# Primate Locomotion: Some Problems in Analysis and Interpretation

E. H. Ashton

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# LOCOMOTION

## Primate locomotion: some problems in analysis and interpretation

By E. H. Ashton
*Department of Anatomy, Medical School, University of Birmingham, Birmingham B15 2JT, U.K.*

Anatomical features biomechanically related to man's upright posture and gait are well defined. But uncertainty surrounds the evolutionary pathway leading to human bipedalism, partly because the anatomical nature of man's immediate ancestors is unknown, and partly because it is sometimes difficult to define and interpret the biomechanical significance of unique constellations of features that obtain in post-cranial remains of fossil hominoids.

In the innominate bone of *Australopithecus* the expanded iliac blade gives some appearance of similarity to that of man and has frequently been taken as indicating that *Australopithecus* had acquired a bipedal posture and gait.

Methods have been developed to define quantitatively those morphological features of the innominate bone that are functionally related to the force pattern impressed during locomotion. On the basis of multivariate comparison of these features with those of extant primate groups representing a wide range of function of the hindlimb, it has been shown: first that the australopithecine innominate bone is unique in form; secondly, that this bone is somewhat better adapted than is that of extant subhuman primates for weight transmission in a bipedal posture; thirdly, that because of a dorsal orientation of the iliac blade *Australopithecus* lacked the means of powerful abduction of the thigh. Thus, any bipedalism practised by this extinct genus must have been quite different from that characteristic of *Homo sapiens*.

Evidence from, for example, the foot, shows that it is quite possible that *Australopithecus* may have used its hindlimb in some form of arboreal locomotion, in addition to possible terrestrial bipedalism (albeit of a non-human type). It is not known whether *Australopithecus* was, or could have been, an ancestor of man. Correspondingly, whether or not such compound use of the hindlimb could have been ancestral to the human type of bipedalism is indeterminate.

## Introduction

The biomechanics of the human upright posture and striding gait, long appreciated from Vesalian inference and amply confirmed by electromyographic and other modern techniques of study, are functionally correlated with aspects of form and proportion that contribute to a distinctive human complex. Many of these features affect the skeleton and, although reflected in, for instance, the curvature of the vertebral column, primarily relate to the hindlimb and pelvic girdle.

Other skeletal features, while of manifest selective significance in the context of the evolutionary emergence of *Homo sapiens*, may not necessarily have a direct biomechanical relationship to the mechanism of bipedal posture and gait. These include, for instance, the retention of free mobility of the forearm, the unique development of a mechanism, arthrological and myological, to permit true opposability of the thumb to each of the fingers in turn, and also the development of distinctive features of the shoulder that permit free mobility of the joint, especially in a plane below the horizontal.

In relation to man's evolutionary history, the biological significance of a bipedal gait and the resulting emancipation of the forelimb is axiomatic. But it is not certain how man's upright posture evolved. Such doubt stems from the fact that the fossil record of the primates is insufficient to permit detailed analysis of when the human and ape lines of descent separated. Thus the anatomical nature of man's immediate ancestors is unknown. Further uncertainty about the derivation of man's upright posture arises because it is difficult to make adequate biomechanical inferences from fossil remains, often fragmentary and of unusual morphological form.

The first of these sources of uncertainty is, and may well remain, intractable. The second is ameliorated by quantitative biomechanical and morphological study.

## Bipedalism in fossil hominoids

Some human types (e.g. *Homo sapiens* from the Upper Palaeolithic together with certain remains of Neanderthal man) are well represented by postcranial skeletal parts so similar to those of living men that there is no real doubt that these now extinct groups stood and walked effectively as does extant man. Despite the remains being less complete, little real variation seems to attach to views about the posture and gait of *Homo erectus*. But earlier members of the hominoid radiation, although represented by relatively abundant postcranial remains (e.g. of *Limnopithecus*, *Proconsul* and *Australopithecus*), differ so much from extant apes and man as to generate doubt not only about overall posture and gait, but even about the likely locomotor use of individual skeletal parts.

