

## The origin of hominid bipedalism re-examined

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### Abstract

The evolution of habitual terrestrial bipedalism in the ancestor of the Hominidae can be reconstructed through an examination of historical transformations of shared-derived morphological-behavioural complexes related to bipedalism in catarrhines. This reconstruction indicates that terrestrial bipedal displays may be of particular importance in understanding the development of habitual terrestrial bipedalism because they are the most recently acquired morphological-behavioural characteristic 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 competition for resources ensued. We propose that the adoption of bipedal displays were the behaviours essential to the success of pre-hominids in this environment in that they allowed for the relatively peaceful resolution of, firstly, intragroup and, eventually, intergroup conflicts. It is hypothesized that the widespread use of bipedal displays for social control in pre-hominids reduced a major source of morbidity and mortality. Bipedal postures, once adopted for social control, probably became common elements of the pre-hominid postural repertoire. With time, this new pre-adaptation to upright standing would have facilitated a multifactorial development of fully habitual terrestrial bipedal locomotion.

Most philosophers and scientists, including Plato, Darwin, Engels, Lamarck, Huxley and Haeckel, have considered bipedalism to be the foremost of human characteristics. In the modern scientific study of human evolution, few topics have elicited as much discussion as that of the origin of bipedalism. McHenry (1982) commented that theories on the origin of hominid bipedalism are both important and speculative: important because they are implicated in the differentiation of the Hominidae; speculative because they require the reconstruction of so many anatomical, behavioural and ecological unknowns. Herein lies both their value and their peril.

In this essay we develop a theory of the origin of hominid bipedalism that explores the nature of the pre-adaptation that facilitated the multifactorial development of habitual terrestrial bipedalism.

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### Previous theories

The history of study into the origin of hominid bipedalism is long and complex and only a highly condensed review of previous theories is possible here.

Both Lamarck and Darwin recognized that the transformation from a quadrupedal to a bipedal posture was initiated by a shift from an arboreal to a terrestrial mode of existence. It is now widely agreed that in an environment that was becoming more open, pre-hominids would have had to spend increasing amounts of time on the ground while transferring from one tree or patch of woodland to another (e.g., Fleagle *et al.* 1981; Susman *et al.* 1984). The question is how bipedalism replaced quadrupedalism as the dominant mode of terrestrial locomotion in this environment.

Many hypotheses about the origin of hominid bipedalism put forward in the latter half of this century have reflected an explicit concern with identifying a specific behaviour or suite of behaviours that would have conferred a selective advantage to the pre-hominids or proto-hominids engaging in them. In this connection, the carrying of objects such as food, tools, offspring and weapons has been repeatedly implicated (e.g., Bartholemew and Birdsell 1953; Hewes 1961; Kortlandt 1967; Lovejoy 1981; Sinclair *et al.*, 1986). Lovejoy contended that evolution of the anatomical adaptations for bipedality required 'consistent, extended periods of upright walking' (Lovejoy 1981:345) and not simply occasional bouts of bipedal walking or upright posture. In this scenario, these extended periods of bipedalism were the key element of a provisioning strategy that directly enhanced reproductive fitness.

Other hypotheses centred around specific pre-adaptive behaviours include those of Jolly (1970) and Rose (1974; 1976) that implicated feeding situations and feeding postures. A common theme in yet other hypotheses has been the linking of the evolution of bipedalism to the avoidance of, or engagement in, agonistic encounters with either predators or conspecifics. In these contexts, bipedal postures were thought to have been utilized as early warning systems (Ravey 1978), in arm-waving or fist-shaking displays (Wescott 1967) or in the wielding of weapons (Dart 1959). The importance of the use of bipedalism in several behavioural contexts such as feeding and carrying has been stressed by Rose (1976) and Sigmon (1971), who have emphasized that natural selection could have acted to promote bipedalism via a complex of positive feedback cycles.

Another category of hypotheses about the origin of

hominid bipedalism has dealt with the pre-adaptive mode of locomotion of the pre-hominid rather than a specific bipedal behaviour that was promoted by natural selection. In this association, brachiation (Keith 1923), arboreal bipedalism (Morton 1935; Yamazaki and Ishida 1984) and knuckle-walking (Washburn 1951; Washburn and Moore 1974) have been viewed as key links between arboreal locomotion and terrestrial bipedalism. Evidence that fully committed bipedalism (*sensu* Rose 1991) had not yet evolved in the earliest known fossil hominids has prompted more recent students to advocate a model in which the proto-hominid was participating in a transitional mode of locomotion such as quadrumanal climbing in which the upper limb was adapted for suspensory postures and the lower limb was adapted for bipedalism (Fleagle *et al.* 1981).

