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1 PRIMATES: A DEFINITION

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INTRODUCTION

Interpretations of primate evolution have undergone radical revision over the past fifty years (Cartmill, 1982). Part of this transformation is, of course, attributable to the impressive accumulation of new evidence, but an equally important part is due to increased clarity and precision in the methodology of phylogenetic reconstruction. With respect to the latter, a major contribution was made by Hennig's concepts, first summarized in German, though not made available in English until later (Hennig, 1950, 1966). As part of the ensuing debate, the present author made a very preliminary attempt to re-examine the question of definition of the order Primates (Martin, 1968). Given the further accumulation of new evidence and interpretations since that time, this is perhaps an appropriate time to reconsider some of the issues involved in defining the primates.

Implicitly or explicitly, definition of the order Primates, and of sub-groups thereof, is an essential component of phylogenetic reconstruction. However, there is also a strong element of circularity because of received notions about membership of the order Primates. This being the case, it is probably preferable to begin the process of definition with those forms whose inclusion in the Primates is largely unquestioned and to proceed thereafter to consider marginal cases. There is now a broad consensus that living primates include at least the lemurs, lorises, tarsiers, monkeys, apes and man, whereas the tree-shrews are a marginal case (see Lockett, 1980 for a recent review). Similarly, little doubt has been expressed about the inclusion of an array of fossil forms extending back to Eocene lemuroids (=Adapidae) and tarsioids (=Omomyidae), now commonly termed "primates of modern aspect" (see Simons, 1972; Szalay & Delson, 1979). On the other hand, there is still some doubt about the status of the early Tertiary Plesiadapiformes ("archaic primates", Simons, 1972). Accordingly, it can be argued that the most reliable procedure is to define living primates to the exclusion of tree-shrews and then to assess the affinities of tree-shrews in relation to that definition. Subsequent examination of the fossil "primates of modern aspect" will permit assessment of fossilizable features included in the definition, and will perhaps lead to some refinement of it. Only then is it appropriate to consider the likely relationships of the "archaic primates" (=Plesiadapiformes).

This leads on to the question of the nature of the definition itself, which may be intended purely for descriptive purposes, but which must be framed

more precisely for purposes of phylogenetic reconstruction. It is in this context that Hennig's contribution (1950, 1966) has been so important. Definitions must clearly be based on similarities shared by species in a group, and it has long been recognised that similarities acquired by convergent evolution should be excluded from consideration (in so far as it is practically possible to identify such similarities). Hennig, however, made the vital observation that it is also necessary to separate homologous similarities into primitive (plesiomorphic) and derived (apomorphic) categories. For any group of animals under consideration, the common ancestral stock must have been characterized by the possession of a particular set of features that are primitive with respect to all later descendants (primitive character states). Shared retention of primitive character states in any descendants provides no information about subsequent branching-points in the evolutionary tree. The existence and nature of later ancestral stocks within the tree is indicated by shared possession of derived character states. Hence, definitions intended for purposes of phylogenetic reconstruction should include only inferred derived character states, whereas purely descriptive definitions may include both primitive and derived character states (e.g. in relation to a taxonomic key for practical identification of specimens). For instance, one might specify "possession of a rhinarium" as a shared feature of strepsirrhine primates (lemurs and lorises), although it is highly probable that possession of a rhinarium is a primitive character state for placental mammals. While it may be useful to cite this feature in a taxonomic key for primates, it does not in itself indicate any special affinity between lemurs and lorises among primates. For the latter purpose, one must cite apparent shared derived features of lemurs and lorises, such as the possession of a tooth-comb, incorporating the canine teeth, in the lower jaw.

This, in fact, ushers in the vexed problem of the relationship between phylogenetic reconstruction and classification (Martin, 1981a). It is, of course, a fundamental tenet of the Hennigian, or cladistic, School that classifications should directly reflect inferred phylogenetic relationships. According to this view, a definition based exclusively on derived character states is required both for phylogenetic reconstruction and for classification (though it still does not follow that taxonomic keys should exclude other kinds of information). But there are numerous reasons, mainly practical, for rejecting the strict Hennigian approach to classification, while accepting the great value of Hennigian concepts for phylogenetic reconstruction. Instead, there is much justification for continuing to use the "classical" approach to primate classification (e.g. see Simpson, 1945; Simons, 1972). This is based on the concept of overall "morphological divergence" and thus depends upon assessments of total homologous similarity (viz. a combination of both primitive and derived character states) and use of the "grade" concept. Regardless of the philosophy of classification adopted, however, it is advisable to maintain a sharp distinction between phylogenetic reconstruction and classification. The former involves inference of the pattern of relationships between species generated by evolutionary divergence over time, while the latter involves construction of a naming system that is compatible with inferred phylogenetic relationships, but requires at least some degree of arbitrary definition. That said, it should be emphasized that the following discussion

is concerned exclusively with the inference of phylogenetic relationships.