In this context, much interest has centred upon the Australopithecinae. The earliest specimen of this group was discovered in 1924. Although predominantly ape-like in the form and proportions of its braincase and facial skeleton (see, for example, Zuckerman 1928), it was immediately hailed by some as a human ancestor because of presumed deviations in certain morphological features of the teeth and skull from those of the extant great apes and apparent approximations to the conditions typical of man (see, for example, Dart 1925). This view was much reiterated when extensive additional fossil material was discovered from the mid-1930s onwards (see, for example: Broom & Schepers, 1946; Le Gros Clark 1947, 1949). But others (e.g. Zuckerman 1950, 1954) repeatedly emphasized the predominantly ape-like proportions and features of the face and cranium.

From the first, claims about supposed morphological deviations of the Australopithecinae from the apes led to inferences about probable posture and gait. Initially (see, for example: Dart 1925; Le Gros Clark 1947) these were based on apparent differences in the position of the foramen magnum on the skull base from that characteristic of extant apes and on a presumed approximation to that characteristic of man. But such deviations from any extant subhuman primates were, at most, marginal and were, for three reasons, of doubtful significance. First the position of the foramen magnum of the fossils actually lay within the range of variation of e.g. *Gorilla* (Ashton & Zuckerman 1951). Secondly, such deviation as was manifest from the mean values of any extant monkeys and apes was, in scale, far less than that obtaining between extant man, on the one hand, and monkeys and apes (adult and immature), on the other. Thirdly, even these much bigger differences, although correlating with contrasts in posture and gait and in the poise of the head, from a functional viewpoint could be explained as reflections of the expansion of man's brain, together with the reduction and resiting of his facial skeleton (Ashton & Zuckerman 1952). Our conclusion was that little can thus be inferred from these features about posture in the Australopithecinae.

But the problem of locomotor pattern in the Australopithecinae was thrown into relief by the discovery (Broom & Robinson 1947) of an almost perfect innominate bone. In this, the iliac blade was broad, as in man, and, in this respect, contrasted with that of extant monkeys and apes, where it is much elongated craniocaudally. On the basis of this and of other features in which the innominate bone appeared to deviate from monkeys and apes, many workers (e.g. Le Gros Clark 1949, 1955) submittted that the morphological configuration of the bone showed that the Australopithecinae were bipeds.

But the bone was not completely like that of man, and a number of features in which it appeared to differ had been noted in certain early descriptions (see, for example, Broom *et al.* 1950). Thus, there was some doubt as to whether or not the bone was better adapted to the transmission of a pattern of forces associated with some form of bipedal gait rather than to the transmission of a force pattern characteristic of some other form of locomotion, possibly one of the types found in subhuman primates, in which the hindlimb subsumes a wide variety of functions.

By the time that this fossil innominate bone was described, an active programme of quantitative enquiry into anatomical similarities and differences between the australopithecine fossils, on the one hand, and extant apes and man on the other, was in progress in the University of Birmingham under the leadership of the then head of the Department of Anatomy, Professor S. Zuckerman. These enquiries included the innominate bone, and certain preliminary studies were made during the first half of the 1950s with, of necessity, limited material and relatively simple (univariate) statistical techniques. These analyses cited in Zuckerman (1966) gave a clear indication that, notwithstanding the relatively wide iliac blade, the proportions of the innominate bone inclined in their totality towards those of extant apes rather than towards those of extant man. It was appreciated that the studies were limited in scope, and equally it was apparent that it would be impossible ever to give a fully adequate representation of the overall morphology of a structure as complex as an innominate bone by the use of dimensions, angles and ratios. It was also realized that, although the earliest forms of electronic computer were then becoming available, it would be a long time before it would become possible to combine more than a limited number of such dimensions in multivariate statistical analysis. Equally, the biomechanical interpretation of such overall mensural complexes would be a virtual impossibility.

