The extent of homoplasy in the trunk and forelimb of the hominoidea

Worthington, Steven

The Extent of Homoplasy in the Trunk and Forelimb of the Hominoidea

A Thesis presented

by

Steven Worthington

to

The Graduate School

For the Degree of

Master of Science

in

Biological Anthropology

Department of Anthropology
University of Durham

June 2002

Declaration

This thesis is the result of my own work, and no part of it has previously been submitted for a degree at any university. Material from the published or unpublished work of others, which is referred to in the thesis, is credited to the source in the text.

Statement of Copyright

Abstract of the Thesis

The Extent of Homoplasy in the Trunk and Forelimb of the Hominoidea

by

Steven Worthington

M.Sc. Thesis
Biological Anthropology

Department of Anthropology
University of Durham

June 2002

For the last century, palaeoprimatologists have questioned whether extant hominoids acquired their trunk and forelimb adaptations (previously interpreted as correlated with forelimb suspension) from a common ancestor, or developed them independently. Various workers have proposed that (1) the adaptations are hominoid synapomorphies; (2) hylobatids acquired these traits independently of hominids; (3) pongines and hylobatids evolved these features independently of each other and the African apes/humans; (4) the adaptations are independently derived in all hominoid genera.

To test between these alternatives, nine characters from the trunk and forelimb are used to determine the evolution of character states in extant and Miocene hominoids. Metric traits from ten extant anthropoid and nine fossil catarrhine genera are used in computer based analyses to reconstruct the ancestral conditions of these traits for a given cladogram. Ancestral morphotypes are compared with conditions exhibited in terminal taxa to identify synapomorphy/homoplasy.

Results suggest that five of the nine characters examined are hominoid synapomorphies. Of the remaining traits, one is shared derived for hominids, one is a synapomorphy of the African ape/human clade, one is not diagnostic for apes at all, and one reflects absolute differences in body size between taxa. Four traits exhibit homoplasy, in the form of convergence or reversal. None of these traits, however, show homoplasy between two or more hominoid taxa. Therefore, it is unlikely that hylobatids, pongines or African apes/humans evolved these traits independently of each other.

Three main conclusions can be drawn from this study: (1) some of the characteristics previously interpreted as synapomorphies for extant and stem hominoids are not in fact shared derived for this clade; (2) there is no homoplasy between extant hominoid genera in the features examined; and, (3) the association of these traits with forelimb suspensory locomotion is unlikely.

Acknowledgements

My sincere thanks go to Dr. Todd C. Rae for his supervision, encouragement, enthusiasm and, on occasions, patience during the research and writing of this thesis. I would also like to thank the administrative staff at the Department of Anthropology, University of Durham, and in particular Pat Barber, for the help I have received. I thank those individuals who allowed me access to the collections of primates in their care, and who provided assistance during my visits: Bob Randal, at the American Museum of Natural History, New York; and, Linda Gordon and Richard Thorington, at the National Museum of Natural History, Washington D.C.

I would like to thank my fellow postgraduate students, and in particular Kate Read and Louise Blundel, for their encouragement, informative discussions and alcoholism. My thanks are also extended to my family and friends, who, over the course of this project have supported me emotionally and financially, despite having to put up with my erratic moods, unsociable work habits and seemingly bizarre interests. Finally, I thank Hilary for her consistently good selection of wines and beverages.

Abbreviations

The following abbreviations are used in the text.

Measurements

BTH	Breadth
LTH	Length

Dimensions

Ant	Anterior
Post	Posterior
Prox	Proximal
Dist	Distal
Med	Medial
Lat	Lateral
Sup	Superior
Inf	Inferior
AP	Anteroposterior
ML	Mediolateral
PD	Proximodistal
CC	Craniocaudal
MID-S	Mid-shaft

Cladogram Statistics

CI	Consistency Index

Museum Accession Prefixes

AMNH	American Museum of Natural History
CGM	Cairo Geological Museum
CP	Can Ponsic
DPC	Duke Primate Centre
IGF	Instituto di Geologia Firenze
IPMC	Institut de Paleontología Miquel Crusafont
" -CL1	Can Llobateres 1
KNM	Kenya National Museum
" -MB	Maboko Island
" -RU	Rusinga Island
" -TH	Tugen Hills
MNHB	Museum of Natural History, Basel
MUZM	Makerere University Zoology Museum
NMNH	National Museum of Natural History
RUD	Rudabánya
UMP	Ugandan Museum of Palaeontology
YPM	Yale Paleological Museum

Others

GFA	Glenoid Fossa Angle
HSC	Homogeneous Subset Coding
LCA	Last Common Ancestor
LTK	Lateral Trochlear Keel
Mya	Million years ago
USP	Ulnar Styloid Process

To my family.