Hennig's distinction between primitive and derived character states is eminently clear at a theoretical level, but application of that distinction in practice is by no means straightforward. Indeed, it must be emphasized that sorting of similarities between species into convergent, primitive and derived character states depends upon the application of a set of guidelines that permit no more than assessments of probability. Such assessments may vary from highly probable to marginally possible. In practice, therefore, one can only speak of inferred convergent, primitive or derived character states, especially where particular character states exhibit a patchy distribution among the species concerned. This being the case, it is best to take an approach that minimizes the likelihood of erroneous inference. A pragmatic approach that meets this requirement is to concentrate, at least in the first instance, on identifying universal or near-universal features of living primates that separate them from all other living placental mammals. Concentration on such universal or near universal features considerably reduces the problem involved in distinguishing primitive from derived character states (though one cannot rule out a priori the possibility that all living primates might universally share certain primitive character states that have been lost in all other placental mammals).

Special Problems of the Fossil Record

Extension of definitions to include fossil forms introduces a set of special problems. There are many reasons for this, most notably the restricted range of characters that can be preserved in the fossil record and the inevitable fact that the common ancestor of a group of living forms must have been more primitive than any of the descendant species. In addition to this, problems of interpretation arise because of a fundamental divergence between the approach taken by those who primarily study living species (neontologists) and the approach taken by those who concentrate mainly on fossil forms (palaeontologists). Although reconstruction of the phylogenetic history of the primates must ultimately rely upon effective fusion of both neontological and palaeontological evidence, there is a marked difference of emphasis that arises from concentrating on either living or fossil primates. The fossil record obviously has unique advantages to offer for reconstruction of phylogenetic relationships (notably with respect to indicating approximate time-scales, adding to the known range of morphology in a group, and permitting tests of inferences based on living forms alone), but it also has unique limitations that may lead to misinterpretation if not explicitly recognised.

The greatest limitation of the fossil record resides in its fragmentary nature, both in terms of preservation of material from individual species and in terms of the sampling of species from the phylogenetic tree. Typically only "hard parts" are preserved in primate fossils and there is a marked disparity in the preservation of individual skeletal elements, with isolated teeth and jaws occurring far more commonly than skulls or associated post-cranial elements. It is important here to distinguish fragmentary fossils, known only from teeth and jaw fragments, and substantial fossils, known

(ideally) from a combination of dental, cranial and postcranial material. Inclusion of fragmentary fossils in any phylogenetic reconstruction can be particularly misleading if those fossils themselves are made to play a central part in the reconstruction process. In the first place, a fragmentary mammalian fossil only permits the class of judgement: "This dentition resembles the dentitions of a particular sub-group rather than the dentitions of other mammals". Since no other characters are preserved, realistic assessment of likely phylogenetic relationships is impossible and allocation of any such fossil to a given group (e.g. the Primates or a particular division thereof) is typically an act of classification (viz. a general assessment of similarity), rather than an act of phylogenetic reconstruction (viz. assessment of the probability that any shared similarities can only be derived rather than convergent). Secondly, this problem can be compounded in the phenomenon of "classificatory accretion", for example with a series of fragmentary fossils allocated to the primate group as a chain of species exhibiting gradually decreasing resemblance to the original primate model. In this process, fragmentary fossils are recognized as "primates" not because of their conformity with an overall framework of primate evolution, but because of serial resemblances between one fragmentary fossil and another. It should be noted in this context that Simpson (1935) linked Plesiadapis to the primates mainly because of dental resemblances to Pelycodus (a fragmentary fossil relative of the Eocene lemuroid Notharctus, itself a substantial fossil exhibiting many similarities to modern primates - see Gregory, 1920). Other fragmentary fossil species now allocated to the Plesiadapiformes ("archaic primates") because of dental resemblances to Plesiadapis bear very little resemblance to the original substantial fossil model (viz. Notharctus) and in some cases the link with primates is tenuous in the extreme, as with Purgatorius and the Picrodontidae. It is therefore advisable to concentrate on substantial fossil species, at least in the first instance, for phylogenetic reconstruction. Table 1 provides an analysis of currently recognised fossil

Table 1: Analysis of numbers of fossil primate species recognised for different Tertiary epochs.
(Data from Szalay and Delson, 1979.)

