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Origin of habitual terrestrial bipedalism in the ancestor of the Hominidae

In this paper, the evolution of habitual terrestrial bipedalism in the stem proto-hominid is reconstructed through an examination of historical transformations of shared derived morphological–behavioural complexes related to bipedalism in catarrhines. This historical reconstruction indicates that the bipedal threat display–appeasement behaviour complex may be of particular importance in understanding the origin of habitual terrestrial bipedalism because it is the most recently acquired morphological–behavioural complex shared by the African great apes and humans.

We suggest that in the late middle and late Miocene of East Africa, as habitats were becoming more open and desiccated and resources more widely separated, increased intraspecific competition among pre-hominids for resources ensued. We propose that bipedal displays and their appeasement were the behaviours essential to the success of pre-hominids in this environment in that they allowed for the relatively peaceful resolution of intragroup and intraspecific conflicts. This theory provides a major, proximate pre-adaptive cause for the later adoption of bipedalism by proposing the use of an existing behaviour in a new environmental context, namely increased use of, and deference to bipedal displays to mitigate violence and make possible the equitable allocation of scarce resources. It is suggested that this increased the evolutionary fitness of pre-hominids by removing a major cause of morbidity and mortality observed in living African apes, i.e. intra- and intergroup aggression.

This theory of the origin of habitual terrestrial bipedalism in the ancestor of the Hominidae differs from others in that it is consistent with available environmental, palaeontological, anatomical and behavioural evidence and known types of social organization in extant hominoids.

Bipedal postures, once adopted for social control, would have become common elements of the pre-hominid locomotor repertoire. With time, this new locomotor mode would have become increasingly multifunctional.

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Introduction

Among primates, humans are unique in their possession of habitually bipedal posture and locomotion. For many years the evolution of upright posture was viewed as a relatively easily accomplished, gradual trend, while the increase in relative brain size was viewed as a rapidly evolved discontinuity that was unique both in its evolutionary mode and in the magnitude of its effect (Gould, 1979). In the last 20 years, however, it has been more widely acknowledged that it is the evolution of habitual bipedalism that is the surprise, while the subsequent enlargement of our brain "is, in anatomical terms, a secondary epiphenomenon, an easy transformation embedded in a general pattern of human evolution" (Gould, 1979:44). We now recognize that bipedalism evolved before the relative cranial capacity of the basal hominid had developed barely beyond the range of modern apes (Eccles, 1989; McHenry, 1982). Habitual bipedalism was not driven by encephalization, but *vice versa*. Bipedalism and subsequent encephalization, in association with the manufacture and use of tools and the emergence of a more sophisticated social organization, have been considered of paramount importance in defining the emergence of the Hominidae from the Hominoidea (Lovejoy, 1981) and bipedalism itself is seen as a prerequisite for subsequent human development (Simons, 1989; Stringer, 1984).

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McHenry (1982) pointed out that theories on the origin of bipedalism are both important and speculative: important because they are implicated in the differentiation of the Hominidae; speculative because they require reconstruction of many anatomical, behavioural and ecological unknowns. We have witnessed in recent years a dramatic growth in the number and sophistication of studies dealing with the anatomical and physiological concomitants of hominid bipedalism, but there remains a shortage of well-reasoned explanatory models to account for its origin. In this paper we develop a theory for the origin of habitual terrestrial bipedalism in the ancestor of the Hominidae that is based on a historical reconstruction of morphological–behavioural complexes in the Hominoidea and that is consistent with our current understanding of the palaeoenvironmental and biogeographical conditions that existed in East Africa when habitual bipedalism in the ancestor of the Hominidae is thought to have been evolving.

The timing of the origin of bipedalism

It is now widely accepted that the footprints at Laetoli were those of habitual, although not necessarily completely modern, upright hominid walkers. Habitual bipedalism was thus established at least before the time of footprints at Laetoli some 3·6 Ma (e.g., Simons, 1989; White, 1980; White & Suwa, 1987). Furthermore, it is possible that this mode of locomotion is 2 or more million years older than that on the basis of putative older East African hominids (Hill & Ward, 1988). Fossil evidence would thus indicate that terrestrial bipedalism emerged in the Hominoidea in the late Miocene, between approximately 10 and 5 Ma.

There now also exists plentiful indirect evidence from geological and palaeoecological studies that bears on the timing of the evolution of hominid bipedalism. The evolution of habitual bipedalism is clearly linked to an increasingly terrestrial habitus and this in turn appears to be closely related to environmental change in Africa during the middle and late Miocene. In East Africa, the transition from closed or evenly forested environments to drier and more open environments with less evenly distributed resources has been related to global climatic events (e.g., Vrba, 1985) and to regional climatic events triggered by the growth of the mountains near the Western Rift Valley (Pickford, 1991, 1992). There now appears to be a consensus that, between 10–5 Ma, an array of potential environments was available in East Africa, including forests and woodlands in well watered areas and mosaics of grassy woodland and wooded grassland elsewhere (Retallack *et al.*, 1990). However, recent studies of the nature and timing of the appearance of grasslands in East Africa have provided evidence that a significant biomass of C_4 grasses did not appear until 8 or 9 Ma (Cerling *et al.*, 1991), and that prior to this time, the landscape was dominated by closed woodland or forest habitats.

Chaline *et al.* (1991) recently proposed that the common ancestor of *Gorilla*, *Pan* and *Homo* was polytypic and consisted of three subspecies that became isolated and subsequently divergently specialized as a result of environmental change by means of a vicariant event.

Theoretical considerations

Any theory purporting to explain the origin of habitual terrestrial bipedalism must be in accord with available environmental, palaeontological, anatomical and behavioural evidence. With respect to environmental considerations the theory must be consistent with information pertaining to the structure of the habitat, including the inferred distribution of food and water resources, thought to have been occupied by pre-hominids. In connection with palaeontological and anatomical evidence the theory must be consistent with what is known of the structure and function of the locomotor system in the earliest known fossil hominids. It must account for the evolution of positional behaviour equally well between both sexes and cannot rely on a unisexual behaviour (Zihlman, pers. comm. quoted in Falk, 1990:343). Further, it must also be compatible with what is known about the degrees and kinds of sexual dimorphism in early hominids. Finally, the theory must be consistent with behavioural information. Many kinds of evidence now support the close phyletic relationship of humans and the African great apes. A theory of the origins of terrestrial bipedalism must take cognizance of the fact that we are seeking to identify a set of behaviours in the common ancestor of hominids and the African great apes that are consistent with the locomotor and postural behaviours of modern humans and the extant African great apes. A theory concerning the origin of habitual terrestrial bipedalism is by definition one that attempts to explain the ultimate causes of speciation or lineage splitting that led to the origin of the Hominidae. Here we explicitly recognize that gorillas and chimpanzees have enjoyed relatively long periods of independent evolution that have resulted in their development of unique behavioural and anatomical specializations. Such a theory must therefore be able to account equally well for the evolution of locomotor and other specializations in the lineage leading to modern hominids and that leading to the modern African great apes.