Consequently, it was necessary (*a*) to develop techniques to attempt to identify dimensional characters directly related to aspects of the force pattern impressed upon the pelvic girdle and thus to locomotor use of the hindlimb, (*b*) to enquire into the extent to which variation in such characters correlates with and mechanically enhances that in the impressed force pattern, and (*c*) to enquire how such a complex of defined 'locomotor' dimensions, in a fossil bone, compares with the corresponding morphological complex in extant Primates. From such comparison, the likely functional use of the hindlimb in a fossil species might be inferred.

## Form and function in primate limbs and limb girdles

Any enquiry into the relationship between even limited numbers of morphological features of the innominate bone and the impressed force pattern is complex. This is because, in all primate species, and irrespective of the way in which the hindlimb is used, the shape of the bone depends upon interaction of weight bearing through the sacro-iliac and hip joints, with the forces produced by the pull of the principal muscle blocks attached to the pelvic girdle.

First it was necessary to establish that it is possible to define and quantify osteological features functionally related to the pattern of impressed forces. A supplementary enquiry was therefore undertaken on the pectoral girdle because here, apart from contact with the sternum at the sternoclavicular joint, the girdle is suspended by attached muscle blocks, which thus provide virtually the entire impressed force pattern. The impressed forces can thus be defined more easily than in the pelvic girdle, where weight bearing and muscular pull interact.

The first step in this ancillary study comprised an analysis (Ashton & Oxnard 1964*a*) of the use of the forelimb in locomotion in different groups of primates. From this, it was possible to define in each group the pattern of forces to which this region is habitually subjected. In some genera from both the Prosimii and Anthropoidea (e.g. *Lemur* and *Macaca*) the locomotor pattern is quadrupedal and the forelimb is thus normally subjected to forces of compression. In other genera of both New and Old World monkeys (e.g. *Alouatta* and *Presbytis*), the animal, while basically quadrupedal, moves on occasion by swinging from its arms, which are thus subjected to forces both of compression and of tension. At the other extreme there are genera in both the Anthropoidea (e.g. *Hylobates*) and Prosimii (e.g. *Perodicticus*) in which the pattern of movement involves a large measure of suspension from the forelimb, which is thus habitually subjected to forces of tension. Although there are definable quantitative differences between practically all primate species, the system thus forming a spectrum, it is possible to delimit not completely arbitrary subdivisions. A forelimb classification into quadrupeds, semibrachiators and brachiators in the Anthropoidea, together with the corresponding categories of quadrupeds and hangers in the Prosimii, proved to be significant in the study of the functional significance of morphological contrasts in the pectoral girdle.

The next stage of enquiry (Ashton & Oxnard 1963) comprised a quantitative study of the disposition and proportions of the major blocks of muscles attached to the shoulder girdle and of their variation between the principal locomotor groups of Prosimii and Anthropoidea as defined by forelimb function. It emerged that significant contrasts in form and proportion exist, for instance in the propulsive muscles and in those responsible for raising the arm above the head. These can be readily related to contrasts in the use of the forelimb.

On the basis of such established muscular contrasts there were defined six osteological features related to the mechanism of arm-raising. These described the extent and orientation of insertion of m. trapezius and the caudal prolongation of the scapula relating to the relative position of insertion of the radiating digitations of m. serratus magnus (this complex forming a muscular couple rotating the scapula), together with the distal extent of insertion of m. deltoideus on the humerus (this measuring the mechanical advantage of abduction of the arm).

Enquiry was first made into the pattern of variation of these quantities between the different forelimb locomotor categories (each comprising several primate genera). A simultaneous study was made of three features mechanically related to the mobility of the shoulder joint (Ashton & Oxnard 1964*b*). These comprised measures of the orientation of the glenoid cavity, of the lateral end of the clavicle and of the extent to which the shoulder projects laterally. It emerged that in all cases there was a clear-cut and progressive pattern of contrast in relation to the extent to which the forelimb was subjected to forces of tension or compression. The pattern was similar in Anthropoidea and Prosimii. Consistently, in the Anthropoidea, brachiators lay at one extreme and quadrupeds at the other, with semi-brachiators in between. Prosimian hangers corresponded with brachiators and semibrachiators, while quadrupeds in the two suborders overlay.