EPOCH	DURATION (my)	TOTAL NO. OF SPECIES	SPECIES BASED ON SUBSTANTIAL FOSSILS
Plio-Pleistocene	7	45	26 (58%)
Miocene	19	46	16 (35%)
Oligocene	12	12	3 (25%)
Eocene	16	83	12 (14%)
Palaeocene	10	64*	5* (8%)
Overall Totals	64	250	62 (25%)

*All "archaic primates" (Plesiadapiformes). No "primates of modern aspect" are known from the Palaeocene as yet.

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primate species (based on Szalay & Delson, 1979), showing that there are comparatively few species (see below) and that only about 25% are based on substantial fossils. Not surprisingly, the proportion of substantial fossils known declines (from 58% to 8%) as one passes back through the Tertiary record.

The fragmentary nature of the fossil record is also important in another respect, in that the sample of past primate species is relatively limited and biased in various ways (e.g. with respect to body size and geographical distribution). As a result, there is a danger that certain fossil species - notably those known only from fragmentary remains (e.g. *Purgatorius*) - may be incorporated into the primate evolutionary tree merely because nothing better is available from the known fossil record. There is a common tendency among primate palaeontologists to treat the primate fossil record as a broadly representative sample, reflecting all the key stages in primate evolution. A direct interpretation of the record yields the picture shown in Fig. 1(A). This suggests that there was an early radiation of "archaic primates" during the Palaeocene and early Eocene in the northern continents. Supposedly, an unspecialized survivor from the base of that radiation gave rise to the subsequent, sustained radiation of "primates of modern aspect", beginning in the northern continents and subsequently spreading to certain southern continents. A direct reading of the fossil record indicates that, following a major radiation during the Eocene, "primates of modern aspect" largely disappeared from the northern continents.

There are, however, numerous flaws in such a direct reading from the fossil record. Very little is known about mammals from Cretaceous, Palaeocene or Eocene deposits of the southern continents (see Savage & Russell, 1983). For Africa, fragmentary fossil mammals are now emerging from Palaeocene and Eocene sites at the northernmost extremity of the continent (Cappetta *et al.*, 1978), but the earliest fossil site to yield substantial mammal (including primate) remains is the Oligocene Fayum site of Egypt. The recent unexpected discovery of an apparent tarsioid, the fragmentary fossil *Afrotarsius*, from the latter site (Simons & Bown, 1985) clearly shows how long it can take competent palaeontologists to unearth remains of small-bodied prosimians even in the best-documented early Tertiary fossil site of Africa. For South America, it is commonly stated that there is a fairly good record of mammalian evolution from the late Cretaceous onwards. However, the known fossil sites for the Cretaceous, Palaeocene and Eocene are very largely restricted to Patagonia and it cannot be claimed that there is an effective sample of fossil mammals for the entire continent during that critical period of mammalian evolution. Hence, it may not be concluded with any confidence that primates were absent from Africa and South America during the Cretaceous-Eocene.

A very crude guide to the effectiveness of our sampling of the primate fossil record can be obtained by means of a simple calculation beginning with the modern fauna of some 180 primate species and involving two assumptions that should, if anything, minimize the possible numbers of primate species that have existed in the course of primate evolution. The first assumption is that the primates originated only 65 million years ago (it is highly unlikely that they originated more recently than this). The