TABLE OF CONTENTS

TABLE OF FIGURES

CHAPTER ONE

INTRODUCTION

Aims and Objectives

The present study is an investigation into the evolution of character states in extant and Miocene hominoids, with specific reference to assessing the extent of homoplasy in the trunk and forelimb of these primates. Several workers (e.g., Simons, 1962, 1967a; Tuttle, 1975a; Larson, 1992, 1998; Begun, 1993) have argued that features in the trunk and forelimb of living apes that exhibit morphological similarity, and which may relate to forelimb-dominated arboreal activities, have evolved independently in these lineages after the divergence from the last common ancestor of the Hominoidea. If this were the case, the morphological similarity in the hominoid trunk and forelimb would not be the result of common ancestry, but could be accounted for by a shared behavioural adaptation to (or structural potential for) suspensory locomotion/vertical climbing/cautious quadrupedalism (Larson, 1998; Lockwood and Fleagle, 1999).

The aim of this study is to test this hypothesis by reconstructing the history of character evolution in nine postcranial characters that have previously been interpreted as shared derived for hominoids and have been implicated in forelimb-dominated arboreal locomotion, and thereby evaluate the extent of homoplasy within the taxonomic group Hominoidea. An assessment of the extent of homoplasy within the Hominoidea is an important exercise for two reasons: (1) it can shed light on the history and sequence of adaptations in clades within the Hominoidea; and, (2) it can highlight the relative strength of the phylogenetic and functional 'signals' in certain characters for this taxon.

Characters that exhibit incongruence are not merely phylogenetic 'noise' (Moore and Willmer, 1997; Alba *et al.*, 2001). Homoplasies are a profitable area of focus in themselves, because they are a valuable source of information about adaptation. In this sense, homoplasies *are* data (Collard and Wood, 2001b). The presence of homoplasies may suggest that different clades responded in similar

ways to similar environmental influences (Collard and Wood, 2001b). This can throw light on the history and sequence of hominoid adaptations.

From a cladistic perspective, homoplasy is detected *a posteriori* as the 'noise' within a cladogram, usually occurring randomly and obscuring a clear, directional phylogenetic signal (Patterson, 1982; Wake, 1996; Moore and Willmer, 1997; Lockwood and Fleagle, 1999). An abundance of homoplasy in a particular taxonomic group or data set, however, can obscure any phylogenetic signal produced, rendering several competing hypotheses of relationship equally parsimonious; thus, homoplasy has a confounding effect on phylogenetic reconstruction (Brooks and McLennon, 1991; Brooks, 1996; Sanderson and Hufford, 1996b; Wake, 1996; Collard and Wood, 2001a).

In the case of hominoids, there has been a vigorous debate concerning the relative strength of cranial versus postcranial evidence *vis-à-vis* homoplasy (Rose, 1986, 1989, 1994, 1997; Andrews and Martin, 1987; Pilbeam *et al.*, 1990; McCrossin and Benefit, 1994; Begun *et al.*, 1997a; C. Ward, 1997; Larson, 1998; Richmond, 1999). Many workers appear to be biased in favour of phylogenies based on craniodental characters, due to an *a priori* assumption that postcranial characters are more subject to homoplasy (Pilbeam, 1996; Pilbeam and Young, 2001).

Many hominoid trunk and forelimb similarities (including the nine characters examined here) have been interpreted as synapomorphies that distinguish these taxa from other anthropoids (Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). If this is not the case, then the phylogenetic reconstruction of hominoid relationships based on postcranial evidence, as favoured by some workers (e.g., Pilbeam, 1996), must be questioned, and (perhaps) craniodental evidence favoured (Begun, 1993; Moyà-Solà and Köhler, 1996; C. Ward, 1997; S. Ward, 1997; Larson, 1998; Richmond, 1999). Also, the basis upon which hominoids are differentiated from other anthropoid taxa must be re-evaluated.