Mayr (1976) pointed out that for almost any biological phenomenon we might want to study there is always a set of proximate causes and a set of ultimate causes that have to be explained and interpreted for a complete understanding of the given phenomenon. In connection with the evolution of bipedalism, the ultimate cause is the environmental change in equatorial Africa described above that led to a fragmentation of the habitats of some Miocene apes and the establishment of ecological barriers between some ape populations (discussed further below). The major proximate cause for the evolution of bipedalism was a pre-adaptation for orthograde posture among apes, related to a vertical climbing habit. A set of more specialized proximate causes for the evolution of bipedalism must also have operated in the history of the Hominoidea and these are described in detail below. The proximate goal of adaptation is improvement in performance of some particular task, whereas the ultimate goal is increase survival of progeny (Oxnard, 1975).

Bioenergetics and the course of evolution of bipedalism

The adoption of a major evolutionary novelty in a population requires that the novelty confer a survival advantage and greater reproductive success to individuals in the population even during the course of its development. This must have been true of the evolution of habitual terrestrial bipedalism, but the specific survival and reproductive advantages of this mode of locomotion have long been disputed.

Some have argued that the rarity of habitual bipedalism can be interpreted as meaning it is inefficient and, therefore, unlikely to evolve (Bartholemew & Birdsell, 1953). Others have suggested that bipedality was more efficient for covering long distances and that it imparted an increased capacity for great physical endurance during locomotion (e.g., Campbell, 1966; Napier, 1963, 1967; Washburn, 1960).

Taylor & Rowntree (1973) demonstrated that for chimpanzees and capuchin monkeys neither of the above postulates appears valid. They demonstrated that these animals expended the same amount of energy whether running on two or four legs. Taylor *et al.*

(1982) showed that metabolic energy consumption (measured as energy cost per stride for each gram of muscle at an equivalent speed) was almost the same for large and small animals and for bipeds or quadrupeds. This reinforced Taylor & Rowntree's earlier conclusion that energy cost should not be used in arguments about the evolution of bipedal locomotion in humans because neither bipedal nor quadrupedal progression could be seen as having an energetic advantage. This judgment has been further strengthened by Alexander's (1991) conclusion that human walking is not significantly more economical in metabolic terms than is quadrupedal walking in mammals.

Rodman & McHenry (1980) compared the energetic costs of the apes tested by Taylor & Rowntree (1973) and humans to the predicted cost for mammals based on the formula of Taylor *et al.* (1970). They found that, as Taylor & Rowntree (1973) had indicated, the locomotor costs of apes were 149% of the predicted value. The humans, in contrast, were more efficient, at only 86% of predicted cost for mammals. From this it was concluded that chimpanzee locomotion was energetically more expensive than that of other mammals and especially as compared to that of humans. Rodman & McHenry (1980) suggested that the energetic advantage offered by bipedalism must have been an important factor in the emergence of bipedalism in one group of hominoids. Following publication of their study, figures for the energetic costs of locomotion in the patas monkey became available and these too were lower than the predicted figure for mammals in general, at 83% (Mahoney, 1980). Therefore, from these results it is clear that no special advantage can be identified for human bipedalism over primate quadrupedalism. As Taylor & Rowntree (1973) suggested, no conclusions should be drawn from energetics to why one form of locomotion was preferred over the other.

The great difference between the energetic costs of locomotion in Taylor & Rowntree's (1973) chimpanzees and humans may indeed have a further explanation. The metabolic expenditure of their chimpanzees was 63% above that of humans at 2·9 km/h (Rodman & McHenry, 1980). This considerable difference was not found by Yamazaki *et al.* (1983), who indicated that chimpanzees were only 16% more costly than humans in bipedal walking. Taylor & Rowntree's (1973) much higher figure may have been due to the younger age of their chimpanzees, as the average weight of their animals was 17·5 kg. Juvenile animals have higher metabolic rates than adults (Kleiber, 1961). Adult chimpanzees at 38 kg have a basal metabolic rate that is approximately 50% lower (Bruhn & Benedict, 1936) than the resting rate of juveniles (assuming it is 1·7 times lower than the *Y*-intercept Taylor *et al.*, 1970) and this difference would be reflected in lower total energetic costs of locomotion in adults.

Unfortunately, there appear to be no direct figures available for metabolic energy expenditure in stationary, bipedally standing apes. Alexander (1991) gave a figure of 0·21 W/kg as the difference between supine and standing humans. This is a higher expenditure than the figures for cattle and sheep, both dedicated standers. Abitbol (1988) rated dogs as much less efficient than humans when just standing, but claimed a lower efficiency than either dogs or adult humans for the compromise morphology of infant humans. Coelho (1986) used figures calculated from human tests to extrapolate energy budgets for baboons. From these he calculated that rearing up on the hind legs was twice as energetically costly as quadrupedal standing. All forms of locomotion were rated the same, approximately 3·5 times higher than bipedal standing. It seems reasonable to infer from the above that with their human infant-like compromise morphology, standing facultatively bipedal apes would consume more energy than do quadrupedally standing apes, and would consume much more than bipedally standing adult humans. Therefore, a distinction must be made between static and moving bipedalism and this distinction must be applied to any theories of the origin of bipedalism derived from studies of energetics.

Rose (1991) pointed out there are profound differences between the bipedalism of humans and non-human primates because of "the lack of commitment" to bipedalism in the positional morphology of nonhuman primates. The relative mechanical efficiencies of a committed bipedal morphology (*sensu* Rose, 1991) in bipedalism and a compromise morphology in facultative bipedalism point to a different bioenergetic interpretation. In facultative bipeds the levels of activity of lower limb muscles, the distribution of body weight and the magnitude of reaction forces of muscles on joints differ significantly from committed bipeds (Okada & Kondo, 1980; Tuttle *et al.*, 1979; Yamazaki & Ishida, 1984). Therefore, a compromise morphology is poorly suited for prolonged bouts of bipedalism because of the high levels of muscular activity necessary to maintain the knee at an angle of 120–140° (Tuttle *et al.*, 1979) and because the lower limb joints are overloaded by the need to maintain flexed positions and to control relatively large excursions of the centre of gravity (Prost, 1980; Rose, 1991; Yamazaki & Ishida, 1984). The increased work of the lower limb musculature in facultative bipedal standing would tend to justify the above supposition that this posture would consume more energy.

We are thus left with the critical question of what adaptive advantage would have accrued to proto-hominids through the adoption of an early form of bipedalism. This form would have been more costly when stationary, neither more nor less metabolically efficient than quadrupedalism for progression, but it would have been less mechanically proficient.

Adaptation usually fulfils one set of selective requirements at a time; occasionally another set of requirements may be satisfied as well, in which case the adaptation to the first set is to be considered pre-adaptive for the second (Mayr, 1970). If, by this means, the mechanical shortcomings of incipient bipedalism were somehow mitigated, the future adoption of habitual bipedalism would have been relieved of its greatest constraint, mechanical awkwardness.