Finally, a different approach was taken by Wheeler (1984; 1991) who argued that bipedalism was promoted because of physiological challenges connected with thermoregulation on the open savannah. He argued that there appeared to be distinct thermoregulatory advantages associated with a bipedal gait under equatorial savannah conditions where levels of solar radiation are high and there is a high risk of hyperthermia and where there may have been need to collect food constantly, from sunrise to sunset.

#### *Requirements of a successful theory of the origin of hominid 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. Many studies have demonstrated that the adaptation to terrestrial bipedalism in the earliest known fossil hominids was not complete and not functionally or physiologically equivalent to the modern human condition (Jungers 1988; McHenry 1986; Rodman and McHenry 1980; Stern and Susman 1983). The fundamental question that emerges is thus what selective advantage did a relatively inefficient form of terrestrial bipedalism confer to stem proto-hominids?

Any theory purporting to explain the origin of habitual terrestrial bipedalism must account for differential reproductive success in pre-hominid populations through either increased fecundity or increased longevity (Lovejoy, 1981) and in either case the evolutionary gain must have been greater than the evolutionary cost. The theory must be consistent with available environmental, palaeontological, anatomical and behavioural evidence. Further, a theory of the origins of terrestrial bipedalism must recognize that we are seeking to identify a set of behaviours in the common ancestry of hominids and the African great apes that are consistent with the locomotor and postural behaviours of modern humans and the extant African apes. A theory concerning the origin of habitual terrestrial bipedalism is by definition one that attempts to explain the ultimate cause of lineage splitting

that led to the origin of the Hominidae. Such a theory must, therefore, 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 apes. To our knowledge none of the previously proposed theories of the origin of habitual terrestrial bipedalism have fulfilled all the criteria that would be expected of the successful hypothesis.

#### *Shared-derived morphological-behavioural complexes and the origin of hominid bipedalism*

It is now widely accepted that the footprints at Laetoli are 3.6 Ma old and are those of habitual upright hominid walkers (White 1980; White and Suwa 1987). Habitual bipedalism was thus established at least by 3.6 Ma and it is possible that it is two or more million years older than that on the basis of putative older East African hominids (Hill and Ward 1988). Fossil evidence would thus indicate that terrestrial bipedalism emerged in the Hominoidea between approximately 10 and 5 Ma and hence long before an increase in hominid relative brain size.

The evolution of habitual bipedalism is clearly linked to an increasingly terrestrial habitus and this, in turn, appears to be closely related to environmental desiccation. There now appears to be a consensus that between 10 and 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). A significant biomass of C4 grasses did not appear until 8 or 9 Ma (Cerling *et al.* 1991); prior to that time the landscape was dominated by closed woodland or forest habitats.

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 as we would study the shared-derived morphologies in a phylogenetic reconstruction. 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 apes, it is often considered inappropriate to derive insights into human behaviours from those of the apes. Surely, however, in attempting to understand the evolution of hominid bipedalism, our ultimate goal must be the elucidation of the historical transformations of shared-derived morphological-behavioural complexes. In this connection, our only opportunity to examine these parameters is in our sister taxa, the African great apes. It is not suggested that the behaviour of the African great apes can be used to assess the behaviour of humans or vice versa. However, where a behaviour influences the pattern of morphological change in a species, we are then dealing with the evolution of a morphological-