In addition, an abundance of homoplasy in any one taxon or anatomical area can confound the classification of fossil taxa. The placement of fossil taxa in a taxonomic scheme is dependent upon the systematic positions assigned to extant taxa (Schoch, 1986; Pilbeam and Young, 2001). Fossil taxa are linked with individual extant taxa on the basis of shared derived characteristics (Hennig,

1966). If characters assumed to be synapomorphic for extant hominoids are found later not to be so, then the phyletic status and relationships of any fossil taxon linked to an extant taxon on the basis of the supposed synapomorphy must be re-evaluated.

Characters that are confirmed to be synapomorphies of the hominoid, hominid or African ape/human clades can be used to help reconstruct the adaptations of the hypothetical common ancestors of these clades. This task, however, relies on traits having a clear correspondence with a particular extant locomotor mode(s), so that specific types of locomotor adaptation can be inferred for (hypothetical) ancestral forms when they are reconstructed as having possessed a certain trait (Richmond *et al.*, 2001). All of the characters used here have been functionally linked with forelimb-dominated arboreal locomotor behaviours (Larson, 1998). If this interpretation were correct, then we would expect a strong functional signal to be associated with these traits. The sampled taxa that engage in forelimb suspensory activities most often (*Hylobates* and *Ateles*) should exhibit the same condition for each of these characters. Traits that do not follow this pattern will have to have their functional significance reassessed.

Homology and Homoplasy

The central problem in assessing similarity, whether morphological or molecular, is the distinction between homology and homoplasy (Moore and Willmer, 1987). Sir Richard Owen first introduced the term 'homology'[1] in 1843 to refer to individual structures or characters that belong to different taxa, but are fundamentally similar because they originated from a common ancestral pattern (Owen, 1848; Panchen, 1994). A key component in the definition of homology is that resemblance is caused by a "continuity of information" (van Valen, 1982:305). The continuity may be phylogenetic or ontogenetic (historical or developmental; Moore and Willmer, 1997). Homology forms the basis on which

[1] The etymological origin of the term homology is from the Greek word *homologia*, which means agreement or assent. *Homologia* is itself derived from the Greek word *homologos*, which means agreeing or consonant. *Homologos* is a union of the words *homos*, which means same or equal and *logos*, which can mean relation, ratio, word or discourse (Brown, 1993).

phylogenetic trees must be constructed, and is thus the hierarchical foundation of comparative biology (Hall, 1994).

Some characters may appear similar in morphology or structure and may perform the same function, but do not reflect phyletic affinity because they are not derived from a structure found in a common ancestor. The term 'homoplasy'[2] was coined by Ray Lankester (1870) and is used to describe these non-homologous, or analogous traits that are useless for phylogenetic reconstruction, but which can reveal important insights into the process of adaptation (Lockwood and Fleagle, 1999).

Homoplasy may be due to one of three different processes: convergent evolution, parallel evolution or character reversal (Wake, 1991, 1996; Cartmill, 1994; Sanderson and Hufford, 1996a). Character reversal occurs when a trait regresses from a derived state back to its primitive condition (Quicke, 1993). Parallel evolution occurs when closely related groups develop similar adaptations separately, despite sharing a recent common ancestor (either because they occupy a similar niche, or because they are developmentally constrained; Wake, 1991, 1996; Brooks, 1996). Characters exhibiting parallelism have evolved independently in at least two closely related lineages. The common ancestor of the lineages does not exhibit the characters, but the descendants have inherited the potential to express them (Moore and Willmer, 1997). Convergence occurs when distantly related groups evolve separately and yet develop similar adaptations (through inhabiting environments or employing strategies that are similar; Brooks and McLennon, 1991; Moore and Willmer, 1997; Lockwood and Fleagle, 1999). Descendants are therefore more alike than were their ancestors (Moore and Willmer, 1997). Characters exhibiting convergence show similar morphology or function but have evolved independently, rather than from a common ancestor. Simpson (1961:78-79) and Gosliner and Ghiselin (1984:258) have distinguished between these two patterns:

> Parallelism is the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channelled by, characteristics of that ancestry. Convergence is the development of similar

[2] The term homoplasy is derived from a union of the Greek words *Homos*, which means same or equal and *plasia*, which is itself derived from the Greek words *plasis*, which means moulding or conformation and *plassien*, which means form or mould (Brown, 1993).