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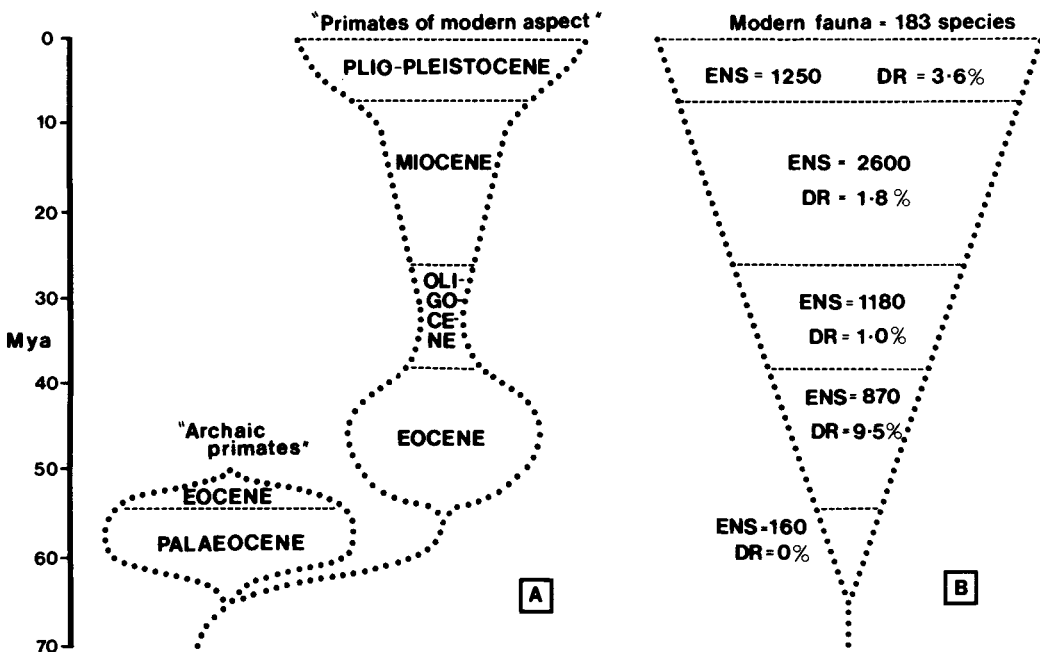
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Figure 1: Two contrasting interpretations of the available primate fossil record:

- A. The relative frequencies of past primate species are seen as a representative sample with no major distortions. According to this view the "archaic primates" underwent a significant radiation during the Palaeocene, only to disappear during the Eocene. An Eocene radiation of "primates of modern aspect", presumably derived from an early relative of the "archaic primates", was apparently succeeded by a marked contraction in species numbers during the Oligocene prior to a further major radiation to produce the modern primate fauna.
- B. A simple calculation based on the modern primate fauna permits inference of the "expected numbers of species" (ENS) for each geological period. The known numbers of fossil species, relative to the expected number, then yields the "discovery rate" (DR). See Table 1 for data (N.B. "archaic primates" excluded).



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second assumption is that the numbers of primate species have expanded progressively since the time of origin (this is a minimal assumption because most authors have indicated an early rapid diversification followed by slower expansion in numbers of species during the evolution of individual mammal groups). Taking a figure of 1 million years as a reasonable approximation to the average lifetime of each fossil primate species (Stanley, 1976, 1978), it can be calculated that about 6000 primate species have existed (as a minimum) during the course of primate evolution. Table 1 indicates that 186 fossil primate species of "modern aspect" may be recognised, representing a 3% sample of past primate species. If the calculation is restricted to substantial fossils (N=57; Table 1), the sample shrinks to 1%. A similar calculation can be made for placental mammals generally, and a similar result emerges. Hence, it would seem that we have a very poor sample of the primate fossil record and of the mammalian record in general. Furthermore, it is a sample which is also affected by a bias against suitable fossil sites in the southern continents.

The simplistic calculation of numbers of past primate species is illustrated in Figure 1(B) alongside the equally simplistic picture produced by direct reading of the available fossil record Figure 1(A). The former also shows a breakdown of possible species numbers for different periods of the Tertiary, giving the ratio of known fossil species to "expected" numbers of species (ENS); this is designated the "discovery rate" (DR). It is striking that no fossil primates of modern aspect have yet been reported from the Palaeocene, although the common ancestor of Eocene lemuroids and tarsuoids and the earliest offshoots thereof must surely have existed prior to the Eocene. By contrast, the inferred discovery rate of 9.5% shown for the Eocene is the highest recorded for any period. Direct reading of the fossil record (Figure 1(A)) would suggest that primates of modern aspect underwent a major radiation during the Eocene, followed by marked contraction. An alternative, reasonable explanation based on the figures in Figure 1(B) is that climatic warming during the Eocene (Wolfe, 1978) led to a northward expansion of primates from the southern continents, which have yet to be effectively sampled. Undoubtedly, such a geographical expansion would have been associated with a temporary global increase in the numbers of primate species during the Eocene, such that the real picture of the evolutionary radiation of the primates would be intermediate between Figure 1(A) and Figure 1(B). Given the alternative interpretation (Figure 1(B)), there is a real danger that the Plesiadapiformes have been inadvertently granted the status of "archaic primates" because we have yet to discover any real "archaic primates" in the fossil record of the southern continents. It should also be noted that with a maximal 3% sample of fossil primate species, any divergence dates that are inferred from known fossils may be much too recent. It is actually quite likely that early "primates of modern aspect" existed prior to 65 million years ago, but have not yet been documented purely because of the very low probability of their discovery. Given all the special difficulties attached to interpretation of the fossil record of primate evolution, there can be little doubt that definition of the living primates provides the correct starting-point for reconstruction of primate evolution history.