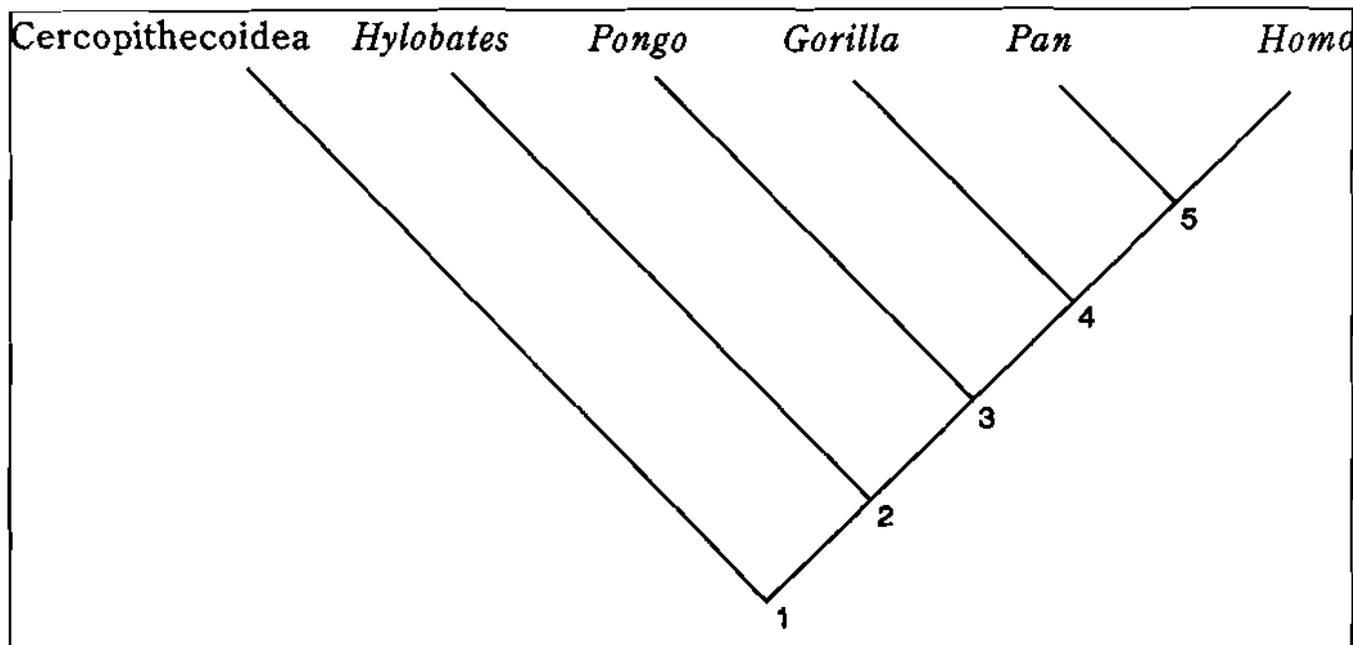


Figure 1. Phylogenetic hypothesis of relationships within the Catarrhini upon which the historical transformations of shared-derived morphological-behavioural complexes related to hominid bipedalism are traced.

behavioural complex. While behaviour is plastic and its mode(s) of inheritance uncertain, behavioural-morphological complexes are neither. Interdependent behavioural-morphological complexes shared between sister taxa are much more likely to be homologous than homoplasious.

In our behavioural reconstruction, we have chosen the phylogenetic hypothesis of relationships within the Catarrhini that is the most strongly supported by anatomical and molecular evidence at this time (Figure 1). It is important to note here that use of the next most strongly supported hypothesis — one that sees a split between the common ancestor of both modern African great apes and the common ancestor of hominids — does not alter the nature of theory proposed here because it is concerned primarily with the pre-adaptive traits that evolved before the splitting of the African ape lineage at Node 4.

From an anatomical perspective, available evidence would indicate that the as yet unknown common ancestor of Old World monkeys and hominoids (Figure 1, Node 1) lacked morphological specializations for upright postures and enjoyed a locomotor repertoire consisting mainly of arboreal quadrupedalism and leaping. Old World monkeys today display compromise morphologies and can accommodate occasional bipedalism in their locomotor and postural repertoires.

Hominoids in general are characterized by locomotor and postural behaviours that routinely involve orthograde postures in suspension, above-branch feeding and arboreal and terrestrial bipedalism. Although the evolutionary history of the Asian apes and the relationship of them to other hominoids remains somewhat unresolved, the shared-derived morphologies and behaviours they display allow us to deduce that the

common ancestor of all the hominoids (Figure 1, Node 2) displayed some postures and locomotor activities involving truncal erectness, including terrestrial bipedalism. The common ancestor of orangutans and the African hominoid clade (Figure 1, Node 3) is also thought to have employed orthograde postures in a variety of contexts.

In addition to the orthograde postures associated with vertical climbing and arboreal bipedalism, the African apes exhibit upright postures in bipedal threat and charging displays on the ground. These displays differ from bipedal walking in that they frequently involve energetic arm waving and the brandishing of a branch or other object. They are used as part of the dominance, appeasement and display routine for maintaining harmony between members of a basic social unit. The presence of such displays in the living African apes and humans strongly indicates that these behaviours were present in the common ancestor of these animals (Figure 1, Node 4). The bipedal displays of chimpanzees are far more varied and elaborate than those of gorillas and the chimpanzee appears better adapted to bipedalism than other nonhuman or non-bipedal primates (Rodman and McHenry 1980). We 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. How then did this ancestral behaviour develop into the uniquely derived characteristic of hominids? We posit here that in pre-hominids bipedal displays became the primary method of social control in pre-hominids and that they were of particular importance in the settling of disputes over resources and mates. Terrestrial bipedalism in pre-hominids involved display rituals for the control of intragroup aggression, the acquisition of mates and the