> characters separately in two or more lineages without a common ancestry pertinent to the similarity but involving adaptation to similar ecological status.
>
> "Parallelism" means that taxa began with the same initial conditions, and independently underwent the same changes. "Convergence" means that the taxa began with different initial conditions and, by different pathways, arrived at a similar condition.

Parallelism and convergence are not entirely separate processes; the distinction between them is continuous (and can be arbitrary), defined by the degree to which the outcome is channelled by common ancestry (Begun, 1993; Moore and Willmer, 1997).

Lockwood and Fleagle (1999) make a distinction between methodological homoplasy and biological homoplasy. Methodological homoplasy can be viewed as an error in the methods used to detect homology. This type of homoplasy depends very much on how characters are defined in the initial stages of phylogenetic analysis (Wiens, 2000; Zelditch *et al.*, 2000). If characters that are actually 'different' are considered (or coded) *a priori* to be the 'same', then they may appear as homoplastic on a cladogram (Lockwood and Fleagle, 1999). Biological homoplasy is the term used when homoplasy is actually occurring in two or more groups of taxa, and is not an artefact of the method(s) used to determine this. In other words, biological homoplasy occurs when identical features are observed in separate taxa that are not present in their most recent common ancestor (Lockwood and Fleagle, 1999).

Systematics and Taxonomy

Extant Primate Systematics and Taxonomy

Throughout this study, the terms 'hominoid' and 'ape' will be used interchangeably to refer to the superfamily Hominoidea. The term 'hominid' (family Hominidae) will be used to refer to the great apes and humans and their fossil relatives (Begun, 1992b, c, 1993, 1994, 2001; Begun and Kordos, 1997). The term 'stem' (lineage, group or taxon) is reserved here for extinct members of a clade that are not members of the crown group; i.e., they exhibit some, but not all of the diagnostic features of the clade (Ax, 1985). The term 'terminal' (group

or taxon) is used to describe existing phyletic groups, in contrast to their (hypothetical) ancestors (Begun, 1994).

Familial systematics within the Hominoidea will not follow any one worker's preferred taxonomic scheme, but will instead consist of a synthesis of previously published schemes whose conclusions are based on molecular and morphological (craniodental and postcranial) evidence[3]. Within the Hominoidea (Infraorder Catarrhini) are included the families Hylobatidae (including the living gibbons and the siamang) and Hominidae, which encompasses the subfamilies Ponginae *sensu stricto* (the orang-utan), Gorillinae (*Gorilla*), Paninae (*Pan*) and Homininae (*Homo*). The subfamilies within Hominidae are not resolved further, due to a lack of consensus concerning the ranking of hominid genera into super-generic categories (see Cela-Conde, 1998).

The classification used for extant taxa in this study will therefore be as follows (only genera discussed in this study are listed):

Order Primates Linnaeus, 1758
Semiorder Haplorhini Pocock, 1918
Suborder Anthropoidea Mivart, 1864
Infraorder Platyrrhini E. Geoffroy, 1812
Superfamily Ceboidea Simpson, 1931
Family Cebidae Swainson, 1835
Subfamily Cebinae Mivart, 1865
Genus *Saimiri* Voigt, 1831
Family Atelidae Gray, 1825
Subfamily Atelinae Miller, 1924
Tribe Alouattini Rosenberger and Strier, 1989
Genus *Alouatta* Lacépède, 1799
Tribe Atelini Rosenberger and Strier, 1989

[3] Although in this classification, hominid taxa are ranked only to the level of subfamily, the author recognises the validity of an African ape/human clade (Sarich and Wilson, 1967), and a chimp/human clade (Yunis and Prakash, 1982; Groves, 1986; Miyamoto *et al.*, 1987; Goodman *et al.*, 1990; Groves and Paterson, 1991; Ruvolo *et al.*, 1991; Begun, 1992b; Goodman *et al.*, 1994; Shoshani *et al.*, 1996; Ruvolo, 1997). Some workers, however, regard the *Gorilla/Pan/Homo* trichotomy as unresolved (e.g., Andrews, 1992; Dean and Delson, 1992). This classification is an attempt to maintain nested monophyletic groups of taxa and avoid the creation of paraphyletic groups, such as the traditionally conceived Family Pongidae (including all the great apes except *Homo*; *sensu* Simpson, 1945).

