover a given distance (Heglund and Taylor, 1988; Kram and Taylor, 1990). The broad girdles exhibited by pit bulls are thought to increase postural stability both by increasing the capacity of the limbs to apply laterally directed forces to the substrate and by increasing limb mobility in abduction and adduction. The circular shape of the pit bull thorax also likely allows greater adduction and abduction of the forelimb (see Ward, 1998). The combination of broad girdles and short limbs lowers the center of gravity of pit bulls, further increasing lateral stability. Thus, the contrasts in stature and girdle breadth illustrated in Figure 1 are thought to reflect selection for economical rapid locomotion in the case of the greyhound and postural stability, lateral strength, and agility in the case of the pit bull.

Compared to *Homo*, australopithecines were characterized by extraordinarily broad pelvic girdles (Fig. 3). The broad hips of australopithecines were due to a relatively wide interacetabular distance as well as a pronounced lateral flare of the iliac blades (Berge and Kazmierczak, 1986; Lovejoy, 1988; Lovejoy et al., 1973; Rak, 1991). Broad hips appear to be a derived condition of *Australopithecus*. Those of nonhuman apes and fossil hominoids are much narrower (Berge and Kazmierczak, 1986; Rak, 1991; Ward, 1997).

The broad hips of australopithecines were unlikely to have conveyed an energetic or mechanical advantage to bipedal walking and running. First, a broad distance between the hip joints increases the gravitational moment arm at the hip joint and would increase the muscular force required of the hip abductor muscles. This may have been partially or fully offset by the long muscle moment arm of the abductor muscles (Berge and Kazmierczak, 1986; Jungers, 1991), but broad hips certainly do not facilitate support of body weight against gravity at the hip joint. Second, broad hips would also increase moments at the hip due to fore-aft ground forces (Carrier, 1990; Fife et al., 2001). In the case of an upright biped these forces would tend to cause body rotation about a vertical axis through the hip joint (i.e., yaw) first in one direction as the body decelerated during the first half of the step and then in the opposite direction as the body accelerated during the second half of the step. To stabilize the body against these moments, relatively larger forces would have been required from the muscles that produce lateral and medial rotation of the limb at the hip joint in australopithecines than in the narrower hipped *Homo*. Finally, if as Rak (1991) suggests broad hips decrease the vertical oscillation of the center of mass during a walking step, the economy of walking would be diminished due to reduced energy cycling through the transfer of potential and kinetic energy (Cavagna et al., 1977).

The impact that the broad hips of australopithecines may have on obstetric function is controversial. A number of people have argued that the pelvis of australopithecines was shaped more to meet the demands of erect posture and bipedal locomotion than to allow an increase in fetal size, which occurred much later in the evolution of hominids (Abitbol, 1987; Rosenberg and Trevathan, 1995; Tague and Lovejoy, 1986). Alternatively, the mediolaterally broad birth canal of early hominids may have been needed to allow passage of the broad shouldered infants (Rosenberg and Trevathan, 1995; Trevathan and Rosenberg, 2000; Wolpoff, 1999). Whether or not the broad hips of early hominids were a function of upright posture and/or obstetric function, the energetics and mechanics of terrestrial locomotion would have been negatively impacted as described above.

Broad hips, however, must have increased the postural stability of australopithecines in two ways. First, broad hips provide a large area of support for the abdominal viscera. This in combination with the cone shaped thorax of australopithecines resulted in a low center of gravity by positioning the viscera low in the trunk (Hunt, 1998). Second, broad hips increase the lateral forces the limbs can apply to the substrate. Although the mechanical advantage of the hip abductors to support body weight in australopithecines appears to have been lower than (Jungers, 1991) or roughly equivalent to (Berge and Kazmierczak, 1986) that in modern humans, the mechanical advantage of the hip abductors for the production of laterally directed forces on the ground, as would be needed when applying a lateral force to an opponent, was much higher in australopithecines than in *Homo*. The muscle moment arms of the *Gluteus medius* and *Gluteus minimus* muscles are determined by the distance from the greater trochanter to the center of rotation of the hip joint, in other words, by the length of the femoral neck. For the production of laterally directed ground forces, the ground force moment arm of the hip abductors is a function of the length of the leg. Hence, the long femoral neck and shorter legs of australopithecines (Jungers, 1982; Ruff, 1988; Wolpoff, 1983, 1999) gave their hip abductors a much greater mechanical advantage to apply lateral forces to the substrate than was present in early *Homo*.

In summary, the exceptionally broad hips of australopithecines are a derived trait of early hominids that does not appear to be related to selection for economical or rapid terrestrial locomotion. Broad hips combined with short limbs do, however, increase postural stability, particularly against laterally directed perturbations. These are characteristics that would likely benefit individuals engaged in physical combat (Table 1). Alternatively, broad hips could have been selected because they increased stability during climbing. However, if this were true why are broad hips a derived character of australopithecines, not found in chimpanzees, gorillas, or the arboreal ancestors of *Australopithecus*? Thus, hip width is a character that should help to distinguish fighting from climbing specialization (Table 1). In contrast, the relatively narrower hips and greater limb length of *Homo* are both consistent with improved locomotor economy.

Hindlimb Length

The short legs of australopithecines have often been equated with inefficient terrestrial locomotion. The argument is that short legs result in short stride lengths and this necessitates a higher stride frequency for a given walking or running speed. As observed by Kramer (1999), however, energetic expenditure is not solely a matter of the number of strides taken, but also of the energy consumed in a single stride. Recent modeling of the gait of australopithecines (Kramer, 1999; Kramer and Eck, 2000) and comparisons to modern children of the similar body proportions to australopithecines (Heglund and Schepens, 2002) suggest that the terrestrial locomotion of australopithecines was not inefficient at low to moderate speeds. The difference between australopithecines and *Homo* suggested by both the modeling and the comparisons to human children is that the energetically optimal walking speed would have been lower in australopithecines, and australopithecines would not have been able to walk and run efficiently at high speeds.