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DEFINITION OF LIVING PRIMATES

Despite the central importance of providing a comprehensive, but succinct definition of living primates, relatively little attention has been paid to this question in the literature. Indeed, numerous authors have relied fairly heavily on the definition provided by Mivart (1873):

"Unguiculate, clavicate placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brain always with a posterior lobe and calcarine fissure; the innermost digit of at least one pair of extremities opposable; hallux with a flat nail or none; a well-developed caecum; penis pendulous; testes scrotal; always two pectoral mammae".

Even quite recently, it was stated that this definition "has withstood the test of time" (Buettner-Janusch, 1966). Some authors have attempted to expand Mivart's definition. Le Gros Clark (1959) listed the following "evolutionary trends", defining the Primates as a "natural group of mammals".

1. Preservation of generalised limb structure with primitive pentadactyly.
2. Enhancement of free mobility of the digits, especially of the pollex and hallux (both used for grasping).
3. Replacement of sharp, compressed claws by flat nails; development of very sensitive tactile pads on the digits.
4. Progressive shortening of the snout.
5. Elaboration of the visual apparatus, with development of varying degrees of binocular vision.
6. Reduction of the olfactory apparatus.
7. Loss of certain elements of the primitive mammalian dentition. Preservation of a simple molar cusp pattern.
8. Progressive expansion and elaboration of the brain especially of the cerebral cortex.
9. Progressive and increasingly efficient development of gestational processes.

Napier & Napier (1967) cited both Mivart's definition and Le Gros Clark's list and added two additional trends to the latter:

10. Prolongation of postnatal life periods.
11. Progressive development of truncal uprightness leading to a facultative bipedalism.

All these attempted definitions of living primates suffer from the inclusion of likely primitive features of placental mammals and features that have arisen by convergent evolution in other mammal groups. Further, it is of little value to include "trends" in any definition of primates, since these refer not to generally shared features of primates, but to major developments found only in some members of the group. As was noted by Napier & Napier (1967), Wood Jones (1929) examined each of Mivart's criteria in turn and concluded that not one constituted a peculiarity of

primates; only the aggregate of the criteria seemed to define them. This is hardly surprising, since Mivart apparently did not believe that the primates are a monophyletic group, descended from a specific common ancestor. Following his much-quoted definition, he considered a list of distinctions between strepsirhine and haplorhine primates and concluded: "...taken together, they render it in the highest degree improbable that the Lemuroids and Apes took origin from any common root-form not equally a progenitor of other Mammalian orders". Clearly, any definition based on the premise that the primates do not form a cohesive phylogenetic unit is unlikely to provide much help in the reconstruction of primate evolution!

It has, in fact, been a common theme throughout the literature on primate evolution that the primates lack any clear-cut diagnostic features of the kind found in other orders of placental mammals. Simpson (1955) specifically noted that primates seem to lack unequivocal identifying features comparable to the wings of bats or the "double-pulley astragalus" of artiodactyls. This view has been widely expressed and was recently repeated in an assessment of the affinities of the plesiadapiforms (MacPhee *et al.*, 1983), "since the order Primates is not clearly definable by unique specialisations, the best grounds for regarding plesiadapiforms as euprimate antecedents are stratigraphic and phenetic". It must be emphasised, however, that the apparent absence of unique, defining features of primates relates to skeletal features identifiable in the fossil record and not to the entire range of features discernible in living primates. Detailed comparisons of living primates reveal that they share numerous universal (or near-universal) features, some of which do seem to be unique. It is possible to define living primates by reference to these apparently unique features, set in the context of other universal features of primates that also occur in other mammals.