Robinson (1963) pointed out that erect standing could be considered an ideal pre-adaptive behaviour, if it could be demonstrated that it brought about sufficient evolutionary benefit or relieved an equally sufficient cost. He reasoned that the adaptive shift to habitual bipedalism occurred in two phases. During the pre-adaptive phase Robinson thought it would be difficult to see how selection for an erect posture as such could have been operating, but during the adaptive phase selection pressures were concerned directly with erect posture. Robinson was unable to offer any explanation of what was causing the changes during the pre-adaptive stage before the adaptive shift occurred. He suggested that sentinel behaviour may have been an influence (as did Ravey, 1978, and others), but considered that the advantage gained from such a behaviour was insufficient to explain the adoption of habitually erect posture (Robinson, 1963, 1972).

In this paper we propose that, among pre-hominids, the adoption of bipedal standing in specific social contexts resulted in a significant selective advantage by relieving morbidity and mortality due to intra- and intergroup aggression. This proximate selective advantage was immediately augmented by those advantages gained from other stationary bipedal behaviours, such as bipedal food procurement, sentinel behaviour or communication.

We suggest, further, that the transitional period of frequent bipedal standing, prior to the evolution of mechanically efficient bipedal progression, would have had significant effects on the pre-hominid anatomy. These would have included changes in the structure and function of the trunk, pelvic girdle, lumbar spine and gluteal muscles and in the neural mechanisms of postural control (Eccles, 1989). Later adaptation from frequent periods of bipedal standing to prolonged ones, would have also necessitated modifications of patterns of cerebral venous drainage (Falk, 1988, 1990; Falk & Conroy, 1983). Once the anatomy of the earliest proto-hominids was sufficiently adapted to enable them to remain upright without discomfort or undue energy expenditure (Abitbol, 1988), they would have benefited from improved bodily cooling (Wheeler, 1988, 1991*b*). This would have been enhanced by improved cooling of the brain facilitated by the changed pattern of cerebral venous drainage (Falk, 1988, 1990). Eventually all these thermoregulatory changes, in addition to a loss of body hair and an increase in the number of cutaneous sweat glands (Wheeler, 1984, 1985, 1991*a*), would have been consolidated into an efficient method for heat dissipation in a hot savannah.

The expected resultant morphology from an original adaptation to stationary bipedalism would appear as a graduated series of compromise morphologies, which slowly shifted in emphasis from arboreal to terrestrial (Robinson, 1972). This mosaic of characters would have contributed to pre- and proto-hominids exhibiting unique modes of locomotion (Fleagle *et al.*, 1981; Oxnard, 1973, 1987; Prost, 1980; Senut, 1980, 1981; Stern & Susman, 1983; Susman *et al.*, 1984). Consequently, this scenario would enable sufficient time for arboreal feeding to be replaced by terrestrial feeding without the need for a sudden change of locomotion to a mechanically inefficient, albeit—as Taylor & Rowntree (1973) showed—apparently not a metabolically inefficient one.

An historical approach to understanding the origin of hominid bipedalism

Rose has recently observed that, "The uncharacteristically committed morphology and single-activity locomotor repertoire of humans must have arisen from a more typical higher primate pattern. This pre-hominid pattern included bipedalism as a minor component of a locomotor repertoire associated with a compromise morphology biased toward the performance of other activities" (Rose, 1991:40). In the reconstruction of the behaviour of the pre-hominid from which the stem proto-hominid evolved, it is profitable to examine the contexts in which bipedalism is used in the closest living relatives of modern humans. In this way we can begin to examine the pattern of specialized or shared-derived behaviours in much the same way as we would examine shared-derived morphologies in the context of phylogenetic reconstruction. An understanding of the evolution of hominid bipedalism requires not only that we appreciate how modern bipedal hominids work, but that we apprehend the exact sequence by which the bipedal hominid morphotype was constructed. This historical biological approach requires the definition of precise historical sequences of changes in anatomical structure–function relationships as well as in behaviour (Lauder, 1981, 1982, 1991).

The living African apes have developed unique morphological and behavioural specializations since they last shared a common ancestor with humans. This fact notwithstanding, it is widely acknowledged that the study of the morphology of the extant African apes is crucial to the understanding of the physical transformation from an essentially quadrupedal to a committed bipedal morphology. While it is considered *de rigueur* to compare anatomical features of humans to those of the apes, it is often considered inappropriate or wrong-headed to derive insights into human behaviours from those of the apes. In attempting to understand the evolution of hominid bipedalism, however, it is critical to explore the behavioural and social contexts in which habitual terrestrial bipedalism first evolved. In this connection, our study must embrace an examination of these contexts in ourselves and our nearest living relatives, the African apes. Our ultimate goal must, therefore, be the elucidation of the historical transformations of shared-derived morphological–behavioural complexes within the Hominoidea.

The behaviour that seems most closely bound to the evolution of stationary bipedalism is connected to the maintenance of social order. Stable dominance relationships are critical to the maintenance of social order in most non-human primate societies in that they permit resolution of conflicts over the rights to mates and resources, usually without recourse to physical violence (Smuts, 1987; Walters & Seyfarth, 1987). Because of the importance of dominance and appeasement behaviours to the survival of the individual performing them—and understanding them—their effect on the phenotype is disproportionate to the amount of time spent performing them. Dominance is principally related to an animal's age and size and other determinants of its fighting abilities, but is also mediated by its physical condition, kin relations and social alliances (Walters & Seyfarth, 1987). Among primates in general, aggression is most commonly expressed as threat displays and gestures, chasing, hitting, grappling and attacks, with attacks often involving biting. The repertoire of threat displays and gestures is varied amongst higher primates, with canine teeth displays of greater importance in cercopithecoids and bipedal standing and charging displays of greater importance in hominoids. Social hierarchies become increasingly important to the maintenance of group stability as group size and the number of interactions between individuals increase. Within primates, intergroup contests are more intense than intragroup conflicts due to consanguineous and other alliances or affiliations that tend to ameliorate the latter. Stable dominance hierarchies prevent injury and wasted effort (Angst, 1987) and when dominance hierarchies are firmly established, dominance disputes become less frequent and less of an impediment to other types of social intercourse such as play (Itani, 1987). Hierarchies are maintained by aggression and ritualized display complexes, with ritualized conflicts of more importance among hominoids.

Dominance display rituals and appeasement behaviours are a species-wide phenomenon and are universal in their application (Moynihan, 1955). Females use the same displays and appeasement behaviours as males, both between themselves and males and more commonly between each other. They are only rarely used by females to defeat adult males, but they defeat subadult males as frequently as they do adult females (Goodall, 1986; de Waal, 1989). Among females displays are used to establish and maintain female hierarchies and to aid in the rearing and protection of offspring of both sexes. Therefore, threat display and appeasement complexes must be the same for both sexes and unambiguously understood by both.