Based on these results, Kramer and Eck (2000) suggest that australopithecines may have been "optimized for a particular ecological niche—slow speed foraging". Although this is certainly a possibility, I view it as unlikely. Specialization for economical slow locomotion requires low-mass limbs (e.g., short limbs of low muscle mass) and slow contracting muscle fibers. These are traits found in low energy specialists such as tortoises (Woledge,

1968). The downside of specialization for this type of economical transport is that low-mass limbs have muscles of small cross-sectional area that cannot produce the large forces needed for rapid acceleration, and slow-contracting muscle fibers that limit maximum running speeds. Thus, if australopithecines were specialized for slow speed foraging, their capacity for acceleration and sprint velocity would have been significantly constrained, as in tortoises. Such specialization seems unlikely in a relatively defenseless terrestrial forager that was confronted by larger and swift terrestrial predators. Alternatively, if their limbs were equipped with large, fast-contracting muscles, australopithecines would have been inefficient at high speeds, but they would have accelerated rapidly and they may have run at relatively high speeds over short distances. This arrangement of short hindlimbs equipped with large, fast-contracting muscles is entirely consistent with specialization for fighting (Table 1).

The argument that short hindlimbs are an adaptation for climbing (Cant, 1987; Cartmill, 1974; Hunt, 1991a; Jungers, 1978) is inconsistent with the relatively long hindlimbs of exceptional climbers such as gibbons and spider monkeys. Indeed, long hindlimbs can be expected to be advantageous in an environment in which the locomotor substrate is limited and unpredictable in its location, allowing more support options than would be available with shorter hindlimbs (Table 1). Thus, the relatively short hindlimbs of chimpanzees and gorillas (Jungers, 1984), as well as those of early hominids, may reflect selection for fighting rather than climbing.

Head and Neck

Another obvious difference between greyhounds and pit bulls is the size and robustness of the head and neck (Fig. 1). Relative to the basal "wolf-like" morphology of domestic dogs the greyhound lineage has lost head mass whereas the reverse is true in the pit bull lineage. In our sample, the mass specific size of the jaw adductors was almost three-fold greater in the pit bulls (11.9 g kg^{-1} , $N = 5$) than in the greyhounds (4.1 g kg^{-1} , $N = 4$; $P < 0.0001$, unpaired t-test; Carrier, unpublished data). In terms of adaptation, we can speculate that the light, streamlined head of greyhounds improves locomotor economy, whereas the robust head and neck of pit bulls provides large biting force and enhances the ability to apply torques to an opponent.

Information that would allow a comparison of the head and neck of australopithecines to that of their arboreal hominoid ancestors does not exist in the current fossil record. Thus, for the sake of argument, and because no other comparison is currently possible, I will assume that the head and neck of the arboreal ancestors of hominids resembled that of modern chimpanzees. Relative to chimpanzees, australopithecines had large heads, due primarily to their exceptionally large faces, and a large area for the attachment of nuchal muscles (Adams and Moore, 1975; Wolpoff, 1999; Fig. 3). In *A. afarensis*, the nuchal plane of the occipital bones was much broader than in chimpanzees, suggesting that the nuchal muscles were well-developed, and reflecting an "emphasis on muscles important in lifting and pulling at the shoulder" (Wolpoff, 1999). Additionally, the mastoid processes of *A. afarensis* are also enlarged relative to that in modern chimpanzees and gorillas (Olson, 1985). Specimens from Hadar (A.L. 333-106 and A.L. 333w-14) show that the spinous processes of the cervical vertebrae were long and robust (Lovejoy et al., 1982), suggesting that the cervical epaxial muscles were also relatively large in *A. afarensis*.

In contrast to most tetrapods, including many primates, the hominid trend towards reduction in canine size (Wolpoff, 1999) suggests that biting and opponent manipulation

were not important functions of the head and neck during fighting in early hominids. Nevertheless, during fighting, the head and neck of hominids serves 1) as the attachment site for external appendicular muscles that raise the shoulder and forelimb, allowing upward (i.e., craniad) swings, strikes, and pushes from the forelimb, and 2) as a relatively vulnerable and fragile target. Powerful, craniad directed forelimb punches or pushes require large force production from the muscles that raise the pectoral girdle on the trunk: sternocleidomastoid, trapezius, levator scapula, rhomboideus minor. When these muscles contract they exert moments on the axial skeleton, specifically on the cervical vertebrae and skull. To stabilize the axial skeleton against these appendicular moments the epaxial and hypaxial muscles must be active (Fife et al., 2001; Gray, 1968). Thus, if we assume that the head and neck of the arboreal ancestors of hominids resembled chimpanzees in build and proportions, then the relatively large cervical and nuchal muscles of australopithecines would suggest fighting specialization (Table 1).

Given that the head and neck are important targets in fighting (see Goodall, 1986; LaBlanc, 1999; Weidenreich, 1943, 1951), buttressing of the face and cranium could be expected if fighting was an important behavior. Although buttressing of the cranium does not appear to have been present in australopithecines (Wolpoff, 1999), buttressing of the face remains a possibility. The large prognathic face that characterizes australopithecines is both a legacy from their hominoid ancestors and a function of their expanded cheek teeth/chewing complex (Wolpoff, 1999). Although it may be very difficult to distinguish masticatory function from protective buttressing, future analyses of structures such as the anterior pillars, zygomatic prominences, and supraorbital ridges should also include functional analysis as possible defensive shielding.

Sexual Dimorphism in Early Hominids

Australopithecines appear to have had a higher level of sexual dimorphism in body size than is observed in *Homo* (Table 2). (Given the lack of consensus on the identity of the limited number of postcranial specimens, I view the level of sexual dimorphism in *A. habilis* and *A. rudolfensis* to be unresolved.) Sexual dimorphism in australopithecines

Table 2. Sexual dimorphism in body size in hominids and extant hominoids (McHenry, 1996; McHenry and Coffing, 2000).