Man was unique in that in features relating to the facilitation of arm-raising he was like types in which the forelimb is habitually subjected to forces of tension (brachiators and hangers). In characters relating to the quadrant in which the shoulder joint is most freely mobile, he was like those in which the forelimb is habitually subjected to forces of compression (quadrupeds). In no instance did he lie in an intermediate position. The overall human complex is thus unique and can be interpreted as implying a shoulder region that gives free mobility, but especially in the quadrant below the horizontal.

Although based initially on univariate statistical comparisons, these findings were subsequently confirmed and further clarified when it became possible to compound the nine locomotor quantities by means of multivariate statistical techniques (Ashton *et al.* 1965*a*).

An attempt was next made to define a second group of eight dimensions of the scapula that could not obviously be related to individual functions of the attached muscle blocks. These included the form of the supraspinous fossa and superior border of the scapula, the relative proportions of the supra- and infraspinous fossae, the projection and shape of the acromion, together with the orientation of the scapular spine (Ashton *et al.* 1965*b*). When these dimensions were combined by multivariate techniques (Ashton *et al.* 1971), the separation of genera correlated to some extent with locomotor rather than taxonomic groupings of living primates. The separation was, however, less marked than for defined locomotor dimensions.

In multivariate combination the two groups of dimensions gave a locomotor separation more pronounced than was evident when either group was taken alone (Ashton *et al.* 1971).

An extension of this study to the arm (Ashton *et al.* 1976) showed that it was again possible to define functionally significant contrasts in the blocks of related skeletal muscles. Related osteological features could be designated, and these, when combined by multivariate statistical techniques, displayed a spectral arrangement of genera correlating with the pattern of locomotor use of the forelimb and thus with the force pattern to which it is subjected. Separation was not, however, so great as with dimensions of the shoulder. It was found that, in contrast to the pectoral girdle, the arm presented other dimensional characters, which, although not varying in phase with locomotor groupings, separated certain major taxonomic divisions of the primates.

In multivariate combination, the two groups of dimensions of the arm gave an overall separation of primate groups in which the major taxonomic categories were differentiated. A locomotor spectrum was apparent within each.

Conversely, when all dimensional characteristics of the shoulder and arm were combined the overall separation of primate genera was basically in accordance with locomotor function (and hence with impressed force pattern), although superimposed upon each region of this spectrum was a measure of separation into taxonomic categories.

It thus appeared that it was possible to define quantitative osteological features of the forelimb functionally related to differences of established locomotor significance in associated muscle blocks. Contrasts between forelimb locomotor groups in these osteometric features were such as to enhance the mechanical significance of contrasts resulting from differences in muscular proportion and arrangement.

We therefore proceeded to analysis of the innominate bone, with the expectation that this will also show features related to the attached muscle blocks. In addition we may expect to find other features dependent upon the direct transmission of weight through the sacro-iliac and hip joints.

Initially, as with the shoulder and arm, a quantitative analysis was made of the locomotor use of the hindlimb and pelvic girdle in different primate groups. Such hindlimb use correlates to only a relatively small extent with that of the forelimb and any attempt to provide an overall scheme of classification, based upon the total locomotor pattern of each species, seemed certain to result in an excessive number of locomotor categories. But, for biomechanical enquiry into the hindlimb and pelvic girdle, it was possible to derive a classification of purely hindlimb use, with reasonable numbers of genera within each category. An initial attempt (Ashton & Oxnard 1964*a*) centred upon the extent to which the hindlimb participates in leaping but proved to be too circumscribed. Later attempts (as summarized by Oxnard (e.g. 1974)) developed a concept in which, from a central core of generalized quadrupeds, there radiated specialized groups in which the hindlimb participated in a variety of types of movement (e.g. leaping, hanging, leaping and clinging, acrobatic activity). This contrasted with the concept describing forelimb use in which there was a progression from forces of compression to those of tension, but it appeared to form a working basis for biomechanical enquiry into the pelvic girdle.