Female displays are used most often in contests for resources. Females are fierce competitors but only contend disputes as hard as the costs are worth the rewards (Lancaster, 1984). Loss of disputes over resources rarely prevents females from passing on their genes. Male disputes include those over access to breeding females and so, in contrast to those of females, male displays are more often concerned with an activity that has a high evolutionary cost and hence can afford to be more intense. The differences between the displays of females and males is not one of type or frequency but one of intensity. Plavcan & van Schaik (1992) have shown that the intensity of competition is more important than its frequency in the development of sexual dimorphism in canine teeth and other dimorphic traits such as body size. Consequently a ritualized display is equally evolved in both sexes, but its expression is most pronounced in the sex most affected in its Darwinian fitness by the outcome of the display.

The idea that light could be shed on the origin of hominid bipedalism from an examination of the bipedal displays of the African apes was first advanced by Livingstone (1962). Livingstone argued that a gorilla-like bipedal charge was important to the pre-hominid in the process of evolving into a "carnivorous, bipedal, open grassland ecological niche" and emphasized that the proto-hominid relied on its "charging ability and powerful forearms to obtain food" through hunting and tool use (1962:304). The possibility that hominid bipedalism developed from the habit of two-legged threat displays or bipedal charging during fighting was mooted again after Livingstone's publication (Guthrie, 1970; Simons, 1972; Wescott, 1967), but has never been fully elaborated.

The first problem to be faced in an historical reconstruction of the evolution of hominid bipedalism is the resolution of a robust phylogenetic hypothesis upon which a history of structural–functional and behavioural transformations can be traced (Lauder, 1981). Determination of the phylogenetic relationship between the great apes and humans, and particularly between humans (H), chimpanzees (C) and gorillas (G), has proven a difficult, stubborn problem, despite concerted attempts of large numbers of morphologists and molecular biologists to solve it. Chromosomal evidence indicates that split in the chimpanzee lineage that gave rise to the bonobo, *Pan paniscus*, south of the Zaire (Congo) River occurred long after the divergence of the chimpanzee and human lineages (Stanyon *et al.*, 1986), and thus after the period of greatest interest of the present investigation. The four possible associations between the three genera include three paired associations, [(G, C), H], [(H, C), G] and [(H, G), C] and a trichotomy [G, C, H]. At present, three out of four of these possibilities are seriously entertained. Difficulty in definitively resolving the African hominoid phylogeny by molecular and karyological methods has led some investigators (e.g., Chaline *et al.*, 1991) to propose a chimpanzee–gorilla–human trichotomy, an arrangement generally considered to be inconsistent with accepted models of speciation. Morphological evidence has been construed to support all four resolutions, but the [(G, C), H] hypothesis is the association most widely favoured (Andrews, 1987). The weight of current biomolecular and cytogenetic data (including those derived by immunological distance, DNA hybridization, amino acid sequencing, mitochondrial DNA (mtDNA) and nuclear DNA sequencing and various chromosomal banding techniques) would resolve the African hominoid trichotomy as [(H, C), G] (for reviews see Hasegawa, 1990; Ruvolo *et al.*, 1991; Stanyon & Chiarelli, 1991).

It is not within the scope of this paper to discuss the relative merits of the phylogenetic hypotheses presented above. For the purpose of our historical reconstruction, the two most strongly favoured patterns of association can be used as the basis for discussion. In Figure 1, the [(G, C), H] arrangement is depicted in (a) and [(H, C), G] in (b).

In Figure 1, the history of bipedal behaviours in the Catarrhini is traced using the two alternative phylogenies discussed above. A listing of the shared-derived behavioural and anatomical characters defining the nodes of cladograms is presented in Table 1. Similar diagrams in which the evolution of locomotor and postural behaviours in hominoids have been traced along alternative phylogenies have been presented before (e.g., McHenry, 1984; Rose, 1991), but to our knowledge this approach has not been utilized previously to trace the history of behaviours and anatomical structural–functional complexes related to bipedalism *per se.*

The bipedal proclivities of non-human primates are well known and those of Old World monkeys have been widely observed. In these animals bipedalism is spontaneous but infrequent and can be elicited in a wide variety of circumstances. In the wild these situations

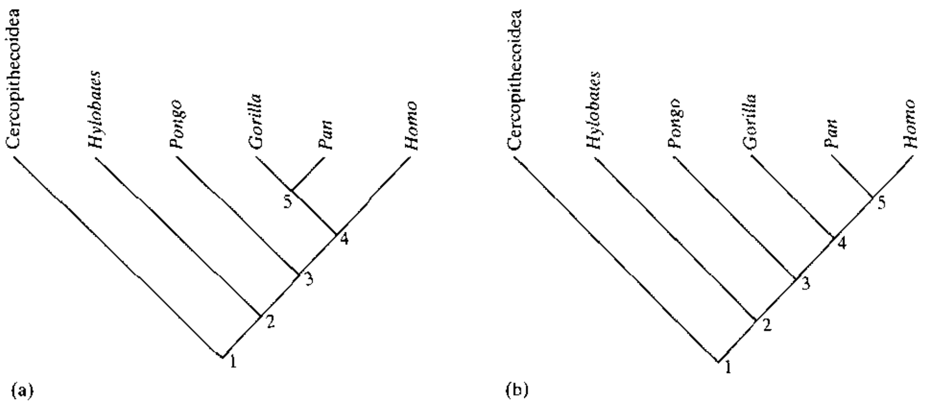

Figure 1. Alternative phylogenetic hypotheses for the Catarrhini. (a) Hypothesis supported more strongly by morphological evidence that shows the basal split in the lineage leading to the large African hominoids being between the ancestor of *Homo* and the common ancestor of *Gorilla* and *Pan*. (b) Hypothesis supported more strongly by biomolecular and cytogenetic evidence that shows the basal split in the large African hominoid lineage being between the ancestor of *Gorilla* and the common ancestor of *Pan* and *Homo*. See text for further discussion.

occur most commonly during feeding and foraging (Rose, 1976). Bipedalism is also associated with lookout behaviours in which animals such as the patas monkey rise to their full height to get a better view of their surroundings. It is also significant that bipedal behaviours in Old World monkeys occur mostly in terrestrial contexts and that they occasionally occur as part of a threat display and appeasement complex. We see among Old World monkeys the emergence of a pattern of threat display and appeasement behaviours that are connected with specific postures. In *Macaca nemestrina* aggressive behaviours such as assaults and biting lead to clear submissive responses such as cringing in the target animal (Strayer & Cummins, 1980). Also, aggressive interactions between males have been reported to include non-injurious struggles in which the individuals grabbed each other by the arm or shoulders and stood bipedally for a brief time before separating and reconciling (de Waal, 1989).

Despite the occasional use of bipedal posture and locomotion in Old World monkeys, these animals display compromise morphologies that permit occasional bipedalism (Rose, 1984, 1991) but lack features of the postcranium that can be construed as adaptations to bipedalism. Amongst hominoids, bipedalism occurs under these conditions as well as others, and so we can surmise that the ancestor of the Old World monkeys and the hominoids exhibited the potential to assume bipedal behaviours spontaneously in the course of feeding, foraging, carrying and displaying while on the ground (Figure 1, node 1). From the anatomical perspective, available evidence would indicate that the (as yet unknown) common ancestor of Old World monkeys and hominoids lacked morphological specializations for upright postures such as those associated with suspensory locomotion, vertical climbing and bipedalism and enjoyed a locomotor repertoire consisting mainly of arboreal quadrupedalism and leaping (Fleagle, 1986).