Taxon	Dates (mya)	Male Mass (kg)	Female Mass (kg)	Male/Female
<i>Australopithecus anamensis</i>	4.2–3.9	51	33	1.54
<i>Australopithecus afarensis</i>	3.9–3.0	45	29	1.55
<i>Australopithecus africanus</i>	3.0–2.4	41	30	1.37
<i>Paranthropus boisei</i>	2.3–1.4	49	34	1.44
<i>Paranthropus robustus</i>	1.9–1.4	40	32	1.25
<i>Australopithecus habilis</i>	1.9–1.6	?	?	?
<i>Australopithecus rudolfensis</i>	2.4–1.6	?	?	?
<i>Homo ergaster</i>	1.9–1.7	66	56	1.18
<i>Homo sapiens</i>	extant	64.9	53.2	1.18
<i>Hylobates lar</i>	extant	6.3	5.6	1.1
<i>Pongo pygmaeus</i>	extant	77.5	37.0	2.1
<i>Gorilla gorilla</i>	extant	169.5	71.5	2.4
<i>Pan paniscus</i>	extant	39.0	31.0	1.3
<i>Pan troglodytes</i>	extant	49	41	1.20

is apparent in their dentition (Kimbel and White, 1988; Wolpoff, 1976), limb bone lengths (McHenry, 1991b), limb bone robustness (Hartwig-Scherer, 1993; Lockwood et al., 1996), and limb joint size (McHenry 1991a, 1992). Based on an analysis of the mandibular corpus, proximal femur and humerus Lockwood and collaborators (1996) suggest that the level of body size sexual dimorphism in *A. afarensis* approached, but did not exceed that of the most dimorphic modern hominoids: gorillas and orangutans. An analysis of the robustness of both fore and hindlimb bones by Hartwig-Scherer (1993) suggests that the ratio of male to female body weight of *A. afarensis* was greater than that of any modern hominoid. Using metrics of the size of hindlimb joints, McHenry (1991a) found that *A. afarensis* had a moderate level of body size sexual dimorphism that was well above that seen in modern humans, somewhat greater than that of the two extant species of chimpanzee, and below the sexual dimorphism of gorilla and orang-utan. Furthermore, the extensive analysis of body weight dimorphism in early hominids by McHenry (1978, 1986, 1991a, b, 1992, 1994, 1996) leads to the conclusion that dimorphism declines through time from *A. afarensis* to *A. africanus* to *P. robustus* with a dramatic reduction in *H. erectus* (McHenry, 1996).

A high level of body size sexual dimorphism may be a basal characteristic of the great ape/hominid clade (Begun et al., 1997). *Oreopithecus bambolii* is a large bodied, late Miocene (8.5–9.0 Ma.) member of the great ape/hominid clade (Harrison, 1987; Sarmineto, 1987), and is represented by a relatively extensive fossil record (Harrison, 1991). Based on the dentition, as well as the cranial and postcranial material, Harrison (1991) estimates that the body mass of males ranged from 30–40 kg, whereas females were ranged from 15–20 kg. Thus, a level of body size sexual dimorphism that exceeds that of *Homo* may be basal for Hominoidea.

The forelimbs of australopithecines appear to have been more dimorphic than the jaws, teeth, or hindlimbs (McHenry, 1996). In *A. afarensis*, for example, the difference between large and small ulnae, radii, and capitates is as great or greater than that between male and female means of the most dimorphic extant apes (McHenry, 1986; 1991a; 1996). Forelimbs also appear to have been relatively dimorphic in both *A. africanus* and *P. boisei* as well (McHenry, 1996). The fact that McHenry's comparisons are based primarily on metrics of articular surfaces at joints is significant because articular surface area is independent of mechanical loading history (Lieberman et al., 2001; Trinkaus et al., 1994). Thus, the relatively high level of sexual dimorphism in the forelimbs of australopithecines must be related to evolution at the species level rather than to gender differences in activity level. Most importantly, the higher level of sexual dimorphism in the forelimb joints than the hindlimb joints suggests that the forelimb dimorphism was due to more than just allometry associated with males being physically larger in body size than females.

Is the relatively high level of sexual dimorphism in body and forelimb size consistent with the hypothesis of high levels of male–male aggression in australopithecines? The functional and behavioral implications of sexual dimorphism in hominids have been discussed by number of authors (Darwin, 1871; Foley and Lee, 1989; Frayer and Wolpoff, 1985; Lovejoy, 1981; McHenry, 1994; 1996; Plavcan and van Schaik, 1997; Wolpoff, 1976). The discussion that follows is similar in theme to that presented by Wolpoff (1976) and McHenry (1994, 1996).

Darwin (1871) proposed two mechanisms of sexual selection that can explain sexual dimorphism. One in which males compete with each other for access to females through direct fighting [or more subtle mechanisms such as sperm competition (Ridely, 1993), and the other in which females choose particular males based on male characters that convey some mating advantage. In cases of female choice, females may prefer handicapped males

because the male's survival indicates his high quality, or females may choose healthy, unparasitized males (Ridley, 1993). Darwin believed that sexual selection would operate more powerfully in polygynous than in monogamous species because the level of selection for adaptations that enable males to gain access to females would be proportional to the number of females a male could possibly monopolize. Darwin's original analysis and subsequent work by others (Andersson, 1994; reviewed in Ridley, 1993) has shown this is largely true; sexual dimorphism is mainly found in polygynous species, and body size sexual dimorphism is generally found in polygynous species in which males compete through fighting or the threat of fighting. Within the Order Primates, monogamous species are always monomorphic and polygynous species are usually dimorphic with males often weighing twice as much as females (Clutton-Brock et al., 1977). Thus, we can be relatively confident that australopithecines were polygynous. But is the relatively high level of sexual dimorphism in body and forelimb size observed in australopithecines consistent with selection due to male-male aggression or with selection due to female choice?