As with the study of the pectoral girdle, the first stage comprised an analysis of the relative proportions and disposition of the principal blocks of muscles attached to the innominate bone (Zuckerman *et al.* 1973). It emerged that the most conspicuous contrasts in all muscle blocks were between man, on the one hand, and subhuman primates, on the other. Most especially, in man the abductors of the hip were more prominent than in any subhuman primate, but the extensors of the hip, despite the great development of the specialized human m. gluteus maximus, were bigger in subhuman primates.

On the basis of these muscular contrasts, a group of five bony features was initially defined (Zuckerman *et al.* 1973). The series was later (Ashton *et al.* 1981) extended to ten dimensions. These included quantities reflecting the length of the ischium, the orientation of the iliac blade, the position of the anterior superior iliac spine relative to the ventral aspect of the bone and to the centre of the acetabulum together with its lateral displacement, the orientation of the rami of the pubis, the craniocaudal dimension of the obturator foramen and the length of the inguinal ligament.

Each of these quantities gave some separation of certain locomotor groups in both Prosimii and Anthropoidea. In the Prosimii the leaper/clingers and the hangers were frequently prominent, while in the Anthropoidea the leapers (facultative and pronounced) were correspondingly conspicuous. But the biggest contrast was consistently between man and most or all subhuman primates. In each of the ten features of this group, *Australopithecus* tended to differ from man and to resemble subhuman primates, especially the great apes.

When these ten locomotor dimensions relating to muscle disposition were compounded by multivariate analysis, the differentiation of locomotor groups among subhuman primates was more complete than that which emerged in the study of any individual dimension. The contrast between man and subhuman primates was also more pronounced. Correspondingly more clear-cut was the association between *Australopithecus* and the apes together with its contrast with man.

Concurrently, a group of osteometric features of the innominate bone was selected, each feature being, so far as could be judged by biomechanical appraisal, directly related functionally to the transmission of weight from the vertebral column, through the sacro-iliac and hip joints, to the femora. There were initially four such dimensions, but the group was later extended to seven. They comprised quantities defining the positions of the acetabulum and the auricular surface of the sacro-iliac joint relative to the boundaries of the innominate bone, the relative separation of these two joints, the angulation of the iliac and ischial arms of the innominate bone, together with the craniocaudal orientation of the acetabulum.

Again, each dimension separated certain locomotor groups to some extent, the leaper/clingers and hangers from the Prosimii, together with the leapers and hindlimb acrobats from the Anthropoidea, often being individually identifiable. But, once more, the biggest contrast was consistently between man and subhuman primates. In this group of dimensions, the extent of contrast was generally greater than that obtained in the locomotor dimensions relating to the disposition of the abductors and extensors of the hip. In each of these seven features relating to the disposition of the sacro-iliac and hip joints, *Australopithecus* consistently resembled man and contrasted with subhuman extant primates.

When the seven dimensions of this group were compounded by multivariate analysis, there was again a measure of separation of locomotor groups, greater than that which resulted from the analysis of any individual dimension. Man contrasted clearly with the subhuman Primates, *Australopithecus* being, in the compound of this group of features, completely like man and thus also contrasting with all subhuman primates.

When all 17 locomotor dimensions were compounded, there was a good separation of locomotor groupings (as based on hindlimb function). This finding verified that the 17 dimensions selected were biomechanically related to locomotor use of the hindlimb and pelvic girdle. But there was effectively no differentiation of major or minor taxonomic categories. For example, quadrupeds, in this instance, from both the Prosimii and the Anthropoidea, clustered as a single group.