Hominoids in general are characterized by locomotor and postural behaviours that routinely involve orthograde postures in suspension, above-branch feeding and terrestrial bipedalism. Gibbons, for instance, utilize vertical climbing, bipedal walking on tree boughs and on level terrestrial surfaces in addition to brachiation. Yamazaki & Ishida (1984)

Table 1 List of hypothesized shared-derived morphological and behavioural characteristics related to the evolution of bipedalism defining the nodes and terminal branches of the cladograms in Figure 1

Figure 1(a) and (b)

Node 1

Postural, locomotor and social behaviours: facultative bipedalism in feeding and sentinel behaviours; a variety of dominance hierarchy some maintained through a display–appeasement complex consisting of canine displays and biting in the aggressor and stature diminution (cringing and cowering) in the target animal.

Morphological features: compromise locomotor morphology; sexually dimorphic canines.

Cercopithecoidea

Postural, locomotor and social behaviours: in addition to the characters listed for Node 1, bipedal standing during aggressive encounters in terrestrial species (e.g., *Macaca arctoides*; de Waal, 1989).

Morphological features: increased sexual dimorphism in body size in terrestrial species.

Node 2

Postural, locomotor and social behaviours: occasional orthograde postures associated with vertical climbing and facultative bipedalism in above-branch feeding and arboreal and terrestrial bipedal walking.

Morphological features: absence of a tail; moderate hip and knee extension possible during bipedalism (Yamazaki & Ishida, 1984).

Hylobates

Postural, locomotor and social behaviours: habitual brachiation involving routine truncal erectness; male and female joint defense of territory.

Morphological features: absence of sexual dimorphism in body size and large, non-dimorphic canines.

Node 3

Postural, locomotor and social behaviours: routine truncal erectness associated with vertical climbing; larger body size with greater sexual dimorphism in weight; moderate canine dimorphism.

Morphological features: modifications of the axial skeleton to accommodate upright postures over a fixed pelvis (Filler, 1981).

Pongo

Postural, locomotor and social behaviours: relatively high frequency of arboreal bipedal standing (Cant, 1987); increase in body size with extreme sexual dimorphism in body size.

Morphological features: evolution of extreme mobility in lower limb joints (Morbeck & Zihlman, 1988).

Figure 1(a) only

Node 4

Postural, locomotor and social behaviours: presence of the terrestrial bipedal threat displays-appeasement behaviour complex consisting of standing bipedal displays and deference shown by cringing and low bowing.

Morphological features: none.

Homo

Postural, locomotor and social behaviours: habitual, committed terrestrial bipedalism.

Morphological features: modifications of the trunk, pelvic girdle, lumbar spine, lower limb joints and gluteal muscles permitting habitual verticality of the trunk and full knee extension, to give a fully committed bipedal morphology (see, e.g., Aiello, 1981; Alexander, 1991; Robinson, 1963, 1972; Stern, 1972; Zuckerman *et al.*, 1973); reduced sexual dimorphism in canine and body size: loss of canine honing facet on lower third premolar.

Node 5

Postural, locomotor and social behaviours: use of knuckle-walking in terrestrial situations.

Morphological features: modifications of the forelimb and, in particular, the hand, related to knuckle-walking.

Gorilla

Postural, locomotor and social behaviours: evolution of largely terrestrial habit; chest-beating display.

Morphological features: evolution of large body size and great bodily sexual dimorphism.

Pan

Postural, locomotor and social behaviours: sophisticated and varied bipedal threat displays and appeasement behaviours.

Morphological features: ability to orient the pelvis to achieve an upright posture when bipedal (Jenkins, 1972).

Table 1 Continued

Figure 1b only

Node 4
  Postural, locomotor and social behaviours: bipedal threat displays and appeasement behaviours.
  Morphological features: none.
Gorilla
  Postural, locomotor and social behaviours: evolution of largely terrestrial habit; chest-beating display.
  Morphological features: evolution of large body size and great bodily sexual dimorphism.
Node 5
  Postural, locomotor and social behaviours: sophisticated and varied bipedal threat displays and appeasement behaviours.
  Morphological features: ability to orient the pelvis to achieve an upright posture when bipedal (Jenkins, 1972).
Pan
  Postural, locomotor and social behaviours: sophisticated and varied bipedal threat display and appeasement behaviours.
  Morphological features: none.
Homo
  Postural, locomotor and social behaviours: habitual, committed terrestrial bipedalism.
  Morphological features: modifications of the trunk, pelvic girdle, lumbar spine, lower limb joints and gluteal muscles permitting habitual verticality of the trunk and full knee extension, to give a fully committed bipedal morphology (see, e.g., Aiello, 1981; Alexander, 1991; Robinson, 1963, 1972; Stern, 1972; Zuckerman *et al.*, 1973); reduced sexual dimorphism in canine and body size; loss of canine honing facet on lower third premolar.

demonstrated that the non-brachiating activities of gibbons led to the development of hip and knee extensions similar to that seen in hominid bipedalism. Although the evolutionary history of the gibbons and the relationship of the gibbons to other hominoids has not been clearly resolved, the shared-derived morphologies and behaviours of the gibbons and the other hominoids allow us to deduce that the common ancestor of all the hominoids displayed some postures and locomotor activities involving truncal erectness, possibly including terrestrial bipedalism (Figure 1, node 2).

Among gibbons, fights are avoided largely through a social structure of contact avoidance that emphasizes boundary calling, small family group size and the driving away of adolescents from the family group (Leighton, 1987). Fights, when they do occur, are swift and effective and involve the biting of an adversary with long, keen canine teeth and clawing with the fingers (Carpenter, 1963). In gibbons, a virtual absence of sexual dimorphism reflects a monogamous social organization and joint defense of ranges.

The nature of the common ancestor of the orang-utan and the African great apes remains a matter of debate (Figure 1, node 3). With respect to posture and locomotion, orang-utans are highly specialized arborealists who are unique among hominoids in their extreme mobility of the hip, knee, ankle and foot (Morbeck & Zihlman, 1988). Upright postures figure in their most common forms of locomotion, arboreal clambering and climbing up and down vertical supports (Cant, 1985), but bipedalism itself is uncommon. Bipedal standing in the trees has been observed as a feeding posture in orang-utans (Cant, 1987), but terrestrial bipedalism appears to be very rare in the wild. Orang-utans are generally solitary animals and, like gibbons, circumvent conflict through a social structure of contact avoidance. When males meet, however, they do still fight.