Analysis of extant taxa suggests that the sexual dimorphism in body and forelimb size in australopithecines was a product of selection for male-male aggression. Although the belief that competing males rarely injure each other remains strongly held by many biologists (Barnett, 1967; Lorenz, 1963; Tinbergen, 1969), male-male aggression that results in serious injury or death is common among both vertebrates and invertebrates (Andersson, 1994; Berzin, 1972; Clutton-Brock, 1982; Daly and Wilson, 1988; de Waal, 1986; Enquist and Leimar, 1990; Geist, 1971; Hamilton 1979; Huntingford and Turner, 1987; Silverman and Dunbar, 1980; Wrangham and Peterson, 1996). When males compete physically, the potential for serious injury needs to be real for a male to achieve dominance (Andersson, 1994; Darwin, 1871; Geist, 1971; Parker, 1983). Hence, it should not come as a surprise that the relative size of male weapons is strongly correlated with both the extent to which males are larger in body size than females and with the level of polygyny (Andersson, 1994; Clutton-Brock et al., 1977, 1980; Hamilton, 1979; Jarman, 1983; Parker, 1983). Kangaroos and gorillas represent particularly relevant examples. Kangaroos use their forelimbs as weapons in fighting. Among species of kangaroos, dimorphism in the mass of the forelimb musculature and length of the forelimbs is most pronounced in polygynous species (Jarman, 1983). Similarly, gorillas fight with their forelimbs (Wrangham and Peterson, 1996). Zihlman and McFarland (2000) found that the greatest sexual dimorphism in lowland gorillas is in the weight of the forelimbs, weight of the forelimb trunk binding muscles, and the epaxial muscles. Finally, given that extant apes most closely related to australopithecines, *Homo*, *Pan*, and *Gorilla*, all use their forelimbs as weapons during male-male aggression (Wrangham and Peterson, 1996), we can be relatively confident that australopithecines did as well. These observations suggest that the high levels of sexual dimorphism in body and arm size in australopithecines were associated with selection for improved performance in male-male aggression.

Robustness of forelimb joint size in both genders might be argued to be consistent with selection for forelimb dominated arboreal behavior in australopithecines. Selection for climbing performance, however, cannot explain the greater sexual dimorphism in forelimb joint size than hindlimb joint size and spine robustness. Thus, the dramatic sexual dimorphism in forelimb robustness of australopithecines is more consistent with specialization for male-male aggression than with specialization for suspension climbing (Table 1). Similarly, given that male gorillas climb less than female gorillas, climbing cannot account for the sexual dimorphism in forelimb robustness in gorillas (Zihlman and McFarland, 2000; see also results in McHenry, 1992).

Relationship between Vertical Climbing, Bipedal Posture, and Fighting with Forelimbs

Specialization for vertical climbing and forelimb suspension preadapts a lineage for fighting with the forelimbs, both because it predisposes an organism to bipedal posture and because it results in long and powerful forelimbs with high mobility. The ancestor of modern hominoids is thought to have been an arboreal catarrhine adapted for vertical climbing and forelimb suspension (Begun et al., 1997; Harrison, 1991; Rose, 1997; Ward, 1997). The out group to extant hominoids for which post-cranial anatomy is best known, *Oreopithecus*, has a suite of characters that suggest it was an adept vertical climber that relied on forelimb suspension (Harrison, 1991). These include features that: 1) strongly differentiated usage of the hind and forelimbs (i.e., long and robust forelimbs relative to hindlimbs), 2) increased ability to raise the forelimbs above the head, 3) greater potential for circumduction at the shoulder and pronation-supination at the elbow and wrist, 4) increased potential for powerful grasping of large diameter vertical supports with the hands, 5) adoption of a more orthograde trunk posture, 6) an increased potential for full extension of the hip and knee joints, 7) greater ranges of rotation at the hip and knee joints and inversion-eversion at the ankle joint, and 8) an increased potential for body weight to be supported by a single hindlimb. Although these eight abilities, present in extant great apes (Gregory, 1916, 1928; Hunt, 1991b; Morton, 1926) and inferred from the postcranial anatomy of Miocene hominoids (Begun et al., 1997; Harrison, 1991; Rose, 1997; Ward, 1997), are associated with selection for climbing and forearm suspension, each ability can be argued to enhance fighting performance. Highly mobile, long and robust forelimbs and hands would increase the potential for striking, grasping, and manipulating opponents with the forelimbs. An increase in orthograde trunk posture (5) and an increased ability to support the body bipedally on the hindlimbs (6, 7, and 8) would free the forelimbs to be used as weapons. Finally, associated with the arboreal behaviors of vertical climbing and forelimb suspension are powerful shoulder and brachial muscles that produce hoisting and lateral transfer of the body (Tuttle et al., 1983; Tuttle and Basmajian, 1974, 1978). These are the same muscles that can be inferred to be employed in arching, over-the-head and roundhouse punches that chimpanzees and gorillas are observed to use when fighting (Goodall, 1986; Wrangham and Peterson, 1996). Thus, selection for improved vertical climbing and forelimb suspension can be argued to preadapt a species for fighting with its forelimbs.

Many quadrupedal mammals adopt a bipedal posture when fighting, such as rats and mice, squirrels, dogs, bears, tigers, and horses. Among apes, both chimpanzees and gorillas adopt a bipedal posture for threat displays (Jablonski and Chaplin, 1993), beating an opponent with the forelimbs (Goodall, 1986; Livingstone, 1962; Wrangham and Peterson, 1996), jumping on an opponent that is lying on the ground (Goodall, 1986), and grabbing an opponent to deliver bites (Goodall, 1986; Wrangham and Peterson, 1996). Chimpanzees also stand bipedally to use weapons such as rocks and clubs (de Waal, 1989; Goodall, 1986; Kortlandt, 1980; Wrangham and Peterson, 1996). Thus, bipedal posture allows the forelimbs to be used as weapons to beat, restrain, and manipulate opponents. For a species that is normally quadrupedal, adoption of an upright bipedal posture also significantly reduces rotational inertia of the body (Carrier et al., 2001; Lee et al., 2001), increasing the speed at which the individual can rotate to face a new direction, as well as increasing the speed, and likely the power with which a round-house blow can be applied to an opponent. Hence, characters that improve balance and strength in a bipedal stance would likely enhance fighting ability in a lineage of quadrupeds that uses forelimbs as weapons. These arguments lead one

to the suggestion that the bipedal posture and locomotion of early australopithecines may have improved their fighting performance relative to that of their more fully arboreal ancestors (Table 1).