Genus *Ateles* E. Geoffroy, 1806

Genus *Brachyteles* Spix, 1823

Genus *Lagothrix* E. Geoffroy, 1812

Infraorder Catarrhini E. Geoffroy, 1812

Superfamily Cercopithecoidea Simpson, 1931

Family Cercopithecidae Gray, 1821

Subfamily Cercopithecinae Blanford, 1888

Genus *Chlorocebus* Gray, 1870

Subfamily Colobinae Elliot, 1913

Genus *Colobus* Illiger, 1811

Superfamily Hominoidea Simpson, 1931

Family Hylobatidae Blyth, 1875

Genus *Hylobates* Illiger, 1811

Family Hominidae Gray, 1825

Subfamily Ponginae Allen, 1925

Genus *Pongo* Lacépède, 1799

Subfamily Gorillinae Hürzeler, 1968

Genus *Gorilla* I. Geoffroy, 1852

Subfamily Paninae Delson, 1977

Genus *Pan* Oken, 1816

Subfamily Homininae Gray, 1825

Genus *Homo* Linnaeus, 1758

Fossil Primate Systematics and Taxonomy

The relationships of the fossil taxa described in this study to extant forms are unclear (Pilbeam, 1996), and therefore their placement in taxonomic groups whose parameters are defined by living primates is difficult. For example, facial features common to both *Sivapithecus* and *Pongo* have been interpreted both as shared derived (Andrews and Cronin, 1982; Pilbeam, 1982; S. Ward and Kimbel, 1983; S. Ward and Pilbeam, 1983; S. Ward and Brown, 1986; Brown and S. Ward, 1988) and shared primitive (Benefit and McCrossin, 1995). If the latter proves to be true, then *Sivapithecus* cannot be grouped in Ponginae. Likewise, cranial and postcranial features of *Dryopithecus* have been used by workers to

link this fossil taxon with the orang-utan (Moyà-Solà and Köhler, 1993, 1995, 1996) and with the African ape/human clade (Begun, 1992b, 1994). In contrast, McCrossin and Benefit (1994) argue that the proximal humeral morphology of *Dryopithecus* and *Equatorius* indicates these taxa may have diverged prior to the last common ancestor of living apes, including hylobatids. They suggest (McCrossin and Benefit, 1994:111) that, "large-bodied hominoids of the middle and late Miocene may merely be avatars, not ancestors, of the extant great apes." In light of the uncertainty surrounding the taxonomy of many fossil primates, and particularly Miocene hominoids, the fossil taxa reviewed in this study will not be formally classified beyond the rank of superfamily.

Previous Phylogenetic Hypotheses

Introduction

The following section is a review of hypotheses concerning the phylogenetic relationships between hominoid genera. Living apes show many craniodental and postcranial similarities (Gebo, 1996; Pilbeam, 1996; Larson, 1998; Rae, 1999). Extensive postcranial similarities have long been noted and have been interpreted as locomotor adaptations to forelimb-dominated arboreal activities, though workers disagree as to whether forelimb suspensory behaviour (Avis, 1962; Lewis, 1969, 1972b; Tuttle, 1975a; Fleagle, 1976; Hunt, 1991b), quadrumanous climbing and bridging behaviours (Cartmill and Milton, 1977), or vertical climbing (Sarmiento, 1987) is most significant. Most of these similarities have been interpreted as synapomorphies (Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). The growth of interest in phylogenies based on postcranial data over the last few decades is a departure from the previously 'craniodentophile' nature of phylogenetic investigations (Pilbeam, 1996, 1997; Pilbeam and Young, 2001). It has led to the recognition that the pattern of craniodental and postcranial similarities between taxa often support conflicting phylogenetic hypotheses (Collard and Wood, 2001b). This incongruence has led some workers to question whether the postcranial similarities of living apes are homoplasies.