Geographical Distribution and Habitat Occupancy

Although it is not customary to include reference to geographical distribution in definitions of mammalian groups, it is significant that living primates are largely confined to tropical and subtropical regions. The prosimian primates (lemurs, lorises and tarsiers) are even more tightly restricted to warmer areas of the world, as a reflection of their generally small body sizes. Since the ancestral primates probably fell within the body size range of modern prosimians, it is quite likely that they were subject to a similar climatic geographical restriction.

Most living primates are essentially arboreal. Only one living prosimian species, *Lemur catta*, exhibits any significant degree of terrestrial activity and it is only among Old World simians that predominant terrestrial activity has become common, though it is still limited to a minority of species. It is most likely that ancestral primates were essentially arboreal inhabitants of tropical/subtropical forest ecosystems.

Locomotor Adaptations

All living primates except man have a grasping foot with a well-developed, divergent hallux. Further, most primates have at least some prehensile capacity in the hand, though the pollex is in fact completely lacking in a few species. Most living primates have flat nails on digits and all species have at least a flat nail on the hallux, reflecting the typical

primate locomotor pattern of grasping arboreal supports rather than clinging to them with claws. The grasping function of the extremities in all living primates is enhanced by possession of tactile pads bearing ridges (dermatoglyphs), which play a dual role (Cartmill, 1974). The ridges resist slipping of the digits along arboreal supports. In addition, they are involved with tactile sensitivity in that dermal counterparts of the ridges enclose Meissner's corpuscles (specialised tactile end-organs), which are apparently unique to primates among placental mammals (Winkelmann, 1963).

The grasping action of the foot, which is dependent upon the divergent hallux, is particularly important for the locomotion of all arboreal primate species. As noted by Morton (1924), the angle between the divergent hallux and the second digit provides the point of thrust during arboreal locomotion (a tarsi-fulcrumating type of foot), in contrast to the typical non-grasping mammalian foot in which the distal ends of the metatarsals of the digits act against the substrate (metatarsi-fulcrumating type). This has direct implications for the dimensions of the tarsal bones in primates exhibiting active arboreal locomotion. One outcome is that in the typical primate foot there is a switch from the probable primitive condition of "alternation" of the tarsus (cuboid in contact with the astragalus) to the apparently unique condition of "reverse alternation" (calcaneus in contact with the navicular; see Lewis, 1980). Although there are numerous features of the primate tarsus that are linked to the requirements of arboreal locomotion, notably with respect to articulation between the astragalus and calcaneus such as to permit inversion and eversion of the foot (Lewis, 1983), most or all of those features are also found in other arboreal mammals (e.g. squirrels). However, living primates do seem to be unique among placental mammals with respect to the ratio between the proximal and distal segments of the calcaneus. It is well known that certain prosimians, notably *Galago* and *Tarsius* species, exhibit pronounced elongation of the distal segment of the calcaneus. Such elongation is also present, though to a lesser degree, in all other primates up to a body weight of about 5 kg (for fairly obvious mechanical reasons, the scope of such elongation of the calcaneus decreases with increasing body size, so any comparisons must take this into account). All living prosimian species and virtually all living simian species weighing 5 kg or less have a longer distal than proximal segment of the calcaneus (viz. a "calcaneal index value" of less than 100%, Walker, 1967), whereas all non-primate placental mammals in that size range have calcaneal index values exceeding 100% (Martin, 1978).

Reliance on the grasping action of the hindfoot in typical primates is associated with hindlimb domination (Walker, 1967; Napier & Walker, 1967; Martin, 1972, 1979; Rollinson & Martin, 1981). This is reflected by two special features that are generally characteristic of primates, but not quite unique to them, since they are also found in a few other arboreal mammals (e.g. the kinkajou). The primary feature is that in the body of a typical primate the centre of gravity is located closer to the hindlimbs than to the forelimbs, such that a greater proportion of the body weight is borne by the hindlimbs (Kimura *et al.*, 1979; Rollinson & Martin, 1981). As a direct consequence of this, the symmetrical walking gait of a typical primate follows a diagonal sequence, as opposed to the lateral sequence typical of non-primate quadrupeds (terms as defined by Hildebrand, 1967).