Man, while linking with the hindlimb acrobats of the Anthropoidea (apes), was uniquely differentiated. *Australopithecus* linked similarly with a different member of the hindlimb acrobats. It was separated to an approximately equal extent from these and from man.

In the extended study of the innominate bone (Ashton *et al.* 1981) an attempt was made, as a result of earlier findings relating to the arm (Ashton *et al.* 1976), to define a further group of features, eight in all, which, so far as could be judged, were not directly related functionally to the locomotor mechanics of the innominate bone, but which described other aspects of pelvic structure, e.g. shape of the birth canal. These comprised the length of the iliac crest, the mediolateral inclination of the iliac blade and ischiopubic rami, the dorsoventral orientation of the acetabulum, and the width and caudolateral orientation of the obturator foramen, together with the lateral displacement of the hip joints and ischial tuberosities.

Analysis of these individual 'residual' dimensions did not produce separation of locomotor groups, but certain dimensions differentiated marginally between major taxonomic categories. Man was, in the group of 'residual' dimensions, generally similar to the apes. *Australopithecus* was in some instances like both man and the apes; in others it differed from these extant Hominoidea and from all other extant primates.

When the eight residual dimensions of this group were compounded by multivariate analysis, separation of genera was broadly in accordance with the taxonomic scheme. Within the Hominoidea, *Australopithecus* and man linked independently to the apes and were again uniquely separated from each other.

When all 25 dimensions (17 locomotor plus eight residual) were combined by multivariate techniques, the principal locomotor groups of subhuman primates separated with a high degree of consistency within both Prosimii and Anthropoidea. These two suborders were well differentiated, while within each there was superimposed upon the locomotor grouping of genera some measure of separation into superfamilies within the Anthropoidea and into infraorders within the Prosimii. Man and *Australopithecus* linked independently to different extant apes and were separated from each other by a distance quite as big as that which separated either from the extant Pongidae.

*Australopithecus* and man thus emerged both in dimensions relating to locomotor function and in those separating taxonomic categories as differing from each other just as much as each differs from the apes. Thus, as man is unique in features relating to locomotion and to taxonomy, so is *Australopithecus* (although differently so). The fossil group is not, in any sense, intermediate in aspects of structure, as defined by these 25 dimensions, between extant apes and man.

## CONCLUSION

From a purely morphological viewpoint, the definition of a unique assemblage of features of the australopithecine innominate bone, some like those of man, others like those of subhuman primates (and especially apes), with yet others differing from both, parallels findings from studies of the skull, teeth and other parts of the postcranial skeleton of this fossil group (e.g. as summarized by Ashton (1981)). Repeatedly, in some aspects of many structural and functional complexes the Australopithecinae emerge as being like man, while in other aspects they are like subhuman primates. In combination, such constellations of features differ uniquely from both those of man and those of subhuman primates and often to an extent as great as these deviate from each other. The Australopithecinae are thus quite different in their overall morphology from any hypothetical creature intermediate in form between men and apes. Such overall morphological uniqueness adds complexity to any attempt to interpret the possible position of this group in the evolution of the higher primates. Thus any conclusions, however tentative, that can be drawn from studies about probable posture and gait of the Australopithecinae do not necessarily bear upon the evolutionary pathways by which man's bipedal posture and gait evolved.

But, viewing the Australopithecinae purely as morphologically unique and thus biomechanically unusual members of the hominoid radiation, it is possible to make certain tentative inferences about their posture and gait.

In the present communication, attention has deliberately been focussed upon the innominate bone, partly because it is so well represented in the Australopithecinae, partly because, from a purely biomechanical viewpoint, it holds a most significant position in relation to posture and gait.

But already, in addition to well known studies of the innominate bone (see, for example, Le Gros Clark 1949, 1955), there have been published several other analyses of parts of the hindlimb. For instance, the proximal end of the femur of *Australopithecus* (McHenry & Corruccini 1976) has also been shown to display a unique combination of human and ape-like features, while a now-classical quantitative study of the distal end of the femur (Kern & Straus 1949) indicated an equally unique assortment of human and monkey-like characteristics.