The fossil record has not revealed a single species that has been universally recognized as the ancestor of all the great apes. *Proconsul* is considered by many to be primitive for Miocene hominoids in features of the postcranium and thus has been thought of as a good candidate for a generalized ancestor of all the great apes and humans (Kelley & Pilbeam, 1986; Pickford, 1986; Walker & Teaford, 1989). The possible locomotor repertoires of *Proconsul* species have been analysed at length by several workers (e.g., Beard *et al.*, 1986; Rose, 1983; Walker & Pickford, 1983) and there is general agreement that the locomotor skeleton of *Proconsul* is unique in its incorporation of cebid and ape-like features. The absence of anatomical features in the postcranium of *Proconsul* related to the more specialized positional capabilities of extant catarrhines is indicative of a potential for a wide range of locomotor abilities including palmigrade quadrupedalism, suspension, climbing (Kelley & Pilbeam, 1986) and, possibly, types of locomotion not seen in extant forms. Although *Proconsul* lacked a tail (Ward *et al.*, 1991), it appears to have lacked obvious indications of fore-limb dominated locomotor patterns. It seems reasonable to speculate that bipedal postures were occasional elements of the behavioural repertoire of *Proconsul* species, but clear anatomical evidence of routine orthograde postures in *Proconsul* and its probable relative *Afropithecus* is lacking (Sanders, 1992).

In addition to the orthograde postures associated with vertical climbing and arboreal bipedalism, the African great apes exhibit terrestrial upright postures in stationary and moving bipedal threat displays (Figure 1, node 4). These displays differ from bipedal walking in that they frequently involve energetic arm waving and the brandishing of a branch or other object.

The nature of the locomotor behaviour and anatomy of the common ancestor of African apes and humans has been debated at length. It is widely acknowledged, however, that the common ancestor of chimpanzees and humans (and thus the ancestor of the Hominidae) was similar in many respects to the chimpanzee (Pickford, 1986). The identity of the common ancestor of the large African hominoids, *Pan*, *Gorilla* and *Homo* (Figure 1, node 4) remains unclear, but it is possible that species of *Kenyapithecus* or *Ouranopithecus* may, when better known, be found to shared-derived characteristics with this group (Kelley & Pilbeam, 1986). In the absence of convincing anatomical or palaeontological information, the nature of the locomotor behaviour of the common ancestor of *Pan*, *Gorilla* and *Homo* is likely to remain a matter of conjecture only. One thing that is certain, however, is that all three of these genera routinely exhibit terrestrial bipedal threat displays. Whether one resolves African hominoid trichotomy according to Figure 1(a) or (b), it can be inferred that the common ancestor at node 4 exhibited bipedal displays.

Among the African apes, the ancestor of the gorilla has remained in an environment similar to the closed, forested habitats thought to have been occupied by the proconsulid ancestor of the great apes and has become very large-bodied and extremely sexually dimorphic. Among gorillas, a majority of groups contain only one dominant adult male, the silverback, to whom all other group members defer. Extreme sexual dimorphism in body size generally prevents aggression being directed toward the silverback; rather, the silverback serves the role of mediator in disputes between other members of the group (Stewart & Harcourt, 1987). Order is maintained through ritualized performances that include vocalizations, gestures and threat displays that often take the form of erect bipedal standing, bipedal charges and cuffing with the hands. In orang-utans and gorillas body size dimorphism exceeds canine dimorphism and reflects the fighting style of the intermale competition. The evolution of more varied and extensive bipedal displays in the gorilla may have been effectively precluded by the mechanical constraints associated with large body size, or by the fact that the dense lower canopy effectively screens bipedal displays except within the immediate vicinity of the group.

The stock from which chimpanzees evolved retained the smaller body size of their putative ancestor and came to occupy a variety of habitats in equatorial Africa ranging from dense closed forest to relatively open woodland and woodland-savannah. In chimpanzee society, conflicts and challenges to dominance are resolved largely by ritual gestures and threat displays, but when attacks occur they are often violent (Goodall, 1986; Smuts, 1987). Bipedal displays in chimpanzees have evolved to become sophisticated and varied. Chimpanzees make use of bipedal standing displays, the bipedal swagger, cuffing with the hands, bipedal mock charges and bluff hits or "pass overs" to maintain dominance and alpha males can be seen to draw themselves up and hunch their shoulders with their hair on end to appear taller (Goodall, 1986; de Waal, 1987). Their appeasement behaviours consist of cringing, low bowing (de Waal, 1989) and even lying prone in some pathological captive chimpanzees (Capitanio, 1986). In chimpanzees both body size and canine dimorphism are lower than in the larger hominoids, but common chimpanzees retain greater canine dimorphism than do bonobos.

Alliances based on dominance rank are used by chimpanzees to gain advantages within their group and are maintained in outside activities such as cooperative hunting and in the driving off of other groups by joint charges (Boesch & Boesch, 1988; Smuts, 1987). While chimpanzees exhibit a species-specific pattern of bipedal displays, these displays have also been shown to be remarkably plastic, exhibiting regionally variable non-verbal "dialects" (Goodall, 1986) and evidence of individual innovation. The bipedal displays of the bonobo seem to be similar to those of common chimpanzees and are used in similar contexts (Susman, 1984; de Waal, 1989).

The greatest, and most novel, specialization of the bonobo seems to have been its evolution of an appeasement strategy built around almost continuous sexual activity, some of which involves bipedalism (de Waal, 1989). Consequently, aggressive incidents are diminished and appear to be less intense than those of the common chimpanzee (Kano, 1982; de Waal, 1989). The anatomy of the bonobo reflects the relative importance of the elements of the behavioural repertoire. Bonobos show less dimorphism in body and canine size, because males do not have to win females by intramale dominance disputes. They also have more prolonged oestrous swellings and a larger penis than common chimpanzees (de Waal, 1989).

Bipedal threat displays and mock fights in humans are often masked by our extensive culture. We are all aware of anecdotal evidence that such displays do exist, for instance that walking tall denotes confidence and, sometimes, aggression, whereas cowering suggests fear and submissiveness (Guthrie, 1970). There is an extensive literature of ethological studies applied to humans that confirms our own experiential anecdotal evidence. Pre-school children have been observed to use primarily hit or push–pull in 75% of their agonistic encounters and similarly 75% of their threat gestures consist of either signals of intention to hit, or face and body postures (Strayer & Strayer, 1980). Biting or threats of biting account for only 1% of all agonistic interactions. Responses to this aggression involved cringing and flinching, passivity or counter-attacking. Diminution of body stature by a child under attack preceded the cessation of aggression a highly significant number of times (Ginsburg, 1980). These findings were reinforced by a longitudinal and cross-sectional study of children through grade and high school (Weisfeld *et al.*, 1980). Although the nature of the interactions of older children and adolescents differed from those of pre-schoolers, the dominance interactions were still mostly manifested in posture. That study concluded that dominance was highly stable, that it was recognized by both sexes, that it seemed to be based on physical traits and was, ". . . expressed by erectness of posture" (Weisfeld *et al.*, 1980:214). In humans, sexual dimorphism in body and canine size is low. The reduction of sexual dimorphism in bonobos mimics that observed in the human lineage (Zihlman *et al.*, 1978). The putative behavioural similarity between human and bonobo is that they have both reduced sexual dimorphism by reducing the relative importance of male–male competition.