successful resolution of intergroup conflicts. It is important to note here that as part of a dominance and appeasement routine, ritualized bipedal displays would have been performed by both sexes. Behaviours related to the establishment of dominance are essential elements of the behavioural repertoires of primate species (Smuts, 1987; de Waal, 1987). In the apes, dominance behaviours by females are used in disputes over resources and offspring, but in males dominance behaviours are also frequently used for the settlement of disputes over access to females.

### *The significance of bipedal displays*

During the course of evolution, each species of African apes has evolved a unique system for the mitigation of violent intragroup aggression and the resolution of intergroup conflicts with varying degrees of success. Pygmy chimpanzees use sexual stimulation to relieve social tension, initiate cooperation and avoid conflict between individuals. Gorillas maintain a more rigid dominance hierarchy within groups than do chimpanzees (Stewart and Hareourt, 1987) and avoid generally conflict with other groups by avoiding contact with them. Common chimpanzees are perhaps the least successful of the African great apes at mitigating intra- and intergroup aggression. Injuries due to intragroup conflict are relatively common and lethal assaults due to intergroup conflict are well-documented (Goodall, 1986). It is important that bipedal displays figure to greater or lesser extents in all of these systems, and we suggest that they were to become of significantly greater importance among Late Miocene pre-hominids.

The idea that light could be shed on the origin of hominid bipedalism from an examination of the bipedal charging displays of the African apes was first advanced by Livingstone (1962), who argued that a gorilla-like bipedal charge was important to the pre-hominid in the process of evolving into what he referred to as a 'carnivorous, bipedal, open grassland ecological niche' (p. 304). The possibility that hominid bipedalism developed from the habit of two-legged threat displays or bipedal charging was mooted again after Livingstone's publication (Simons 1972; Wescott 1967) but has never been fully elaborated.

When palaeontological, anatomical and behavioural information are coupled with biogeographic and palaeoenvironmental evidence, a coherent scenario of the evolution of hominoid locomotion can be formulated. 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 African hominoids. In this scenario, the lineages leading to *Gorilla*, *Pan*, and *Homo* arise from two dichotomous branching events that occurred as a result of habitat fragmentation in equatorial Africa. Among the African apes, the ancestor of the gorilla has remained in an environment similar to the closed, forested habitats occupied by its hominoid

ancestor and has become very large-bodied and sexually dimorphic.

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. Bipedal displays in chimpanzees evolved to become sophisticated and varied. Chimpanzees exhibit a species-specific pattern of bipedal displays, but their displays have also been shown to be remarkably plastic, exhibiting regionally variable nonverbal dialects and evidence of individual innovation (Goodall, 1986).

In the most marginal situation of all in East Africa, in a habitat composed largely of open wooded grasslands, evolved the ancestor of the Hominidae. In such habitats, food and water resources were not evenly distributed and animals evolved strategies to cope with the increased patchiness of their environment (e.g., Foley and Lee, 1989). As habitats became more fragmented and desiccated, and resources more widely spaced, increased competition for resources probably ensued. We suggest that bipedal displays 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 intergroup conflicts, including those over scarce resources. We propose that the bipedal displays of pre-hominids differed from those of the living African great apes and their immediate ancestors in several respects. The most important of these is that they had become more important in the dominance-appeasement regime of pre-hominids and as such occurred more frequently than they did in other hominoid lineages. It is suggested that in pre-hominids bipedal displays had become the prime mechanisms for the settling of dominance between group members of both sexes over food and water that would have occurred at high frequencies in an open environment.

We suggest that in pre-hominids bipedal displays were established first as mechanisms for the peaceful resolution of intragroup conflicts. It is thought that the bipedal displays of pre-hominids led to resolution of intragroup conflict almost exclusively by ritualized display and gestural behaviours and only very rarely deteriorated into injurious attacks. It is noteworthy that in pygmy chimpanzees display and appeasement behaviours can take the form of genital-to-genital contact in upright postures. The bipedal displays of pre-hominids probably included stationary displays such as standing erect, arm waving with and without such things as branches, mock fights involving clubbing and pounding with the soft padded eminences of the hand and moving displays like bipedal runs and pass-overs and appeasement behaviours such as cowering and, possibly, bipedal grooming. We suggest that groups practicing such displays would suffer lowered morbidity due to fight-related injuries and so would slowly but steadily increase in size and number and come to be more reliant on these behaviours.