The idea that selection for aggressive behavior may have played a role in the evolution of hominid bipedalism is not new. Wescott (1967) suggested the evolution of bipedalism allowed agonistic exhibitionism in which bipedal behavior made the individual appear larger and more threatening. Jablonski and Chaplin (1993) have argued that the bipedal activities that were critical to the differentiation of the Hominidae were those involved in the control of intragroup aggression, the successful resolution of intergroup conflicts, and the acquisition of mates. The most important behaviors in this context, they suggest, were bipedal displays, bipedal charges, and bipedal mock fights and deference to these behaviors. Livingstone (1962) used observations of aggressive bipedal chest-thumping, charging, and fighting in gorillas to argue that aggression was fundamental to the evolution of hominid bipedalism. Both Washburn (1967, cited in Guthrie (1970)) and Guthrie, (1970) have suggested that as forelimbs became more important in aggression in the lineage from which hominids evolved, a bipedal posture was adopted not only in fighting but also to present a more formidable appearance in height and breadth. Kortlandt (1980) suggested that early hominids adopted an upright posture and gait to be able to wield thorn branches as a defense against their predators.

In addition to using bipedal posture when fighting, male chimpanzees and bonobos appear to prefer to fight while on the ground rather than from an arboreal perch. The most violent and serious fights in both chimpanzees and bonobos occur on the ground (de Waal, 1986, 1989; Goodall, 1986; Kano, 1992; Wrangham and Peterson, 1996). In contrast, when attempting to avoid physical aggression from other males, both chimpanzees and bonobos retreat by climbing into trees (de Waal, 1989; Goodall, 1986; Kano, 1992). These observations highlight the importance of the terrestrial substrate during fighting in our closest living relatives and are consistent with the hypothesis that specialization for balance and strength in bipedal posture may have improved fighting ability in early hominids.

Thus, selection for increased male–male aggression may have helped draw the early hominids to the ground. Alternatively, the necessity of greater terrestrial specialization, due to the opening of the habitat, may have opened the door for greater fighting specialization in early australopithecines by freeing the forelimbs from their primary role in climbing. In either case, it is likely that as a consequence of terrestrial specializations early australopithecines had greater fighting abilities and were more dangerous opponents than were their arboreal ancestors.

Summary

Several lines of evidence lead to the suggestion that australopithecines were specialized for male–male aggression. First, relative to *Homo*, many aspects of the australopithecine musculoskeletal system appear to have conferred high potential for fighting with the forelimbs: long powerful forelimbs, short hindlimbs, broad pelvic girdles, limited potential for storage and recovery of elastic strain energy in muscle-tendon systems, robust muscles that raise the pectoral girdle on the trunk, and proficiency in bipedal stance and gait. Although some of these features were characters inherited from arboreal ancestors, they would have conferred high fighting performance in the first hominids. Most importantly, the high ratio of forelimb to hindlimb joint robustness, the very wide hips, relatively short hindlimbs, and the robust axial and appendicular muscles of the head and neck are more

consistent with specialization for fighting with the forelimbs than with specialization for suspension climbing or terrestrial locomotion. Second, the high level of sexual dimorphism in body and forelimb size in early australopithecines is also more consistent with high levels of male–male aggression than with specialization for climbing. Third, it can be argued that specialization for terrestrial locomotion and bipedal posture likely improved the fighting performance of australopithecines relative to their arboreal ancestors. Thus, australopithecines appear to have been apes that were specialized for both a terrestrial habitat and for male–male aggression.

IMPLICATIONS OF THE RUNNING-FIGHTING DICHOTOMY TO THE EVOLUTION OF *HOMO*

Homo sapiens is a violent species, and the pattern of modern violence indicates that homicide and warfare are often causally tied to male–male competition for access to reproductive females (Daly and Wilson, 1988; Keeley, 1996; Wilkinson, 1997; Willey, 1990; Wrangham and Peterson, 1996). The analyses by Daly and Wilson (1988) have shown that the predominant form of homicide by humans involves males killing other males. Across cultures, same-sex homicides are on average 27 times more likely to be among males than among females. Daly and Wilson (1988) argue that sexual selection theory (Bateman, 1948; Trivers, 1972) predicts the cross-cultural universality of this enormous sexual difference in the incidence of same-sex homicide. They also relate a young man's social standing and life prospects to the probability that he will turn to violence in his pursuit of status, resources, and women. Hence, evidence from modern humans indicates that we are a violent species and the evolutionary basis of much human violence appears to be the result of sexual selection for male–male competition.

Yet a comparison of *Homo* and *Australopithecus*, indicates there is less anatomical specialization for fighting in *Homo* than was the case in early hominids. Some of the most conspicuous changes that occurred in the evolution of *Homo* from an australopithecine ancestor include an increase in body size, a reduction in relative forelimb length and robustness, a lengthening of the hindlimb, a reduction in the relative size of the feet, a relative narrowing of the pelvis, development of a more barrel-shaped chest, reduction in relative head mass, reduction of relative gut size, larger surface to volume ratio, and a drop in sexual dimorphism. Each of these changes can be argued to represent anatomical changes that would have facilitated economical transport and locomotor stamina (see above discussion; Bramble, 1990, 2000; Carrier, 1984; Jungers, 1991; Kramer and Eck, 2000; McHenry, 1994; Ruff, 1991, 1994; Wolpoff, 1999). Within the context of the locomotor-fighting dichotomy, however, they are also changes in body configuration (excluding the increase in body mass) that would reduce male fighting ability. Nevertheless, if modern *Homo sapiens* are representative of the genus, male–male aggression and propensity for male violence are unlikely to have abated with the emergence of *Homo* (see for example Daly and Wilson, 1988; Frayer, 1997; Keeley, 1996; LeBlanc, 1999; Wrangham and Peterson, 1996). Thus, our species is specialized both for locomotor stamina and male–male aggression, and this appears to be in conflict with the suggestion that there are functional tradeoffs between specialization for fighting performance and specialization for locomotor economy. Are the functional tradeoffs between running and fighting a false dichotomy?

The distinctions that I wish to raise between *Australopithecus* and *Homo* are based on body shape and locomotor anatomy. Hence, in this discussion I will follow the division

proposed by Wood and Collard (1999) and Wolpoff (1999) in which *Paranthropus* and *H. habilis* and *H. rudolfensis* are grouped with the australopithecines and the genus *Homo* is represented by *H. ergaster*, *H. erectus*, *H. neanderthalensis*, and *H. sapiens* [i.e., *H. sapiens* (Wolpoff, 1999)].