The fossil record has yet to yield any remains that can be convincingly attributed to the *common ancestor of chimpanzees and humans [Figure 1(b), node 5], and the detailed* evolutionary history of the chimpanzee is completely unknown. In contrast, early hominid fossils are known, but interpretation of their affinities has been marked with controversy. This has been especially true of the earliest known hominid remains from Hadar, where the question has arisen as to whether we are observing one highly dimorphic species or two species with lesser amounts of dimorphism. Interpretations based on these views see either lessened sexual dimorphism in canine tooth size but relatively larger dimorphism in stature or, alternatively, a gradual lessening of total dimorphism during the course of hominid evolution. If the Hadar remains are interpreted as belonging to one species, *Australopithecus afarensis*, the degree of sexual dimorphism in canine size, stature and body size observed can be interpreted as exceeding that of *Pan troglodytes* and *Pan paniscus*, but not exceeding that of the gorilla, with females exhibiting 56–65% of male weight and female stature an average of approximately 70% of males' (based on figures provided in McHenry, 1991*a*,*b*). If two species are seen at Hadar, the sexual dimorphism in both would have already been approaching modern human levels. It is worth noting that the maxillary canine teeth of *A. afarensis* do not bear honing wear facets that would have indicated that the canines had been used as weapons (Greenfield, 1990).

Following the phylogeny in Figure 1(a), we can suggest that the common ancestor of gorillas, chimpanzees and humans was adept at bipedal displays, but that this ability was diminished in gorillas with the evolution of greater body size. Following the alternative phylogeny in Figure 1(b), we can posit that a more primitive form of bipedal threat displays existed in the common ancestor of *Gorilla* and the *Pan–Homo* clade, and that a more derived form evolved in the *Pan–Homo* clade following separation from the *Gorilla* lineage. That *bipedal displays are a shared derived characteristic of the African great ape lineage is without* doubt. How this ancestral behaviour was developed into a uniquely derived characteristic of hominids needs further elaboration.

Bipedal displays and the origin of hominid bipedalism

The historical reconstruction detailed above would indicate that the complex of bipedal threat displays and appeasement behaviours was of particular importance in understanding the origin of habitual terrestrial bipedalism because this is the most recently acquired morphological–behavioural complex shared by the African great apes and humans. We posit here 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. These activities were stationary bipedal displays, bipedal charges and bipedal mock fights and deference to these behaviours.

During the course of evolution, each species of African ape has evolved a unique system for the mitigation of violent intragroup aggression. Bipedal threat displays figure to greater or lesser extents in all of these systems, and it is our suggestion that they became of significantly greater importance among Late Miocene pre-hominids. The climatic deterioration of the late middle and late Miocene led to the gradual fragmentation of the forests of equatorial

Africa and the fragmentation of the ranges of several species of ancestral hominoids. In the most marginal habitat of all evolved the ancestor of the Hominidae.

Late Miocene hominoids living in an open, wooded grassland environment would have probably ranged over relatively large areas in search of food, in a manner similar to that of modern chimpanzees from sparsely wooded, relatively arid regions (Nishida & Hiraiwa-Hasegawa, 1987). The combined effect of large group size and a distribution of food resources that was more patchy, less dense and more seasonally variable than that of the forest would have contributed to higher frequencies of intragroup and intergroup interactions within these hominoid populations. Such interactions probably were mostly peaceable, with most aggression controlled by ritualized displays of dominance and appeasement. Among the African great apes today, however, there are occasions when intragroup tensions and conflicts escalate, leading to fights or the disruption of cooperative alliances. Fights within groups are generally not severe and seldom result in serious injury, but have been known to result occasionally in serious morbidity through biting injuries (Goodall, 1986). It is known that two dominance struggles in captive breeding colonies maintained under semi-natural conditions resulted in the death of one of the contestants (Goodall, 1986; de Waal, 1989).

In habitats where food and water resources were not evenly distributed, pre-hominids evolved strategies to cope with the increased "patchiness" of their environment..As habitats became even more fragmented and desiccated, and resources more widely separated, increased competition for resources probably ensued. We suggest that bipedal displays and increased deference to them were the behaviours essential to the success of pre-hominids in this environment in that they allowed for the relatively peaceful resolution of intragroup conflicts, including those over scarce resources. The bipedal displays of pre-hominids differed from those of living apes in several respects. The behaviours, including the bipedal displays, of pre-hominids were performed by a different species in a different environment. The fact that they occurred in a different environmental context from those of other African hominoids is significant. In this more open habitat, competition was more frequent and intense than it would have been in areas where resources were more evenly and densely distributed. With the increased competition caused by this environment, displays would have probably occurred more frequently than they did in other hominoid lineages. In addition, the bipedal displays of pre-hominids in this environment would have been more visible than those of other hominoids in more closed situations.

We suggest that in pre-hominids bipedal displays and bipedal mock fights were established through the evolution of increased deference and used first as mechanisms for the peaceful resolution of intragroup conflicts. The bipedal displays of pre-hominids probably included standing erect, bipedal runs and "pass overs", and mock fights involving clubbing and pounding with the soft eminences of the hand. In clubbing and pounding, blows would have been generally non-injurious as they were aimed at well protected parts of the body, a phenomenon seen in play and real fights between modern chimpanzees and, in particular, in the play of gorillas and human children. We propose that the bipedal displays of pre-hominids led to resolution of intragroup conflict almost exclusively by ritual and gesture and only very rarely deteriorated into injurious attacks. The reduction of fight-related morbidity and occasional mortality would have been an immediate, albeit slight, advantage to individual and hence group survival. In an environment in which key resources were sparsely and unevenly distributed and conflicts over resources were frequent, the evolution of behaviours that made possible the peaceful resolution of routine dominance disputes were favoured. We suggest that groups practising such displays and suffering lowered morbidty due to fight-related injuries would slowly but steadily increase in size and number and would come to be more reliant on these behaviours.

Among chimpanzees and gorillas, bipedal displays involving standing, running and charging help to mediate social interactions within the group, but also figure prominently in aggressive intergroup encounters. In the common chimpanzee, the mountain gorilla and the bonobo transfer between bisexual groups is effected by females and intergroup aggression is related primarily to the defense and acquisition of females (Cheney, 1987; Goodall, 1986; Kano, 1982; Nishida & Hiraiwa-Hasegawa, 1987). In these species female transfer appears to be voluntary, with females being attracted to high-ranking or alpha males from their own or rival groups who have overcome challenges within the group or who have defeated opponents in intergroup contests. In mountain gorillas bipedal displays are central to such contests, with 80% of male–male encounters involving vigorous bipedal threat displays often with foliage slapping and runs, and 50% of these encounters degenerating into fights with physical contact (Stewart & Harcourt, 1987). In chimpanzees, bipedal displays appear less critical to the success of male–male encounters than they are in gorillas, but the bipedal swagger and upright running with arm waving are important components of the non-vocal display that one male would direct toward another (Goodall, 1986) in an encounter within or between groups. High ranking or alpha male chimpanzees are known to achieve a high mating success with ovulating females (Nishida & Hiraiwa-Hasegawa, 1987).