Among chimpanzees and gorillas, bipedal displays

including running and charging help to mediate social interactions within the group, but also figure prominently in aggressive intergroup encounters (Goodall 1986; Stewart and Harcourt 1987). In the common chimpanzee, the mountain gorilla and, possibly, the pygmy chimpanzee, transfer between bisexual groups is effected by females and, generally, intergroup aggression is related primarily to the defence and acquisition of females (Cheney 1987; Goodall 1986; Nishida and 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 rival groups or who have defeated opponents in intergroup contests. High-ranking or alpha male chimpanzees are known to achieve a high mating success with ovulating females (Nishida and Hiraiwa-Hasegawa 1987).

We theorise that in pre-hominids, the transfer of females from relatively peaceable groups in which bipedal displays were common to other groups would have led to the slow 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 probably spread in the same manner.

As bipedal displays became widely adopted, we propose that this led to a marked increase in fitness in pre-hominid groups by greatly reducing the morbidity and mortality incurred as a result of one of the most common causes of disability in the African apes, that is intergroup conflict (Goodall 1986). Once bipedal displays were thoroughly incorporated among pre-hominids in the context of threat, bluff and display, they became increasingly important parts of the total behavioural repertoires of the animals. Dominance rituals and displays related to the establishment of dominance occupy a significant amount of the time budgets of the living African apes. Such displays are frequent and important and the selective advantage of good performers appears great (Goodall 1986). We suggest that in pre-hominids, natural selection favoured those animals adept at bipedal displays. The adaptation to stationary bipedal displays would have involved the anatomical changes of the pelvis and hip joint outlined by Robinson (1963) as necessary pre-adaptations to habitual bipedalism and its further refinement. An important development would have been the incorporation of bipedal displays into the play and rehearsal behaviours of juveniles and subadults, in much the same way as innovative behaviours in chimps are imitated by younger animals (Goodall 1986). Individual and group variation in the performance and interpretation of such displays would have quickly led to their becoming more varied, multifunctional, and increasingly involved in play and carrying. This marked the beginning of truly habitual terrestrial bipedal progression and the opening of entirely new behavioural

horizons. We posit that 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 locomotion required. Increased encephalization proceeded slowly at first, in response to the increased need for postural control (Eceles, 1989) and only later escalated as the uses of the hand in manipulation and tool-making became more varied. The more egalitarian society that had evolved would auger further changes in social organization and would presage the acquisition of language. All of the other benefits brought about by habitual bipedalism and the subsequent freeing of the hands, which have often been cited as theories for a first cause for the evolution of bipedalism by others, would have then followed in train.

#### *Why chimpanzees aren't human*

The question of why the immediate ancestors of other African great apes did not evolve along the same trajectory as pre-hominids is important and needs to be addressed. As mentioned above, gorillas too evolved their own strategy involving the establishment of rigid and long-lasting dominance hierarchies. Pygmy chimpanzees perhaps came closest to hominids by evolving an alternative strategy to alleviate intragroup aggression that involves sexual pacification. It is highly significant that pygmy chimpanzees and gorillas inhabit forests that closely resemble the original environments in which their common ancestor lived and in which the distribution of resources is relatively even and at times abundant; in such environments contact between groups can be avoided for the most part. The common chimpanzee, in contrast, inhabits a variety of environments, some of which resemble that inhabited by pre-hominids. Alliances and allegiances are formed and broken within the groups, in which dominance and threat remain real and not ritualized. Here we see recurring violence between groups (Goodall 1986; Nishida and Hiraiwa-Hasegawa 1987). 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). The failure of chimpanzees to develop a more stable dominance hierarchy that utilizes a peaceful method of settling disputes has retarded the evolution of chimpanzees into a more egalitarian society. Such a society is necessary for the sharing of scarce or sparsely distributed resources. Chimpanzees have remained trapped in a semi-arboreal niche and have never been able to fully take advantage of the new vistas which opened up as the forests declined. In this environment they were out-competed by the lineage that would continue to flourish, hominids.

#### *Conclusions*

In this essay, we have presented evidence 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 bipedal displays of pre-hominids that permitted the mostly peaceful resolution of intra- and intergroup conflicts, including those over patchy and scarce resources. This reduced a major source of morbidity and led to the diversification of bipedal displays 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 occurred as bipedal behaviours were becoming more widely incorporated into pre-hominid behavioural repertoires. 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 the open habitats of Africa in the Pliocene.

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