Theories concerning the phyletic relationships between hominoid taxa are not new, they have been expounded for most of the last century (Tuttle, 1974). Many workers (e.g., Straus, 1949; Le Gros Clark and Thomas, 1951; Napier and Davis, 1959; Avis, 1962; Simons, 1962, 1967a; Ashton and Oxnard, 1963, 1964a; Washburn, 1963; Lewis, 1969, 1971a, b, 1972a, b; Lewis *et al.*, 1970; Groves, 1972; Cartmill and Milton, 1974, 1977; Tuttle, 1975a; Andrews and Groves, 1976; Corruccini *et al.*, 1976; Corruccini, 1978b; Harrison, 1982, 1986a, b, c, 1987, 1991; Ciochon, 1983; Hollihn, 1984; Andrews, 1985, 1992; Martin, 1986; Pilbeam, 1986, 1996, 1997; Andrews and Martin, 1987; Sarmiento, 1987; Pilbeam *et al.*, 1990; Begun, 1992b, 1993, 1994, 2001; Larson, 1992, 1998; McCrossin and Benefit, 1994; Benefit and McCrossin, 1995; Begun and Kordos, 1997; Harrison and Rook, 1997; Alba *et al.*, 2001; Köhler *et al.*, 2001; Pilbeam and Young, 2001; Richmond and Whalen, 2001) have pondered the extent of homoplasy in the Hominoidea, and opinions on this subject can be roughly divided into four categories: (1) the trunk and forelimb similarities of extant hominoids are synapomorphies; (2) *Hylobates* evolved trunk and forelimb adaptations independently of hominids; (3) *Pongo* and *Hylobates* evolved their trunk and forelimb morphology independently of each other and the African ape/human clade; and, (4) certain features of the extant hominoid postcrania are independently derived in all genera.

References to postcranial homoplasy among hominoids are numerous in the published literature. Most, however, are no more than passing comments, rarely specifying which similarities may be homoplasies, the reasons for supposing this, or even which genera developed the similarities independently. The following review will outline some of the more detailed references and try to make explicit each worker's justification for subscribing to a particular hypothesis and any evidence they cite in its favour.

Hominoid Trunk and Forelimb Synapomorphy

Many workers regard the trunk and forelimb similarities evident in the extant hominoids to be inherited from their most recent common ancestor (i.e., to be synapomorphies). Several researchers (e.g., Straus, 1949; Washburn, 1963; Gebo, 1996) do not cite specific evidence in favour of this hypothesis, preferring

to assume that, in the absence of evidence to the contrary, the upper body and forelimb anatomy of living apes evolved only once.

Other workers (e.g., Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987) have delineated the sequence of character evolution, as they see it, at each of the ancestral nodes within Anthropoidea. All of these workers agree that most of the trunk and forelimb similarities exhibited by extant hominoids (including the nine examined in the present study) are synapomorphies. None of these workers, however, performed a phylogenetic analysis using these characters. Since this is the final arbiter in distinguishing synapomorphy from homoplasy (Patterson, 1982; Farris, 1983; Schoch, 1986), their conclusions are no more than assumptions.

Lewis (1969, 1971b, 1972b) has pointed out that some non-hominoid anthropoid taxa (e.g., *Ateles*) that engage in forelimb suspension lack some of the trunk and forelimb similarities shared by living apes, and that this fact reduces the plausibility of these features being independently derived in extant hominoids. The logic of this argument is that similarity (through convergence) should be expected in such taxa if these traits are frequently subject to homoplasy, because trunk and forelimb morphology is put to the same functional use in atelins and (some) hominoids.

Lewis (1969, 1971a, b, 1972a, b; Lewis *et al.*, 1970) has used this argument to suggest that the derived wrist morphology in living apes was acquired only once, in their last common ancestor. Lewis (1971b) points out that if extant hominoid wrist morphology were the product of parallelism, due to similar functional usage or developmental constraint, then we would expect similar wrist morphology to have evolved convergently in atelin monkeys, who exhibit similar locomotor patterns. The fact that it has not, he claims, suggests that wrist morphology in living apes represents a "monophyletic acquisition" (Lewis, 1971b:254).