It can be envisioned that the performance of unique bipedal displays occasionally resulted, by dint of their sheer novelty, in the winning of encounters between males from different groups by their surprising effect. As in living apes, the success of pre-hominid males winning status by performing such displays would have been immediately reflected by their greater mating success with receptive females. Similarly, females winning such contests would have had access to more resources and may have protected their offspring more successfully.

In pre-hominids, the transfer of females from such peaceable groups in which bipedal displays were common to other groups would also have led to the slow and passive transmission of this behavioural tendency. Female transfer would have spread the bipedal display and the trend toward deference to the bipedal display into non-bipedally displaying groups. Incipient modifications of the musculoskeletal system to accommodate more frequent and prolonged bouts of bipedalism spread in the same manner in both sexes. The offspring of such migrating females may have stood up more and thus achieved higher status by this novel behaviour. Alternatively, the behaviour may have been passed on passively and would have slowly spread into the group without notice. Therefore, the proliferation of this style of bipedal display was brought about passively by female transfer or migration. This obviated the need for males to join in combat with more aggressive individuals, which they would naturally be more inclined to lose.

As this behaviour became widely adopted, it led to a marked increase in fitness in pre-hominid groups by greatly reducing the morbidity and mortality incurred as a result of the most common non-pathological cause of disability in the African apes, intergroup conflict (Goodall, 1986). In relatively open country, bipedal displays could have been observed *en masse* at a distance and deference to such displays would have avoided conflict and mortality.

Once these displays were thoroughly incorporated among pre-hominids in the context of threat, bluff and display, we suggest that they became increasingly important parts of the total behavioural repertoires of the animals. An important development would have been the incorporation of bipedal displays into the play and rehearsal behaviours of juveniles and subadults. Individual and group variation in the performance and interpretation of such displays would have quickly led to their becoming more varied and multifunctional. This marked the beginning of truly habitual terrestrial bipedalism and the opening of entirely new behavioural horizons. At this point, strong positive selection for this suite of bipedal behaviours favoured the rapid acquisition of the several major anatomical changes that the new habitual posture required. Increased encephalization proceeded slowly at first, in response to the increased need for postural control, and only later escalated as the uses of the hand in manipulation and tool-making became more varied. All of the other benefits brought about by habitual bipedalism and the subsequent freeing of the hands, which have been cited as first causes for the evolution of bipedalism by others, would have then followed in train. Enhanced evolutionary fitness due to the acquisition of habitual bipedalism and the many co-dependent adaptations to an open environment arising as a result of bipedalism would have made possible the massive radiations of hominid species that occurred during the Pliocene.

Discussion and conclusions

An understanding of the processes of bipedalization and the diversification of the Plio–Pleistocene African Hominoidea requires integration of palaeontological, anatomical, behavioural and palaeoenvironmental evidence. Evidence has been presented that supports the hypothesis that the origin of habitual terrestrial bipedalism in the ancestor of the Hominidae was the key innovation that permitted hominid colonization of open environments in Africa in the late Miocene and Pliocene. The roots of this innovation can be traced to the performance of and deference to bipedal displays of pre-hominids that permitted the mostly peaceful resolution of intra- and intergroup conflicts, including those over scarce resources. This argument is based on the observation that the bipedal threat display and appeasement complex is a shared derived characteristic of *Gorilla*, *Pan* and *Homo*. We suggest that the bipedal displays that can be observed in extant African apes closely resemble the behaviours we posit for the putative ancestor of these animals and ourselves. It is not that these displays were any more effective at mitigating the effects of higher rates of aggression than another possible non-injurious mechanism would have been. It is just that these were the non-injurious behaviours that were already being employed in the social context of peacemaking. Any alternative argument—that such displays were uniquely derived in each of *Gorilla*, *Pan* and *Homo*—would have to account for the evolution of bipedal displays in terms of the convergent emergence of the same behavioural complex in different lineages in different environments.

To our knowledge, ours is the only hypothesis concerned with bipedalization and the origin of the Hominidae that provides a causal explanation for the kinds and degrees of sexual dimorphism observed in humans. As pointed out the reduction of sexual dimorphism in bonobos, which mimics that observed in the human lineage, supports the argument that hominids had similarly found a method to reduce agonism. Just as bonobos have enhanced their display equipment, so did hominids enhance theirs by becoming better at being bipedal.

If the habitual terrestrial bipedalism of hominids evolved as an outgrowth from the bipedal threat display, we would expect to see this reflected in the amount and type of sexual dimorphism in Hominoidea because of the element of male–male competition in that display. Our hypothesis is consistent with both interpretations of the hominid fossil remains from Hadar, although it is only supported by the single species model. The relatively large amounts of sexual dimorphism in body size and stature, but decreased amounts of dimorphism in canine size, observed in a single species of *A. afarensis* suggest that these dimorphisms were a result of the success of bipedal displays, which brought about a reduction in the importance of canine teeth in fighting.

We suggest that because female migration is common in the African great apes that it was responsible for the widespread transmission of the bipedal display and appeasement behaviour complex into a species-wide phenomenon in pre-hominids. On the face of it, a somewhat passive and indeed pacifist behaviour would not have had a chance to spread throughout pre-hominid populations without such a mechanism. As several authors have recently pointed out, primates have evolved a wide variety of behavioural patterns to counteract violent aggression and its sequelae (e.g., Goodall, 1986; Hodgson, 1990; de Waal, 1989). The deflection and control of aggression and the mechanisms of peacemaking in primate societies are of considerable importance, and we argue that these phenomena were of paramount importance in the survival and ultimate success of pre-hominid populations. We propose that *female transmission ultimately led to the successful establishment of habitual terrestrial* bipedalism, which evolved from increased deference to nonviolent bipedal threat displays. We suggest that the initial success of bipedal displays was in reducing morbidity and mortality in intra- and intergroup conflict in the context of social control, a reduction which led to a major improvement in individual Darwinian fitness.

The success of bipedal displays led to their diversification through individual innovation and the spread of bipedalism into other social contexts, notably play and rehearsal behaviours. Natural selection for modifications of the musculoskeletal system probably occurred as bipedal behaviours were becoming more widely incorporated into pre-hominid behavioural repertoires and as bipedal displays evolved to include more prolonged periods of standing. Increased evolutionary fitness accrued to pre- and proto-hominid populations at every step in this process and, ultimately, the success of habitual bipedalism made possible the radiation of early hominids into open habitats throughout much of Africa in the Pliocene. The increase in relative brain size, an important trend in the Hominidae, began slowly in response to the increased need for postural and locomotor control. The rate of encephalization increased as the freed hands began to be employed for more sophisticated types of manipulation, gesturing, carrying and tool-making.

It is noteworthy that the uniqueness of humankind may have originated from the leaving behind of "nature red in tooth and claw" for a society based on ritualized display and appeasement.

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