Cervids, Bovids, Antilocapra, and Macropods

Humans are not the only species that are both locomotor and fighting specialists. In terms of running speed and stamina three families of artiodactyls appear to be the top performers. Although cheetahs are often recognized as being the fastest runners on the planet, species in the artiodactyls families Cervidae, Bovidae, and Antilocapridae run almost as fast, and are known to have much greater stamina than the fastest cat (Lindstedt et al., 1991; Nowak and Paradiso, 1983). Yet these three families of artiodactyls are also recognized for their polygynous mating systems with intense male competition and male-male aggression (Andersson, 1994; Geist, 1971; Jarman, 1989). At first glance, these artiodactyl families appear to falsify the hypothesis of a running-fighting dichotomy.

Alternatively, these artiodactyl lineages may have circumvented the limits imposed by the dichotomy. Each of these groups, apparently independently (Janus, 1982), evolved a new weapon system, horns or antlers, which is largely independent of the locomotor system. The basal weapons of mammals are teeth, claws, and limbs. But cervids, bovids, and antilocaprids evolved teeth that are grinding machines for tough, fibrous plant material, and evolved limbs that function primarily as pogo sticks for economical transport. In other words, their basal weapons have become so specialized for feeding and locomotion that they no longer function as effective weapons. The evolution of new weapons, horns or antlers, in each of these lineages very likely made extreme specialization of teeth and limbs possible.

If the evolution of new weapons systems that are independent of locomotor function can circumvent the functional conflicts between running and fighting, then two predictions can be made. First, artiodactyls with horns or antlers should be better runners than artiodactyls without these weapons. Second, artiodactyls with horns or antlers should be better runners than other cursorial mammals. Figure 4 shows that these predictions are largely true in regards to running speed. Thus, the evolution of horns or antlers in three families of artiodactyls may have circumvented the locomotor-fighting dichotomy, allowing greater specialization for running speed and stamina than is possible in other mammalian lineages.

In this context, kangaroos also warrant consideration. Although not as fast as many species of artiodactyls, kangaroos are among the most economical of runners. The hindlimbs of kangaroos function so well in the storage and recovery of elastic strain energy (Biewener et al., 1998) that the energetic cost to run a given distance actually decreases as running speed increases in the species *Macropus rufus* (Dawson and Taylor, 1973). This high capacity for elastic storage is expected to diminish fighting ability (see discussion above), yet larger species of kangaroo such as *M. rufus* are noted for fierce fighting among males over access to females. Kangaroos fight with their forelimbs. They use their forelimbs to punch, and to hold their opponent around the head, neck and shoulders while they bite (Jarman, 1989). Other species hold the opponent at arm's length, clawing at the face and positioning him for a kick with the hind feet. Consistent with forelimbs being weapons, sexual dimorphism in muscular strength and length of forelimbs is highly correlated with the level of sexual dimorphism in body mass (Jarman, 1989). Hence, adoption of a bipedal hopping gait has allowed the forelimbs to become specialized for fighting. Specialization of the forelimbs