But, notwithstanding this considerable volume of morphological study, there have persisted, throughout the 30 years following the discovery of the almost complete australopithecine innominate bone upon which the present analyses have been based, many views about the likely posture and gait of this fossil group.

On the one hand, workers, such as, for instance, Le Gros Clark (1949, 1955), regarded the group as having acquired the posture and gait distinctive of the family Hominidae, a view that was only marginally later modified (see, for example, Le Gros Clark 1967). Such views, sometimes expressed in an even more extreme form, continue to be held by certain workers. Lovejoy *et al.* (1973), for instance, were unable to find pelvic features of the Australopithecinae that 'distinguish their gait pattern from that of modern man'. Robinson (1972) also submitted that the fossil evidence supports the view that the Australopithecinae had developed a 'uniquely human method of balance control'. This, coupled with an orientation of the pelvis as in modern man, resulted, in his view, in a full development of the capacity of the Australopithecinae to stride.

On the other hand, certain other workers (e.g. Zuckerman 1954, 1966) repeatedly and forcefully expressed doubt about the possible bipedality (habitual or facultative) of the Australopithecinae.

Even among those inclining towards the view that the Australopithecinae were habitual bipeds, some (e.g. Napier 1967) pointed to features of the australopithecine pelvic girdle that would be inconsistent with the 'heel–toe' type of striding gait characteristic of *Homo sapiens*. The analysis in the present study of locomotor–related features of the innominate bone re-emphasizes such differences. When the Australopithecinae walked bipedally (as most subhuman primates sometimes do), the relative disposition of their sacro-iliac and hip joints would seem to have permitted weight to be transmitted from the trunk to the lower limb more efficiently than in any extant subhuman primate. But a human-like disposition of the sacro-iliac and hip joints does not necessarily mean that *Australopithecus* was habitually bipedal and, in fact, certain of the findings of the present study relating to the disposition of the principal blocks of the pelvic muscles could be interpreted as indicating this not to be so. For instance, the orientation of the iliac blade and the position of the anterior superior iliac spine in the fossil group are such as to make it virtually certain that the lesser gluteal muscles were not disposed as in man, where they are abductors of the hip and thus provide strong stabilizing power during the human type of striding bipedalism. In fact, when *Australopithecus* walked bipedally, its gait must have been of the rolling type that obtains when subhuman primates attempt to walk upright.

But, just as some groups of subhuman primates use their limbs in different ways when carrying out different types of locomotion (e.g. semibrachiators sometimes use their forelimb to support the body during quadrupedal locomotion and at others to suspend it during progression by arm-swinging; hindlimb acrobats sometimes use the hindlimb during quadrupedal locomotion, while at others it can take part in a wide variety of suspensory and related functions), it is possible that the hindlimb of *Australopithecus* may also have subsumed several different functions.

Such a view has been put forward by Prost (1980), who, on the basis of analysis of the intermixture of human and subhuman primate features in both the forelimb and hindlimb of *Australopithecus*, concluded that the Australopithecinae 'must have been adapted to arboreal quadrupedal vertical climbing, having the capacity, at the same time, to perform facultative terrestrial bipedalism, moving on the ground in a manner visually identical to that of humans'.

The view is even more strongly reinforced by the recent work of Oxnard & Lisowski (1980) on the foot. A detailed and highly critical appraisal of the available osteological evidence has shown, once again, many functionally significant contrasts with man, together with a total functional complex that suggests 'usage as in an arboreal species that also walks bipedally with flattened arches (like a chimpanzee or gorilla) rather than with the high arches of Man'.

Such a creature would have been very different from all living primates (human and subhuman). Whether or not its gait could have been ancestral to the human type of bipedalism remains indeterminate.

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