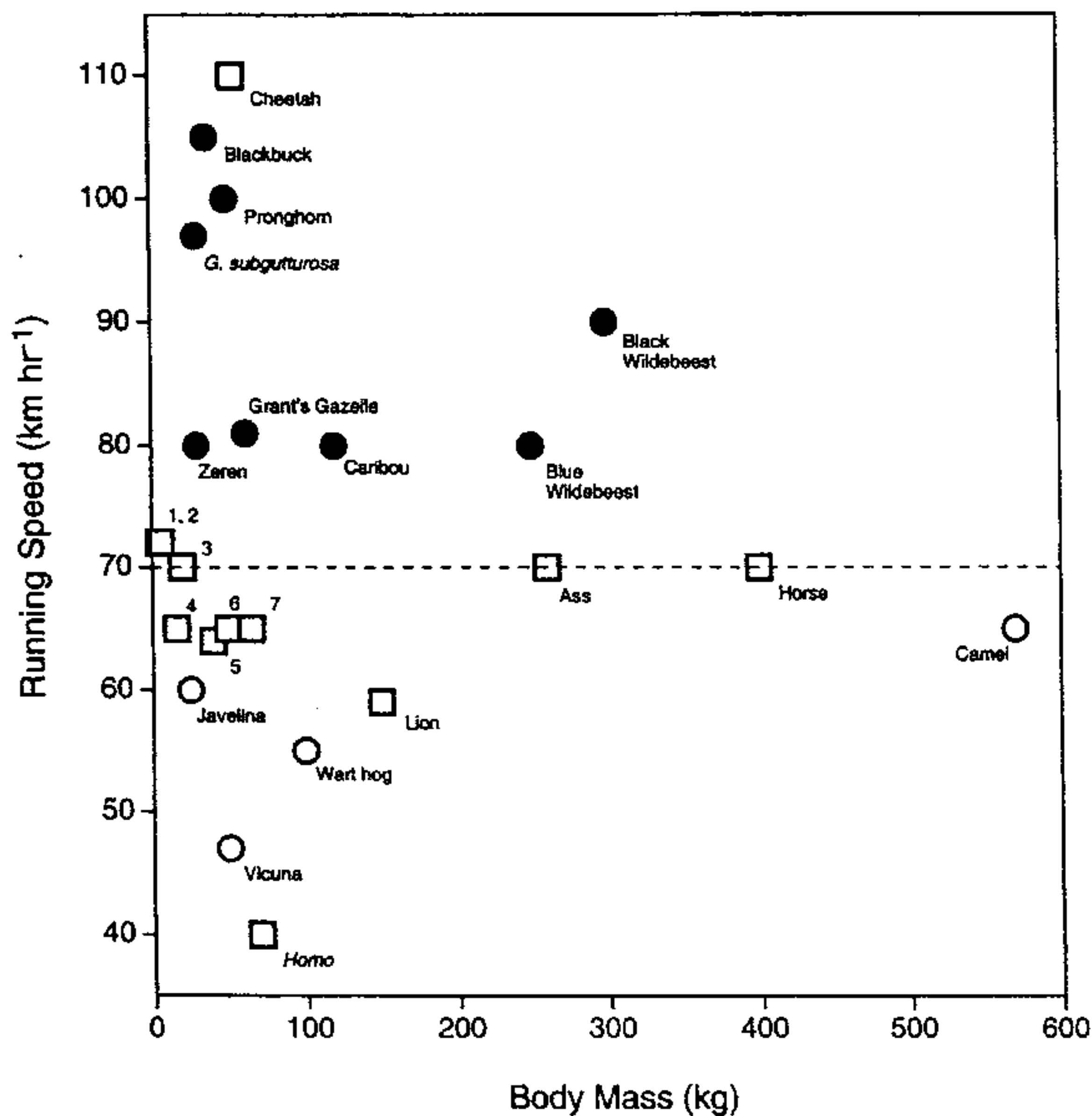


Figure 4. Maximum running speeds for representative cursorial mammals plotted against the average body mass of the species. Solid circles are species with horns or antlers from three artiodactyl families: Bovidae, Antilocapridae, and Cervidae. Open circles are species of artiodactyls that lack horns or antlers from two families: Suidae and Camelidae. The open squares are species of other cursorial mammals that also lack horns or antlers: 1) antelope jackrabbit, 2) fox (*Vulpes fulva*), 3) African hunting dog, 4) coyote, 5) gray wolf, 6) red kangaroo, 7) spotted hyena. Thus, the fastest artiodactyls with horns or antlers are faster runners than artiodactyls without these weapons. The fastest artiodactyls with horns or antlers are also faster runners than other cursorial mammals, with the exception of cheetahs. All speed records come from a compilation by Garland (1983), except for those of the Suidae and Camelidae that are from Nowak and Paradiso (1983). The speed of javelinas is an estimate based on their ability to out maneuver and escape coyotes (Nowak and Paradiso, 1983).

for fighting may, in turn, have allowed the hindlimbs to become more highly specialized for storage and recovery of elastic strain energy during running.

Invention of New Weapon Technology and the Evolution of *Homo*

Analogous to the evolution of new weapons in bovids, cervids, and antilocapra, the invention of weapon technology by early hominids may have reduced the conflict between selection for locomotor stamina versus selection for male–male aggression, and allowed a greater independence in the evolution of characters associated with running and fighting. In other words, the invention of new weapons may have allowed the evolution of locomotor specialization in the human lineage.

Among cursorial mammals, modern humans are one of the best distance runners (Carrier, 1984). Humans are not fast runners, but we do have an ability to cover great distances more rapidly than most species. This ability is remarkable given our relatively

recent arboreal ancestors and the relatively high energetic cost of human running. The physiological mechanisms that allow humans to be elite distance runners, in spite of their high cost of transport, are not well understood. Humans have been suggested to have 1) superior abilities to dissipate metabolic heat (Carrier, 1984; Porter, 1993; Wheeler, 1984, 1991), and 2) an uncoupling of locomotor, ventilatory, and thermoregulatory functions that facilitates sustained vigorous running (Carrier, 1984). Recent work in sheep and dogs indicates that, in species that pant to thermoregulate and couple their ventilation to the locomotor cycle, regulation of body temperature during running does compete with both the minimization of ventilatory work and pH balance (Entin et al., 1998, 1999; Wagner et al., 1997). Thus, independence of locomotor and ventilatory cycles, as well as cutaneous evaporative cooling, may indeed give humans an advantage in endurance running relative to many other species. In any case, humans are elite endurance runners and hominids evolved this capacity in a relatively short period of time from ancestors that were not specialized for running.

Anatomical features indicating cursorial specialization of *Homo* appeared in the fossil record approximately 2.0 to 1.8 my ago (Klein, 1999; Wolpoff, 1999). The earliest stone tools appeared somewhat earlier, just over 2.5 my ago (Harris and Capaldo, 1993). Foley (1987) has argued on the basis of tool use by chimpanzees (Boesch and Boesch, 1983; Goodall, 1970), that simple tool use is an ancestral hominid trait that may have had its origin in Miocene hominoids. Use of weapons, a category of tool, also likely predate the origin of hominids. Although the primary weapons of our closest living relatives are forelimbs and teeth, chimpanzees also occasionally attack by throwing rocks (de Waal, 1989; Goodall, 1986; Kortlandt, 1980) and wielding branches as clubs (Kortlandt, 1980). Given that the two extant hominoids most closely related to basal hominids, chimps and humans, use weapons, we can be relatively confident that early australopithecines used simple weapons as well.

The first weapons used by hominids in intraspecific aggression would have been relatively simple, such as the stones and tree branches used rather ineffectively by extant chimpanzees. Nevertheless, at the inception of weapons that concentrate force in order to pierce tissue, such as pointed wooden spears, or weapons that optimize the energy imparted in a blow to an opponent, such as clubs of the correct mass and rotational inertia, success in physical combat would have begun to shift from the opponent with the advantage in physical strength and quickness to the opponent with the best weapon design. In this context, it is worth noting that the history of human warfare, and therefore the course of human history, has been substantially influenced by weapon innovation and dissemination (LeBlanc, 1999; O'Connell, 1989; van Creveld, 1991). Thus, the invention of new weapon technology may have shifted the effect of selection for aggressive behavior from favoring physical performance to favoring creativity and technical innovation in the lineage from which *Homo* evolved.

If the invention of weapon technology did allow greater specialization for locomotor stamina in hominids, two predictions can be made. First, one would predict a reduction in sexual dimorphism in body and forelimb size with the appearance of specialization for locomotor stamina. Second, evidence of injuries from weapon use could be expected in the fossilized bone of individuals that have specializations for locomotor stamina.

✱ The changes in sexual dimorphism in body size during hominid evolution are consistent with weapon innovation achieving greater importance in male–male aggression at the time of emergence of *Homo*. Sexual dimorphism in body size declined from the early australopithecines to *Homo ergaster* (McHenry, 1996). This decline has been interpreted to

represent a decline in male–male aggression (McHenry, 1996). Alternatively, the invention of new weapon technology may have diminished the selective value of relatively large brawny males, and favored males and females of more similar size and shape for the sake of economical distance transport.

The incidence of healed cranial injuries also appears to be consistent with weapon innovation being associated with the evolution of *Homo*. Although there appears to be a high incidence of healed cranial fractures in early *Homo*, such injuries are not known in the fossil record of *Australopithecus* (Wolpoff, 1999). The clearest examples of healed cranial fractures come from the Zhou-Kou-Dian and Ngandong Middle Pleistocene *Homo erectus* sample (Weidenreich, 1943, 1951) and from the Neandertal sample (Berger and Trinkaus, 1995; Zollikofer et al., 2002). Of the eleven crania represented in the Ngandong sample, Weidenreich (1951) discusses healed cranial injuries in three skulls (I, IV, and VI). He attributes the injuries in skulls IV and VI to interpersonal violence, and “to have resulted from the effect of cutting blows (Skull IV), and the wielding of blunt weapons (Skull VI) . . .”. In an analysis of the anatomical distribution of traumatic lesions, Berger and Trinkaus (1995) found a similar incidence of head and neck injuries in Neandertals. Thirty percent of the specimens exhibited evidence of head or neck trauma. They found a tight correspondence between the pattern of injuries in the Neandertal sample and that of modern Rodeo athletes and, therefore, speculated that the Neandertal pattern of injury might have been the result of trauma sustained during predation on large game animals. Berger and Trinkaus, however, do acknowledge the possibility that the Neandertal injuries were caused by interpersonal violence and there does not appear to be evidence to exclude this possibility. The recently described healed fracture in the St. Césaire Neandertal is suggested to have resulted from interpersonal violence (Zollikofer et al., 2002). Finally, the Dmanisi 2280 skull provides evidence of large cranial injuries in *Homo* dating back to 1.7 million years ago (Wolpoff, per. com.). Given that neither modern humans nor nonhuman apes have the ability to crush the skulls of adult conspecifics with their bare hands, these examples of cranial injury in early *Homo* may be evidence of head-crushing weapons.

Structural buttressing and thickening of the cranium distinguishes early *Homo* from *Australopithecus* and may be related to the increased incidence of cranial injury. Cranial buttressing that separate *H. ergaster* and *H. erectus* from *Australopithecus* (including *A. habilis*) include the formation of a pronounced supraorbital torus (i.e., browridge) with a supratrochlear sulcus; an occipital torus (Klein, 1999); a torus along the temporal lines; one along the top of the cranium, and tori above the mastoids and ears (Weidenreich, 1943; Wolpoff, 1999). This buttressing, in particular the supraorbital torus, does not appear to be a function of mechanical loading due to mastication (Hylander and Ravosa, 1992; Lieberman, 2000; Ross and Hylander, 1996). Lieberman (2000) provides a review of the developmental basis of the supraorbital torus and relates differences in projection of the torus among groups of *Homo* to differences in facial projection and the cranial base. Formation of large occipital tori in the crania of early *Homo* has been suggested to be associated with enlarged occipital muscles necessary for head stabilization during running (Bramble, 1991, 2000). Independent of the developmental basis of cranial buttressing and possible functional implications to mastication and locomotion, cranial buttressing in early *Homo* must have resulted in a general strengthening of the cranial vault (Weidenreich, 1943; Wolpoff, 1999). Additionally, the cranial bones of early *Homo* were often much thicker than those in either *A. africanus* or *A. habilis* (Weidenreich, 1943; Wolpoff, 1999). This thickening of the cranium may be a developmental response to increased intensity of locomotor activity, as suggested by

Lieberman (1996). Nevertheless, evidence from the limb bones of domestic dogs indicates that bone thickness can be highly heritable (Chase et al., 2002; Lark pers. com.). These observations raise the possibility that the buttressing and increased thickness of the crania observed in *H. ergaster* and *H. erectus* may have been an adaptive response to an increased likelihood of cranial injury.

Summary

The observation that modern humans are both elite distance runners and a physically violent species appears to defy the hypothesis of functional tradeoffs between specialization for locomotion and specialization for fighting. Humans, as well as bovids, cervids, and antilocapra, however, may be the exceptions that prove the running-fighting dichotomy. All four groups appear to have evolved exceptional locomotor performance in association with the evolution or invention of new weapon systems that are largely independent of locomotion. In the case of hominids, the evolution of *Homo* may have been dependent on the invention of weapons that allowed specialization for locomotion and fighting to proceed independently.

CONCLUSIONS

Many aspects of their musculoskeletal system, as well as a high level of sexual dimorphism in body and forelimb size, suggest that australopithecines had a high level of male–male aggression. Furthermore, the adoption of bipedal posture and a terrestrial habitat are likely to have improved fighting performance in the early australopithecines relative to their arboreal ancestors. Indeed, selection for fighting performance may be one of the factors that led the ancestors of hominids to spend more time on the ground and adopt a bipedal striding gait. Thus, australopithecines appear to have been fighting specialists.

The characters that made australopithecines adept fighters, however, must also have limited their terrestrial locomotion. Their pronounced forelimb strength, short stature, limited potential for storage and recovery of elastic strain energy in the muscle-tendon systems of the limbs, wide hips, and robust head and neck would likely have made australopithecines inefficient runners by modern human standards. Nevertheless, in a relatively short period of a few million years, hominids evolved from arboreal climbers into a species that is one of the best distance runners on the planet. If the functional tradeoffs entailed in the running-fighting dichotomy are real, the evolution of elite endurance capacity in a lineage that was specialized for fighting represents a fundamental change in evolutionary trajectory. Gaining an understanding of the causes of this change in evolutionary pathway will likely improve our understanding of human nature and help explain why humans evolved.

Rather than trading fighting performance for locomotor stamina, I suggest that selection for male–male aggression resulted in the invention of weapon technology in the ancestors of *Homo*. By reducing inherent functional conflicts, the new weapons allowed the evolution of increased locomotor speed and stamina. With the invention of the first effective weapons selection for aggression in early hominids would have shifted from favoring greater physical strength and agility to favoring creative innovation. In this scenario, the emergence of *Homo* is: 1) dependent on the invention of new weapons, and 2) represents both greatly improved

distance transport and increased lethality in a lineage that was already specialized for fighting.

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