One problem with this argument is that it is based on the premise that atelin monkeys engage in the same patterns of locomotion, in the same way as living apes, without having evolved similar morphological responses. All three genera of atelin monkey, however, possess a crucial morphological difference to the living apes, a fifth limb or prehensile tail (Rosenberger and Strier, 1989). The prehensile tail aids the support of these primates during forelimb suspension,

obviating the functional need that extant hominoids display for an increased range of pronation/supination in the forearm (achieved through ulnar deviation). Another problem is that some atelin taxa (in particular *Ateles*) display marked similarities with extant hominoids in other areas (e.g., pectoral girdle; Gebo, 1996); therefore, even if wrist morphology is synapomorphic in hominoids, other anatomical areas may be subject to homoplasy. A further problem is that some features of the hominoid wrist are found in a convergent condition in lorises (e.g., *Nycticebus*), suggesting that hominoid-like specialisations of the wrist may not be functionally correlated with suspensory locomotion, but rather with cautious quadrupedalism (Cartmill and Milton, 1977). The fact that some hominoid wrist traits have undergone convergence in other non-hominoid taxa invalidates Lewis's (1969) hypothesis that hominoid wrist morphology is unique among primates, and therefore synapomorphic.

Another argument sometimes proposed is that similarities among hominoids are so detailed and pervasive that they must be homologous (and synapomorphic, if they differ in expression from the nearest outgroup). Sarmiento (1987) uses this argument to suggest that all living apes and the late Miocene ape *Oreopithecus* must have derived their trunk and forelimb adaptations from a common ancestor. He points out that, like extant hominoids, *Oreopithecus* exhibits a forelimb specialisation that facilitates the climbing of large diameter vertical supports. This adaptation is anatomically manifest in the joint complex for forearm and shoulder rotation. Sarmiento (1987:2) suggests that:

> The large number of anatomical elements incorporated into this specialisation and the one-to-one correspondence of these elements in *Oreopithecus* and hominoids strongly argue for a uniquely shared evolutionary history.

It certainly does appear that *Oreopithecus* shares numerous postcranial similarities with the living hominoids, which have usually been interpreted as shared derived (e.g., Harrison, 1986a; Harrison and Rook, 1997). If these traits were hypothesized to have originated in the common ancestor of the Hominoidea, however, we would expect to see these features exhibited in all members of the oreopithecid lineage. The fact that *Nyanzapithecus*, an early Miocene taxon linked to *Oreopithecus* on the bases of dental similarity (Benefit and McCrossin, 1997),

displays the primitive condition for many of these traits in the proximal humerus (McCrossin, 1992), suggests that the derived proximal humerus characters in *Oreopithecus* evolved independently[4] (Benefit and McCrossin, 1995; McCrossin and Benefit, 1997). Sarmiento (1987:23) later states that, "because *Oreopithecus* and [extant] hominoids have arrived at the same morphological solutions to the mechanical problems imposed by climbing behaviours, convergence is a very unlikely supposition." This appears to be a very curious statement, since the employment of similar morphological solutions to similar functional/mechanical problems by different taxa is the epitome of homoplastic evolution (Simpson, 1961; Lockwood and Fleagle, 1999).

Pilbeam (1996) also uses the argument that extant hominoid postcranial similarities are too detailed to be homoplasies. He concedes (Pilbeam, 1996:160) that it is, "likely that some fraction of hominoid postcranial similarities . . . represent homoplasies" but goes on to say that he "doubt[s] that this is a significant fraction." He bases these doubts (Pilbeam, 1996:160) on the premise that axial and appendicular skeletal similarities are "widespread and marked" within the Hominoidea. It is true, when compared with other anthropoid taxa, that hominoids share many postcranial similarities, but it has also been pointed out by some workers (e.g., Larson, 1998) that there are marked differences in trunk and forelimb morphology between extant hominoid genera, and where similarities exist they manifest themselves in varying degrees of expression in each taxon. An assessment of the validity of this argument will have to wait until the degree of trunk and forelimb similarity in hominoids has been ascertained.

Harrison (1982, 1986a, b, 1987, 1991) is another worker who has used the argument that trunk and forelimb similarities in the Hominoidea are too detailed to be homoplasies. He suggests (Harrison, 1986a:573) that:

> *Oreopithecus* . . . has a range of unique synapomorphies with the living hominoids that is so detailed and pervades so many functional complexes that there seems little possibility that these traits could have been independently acquired in the two taxa.

[4] Harrison and Rook (1997), however, conclude that the dental similarities between *Oreopithecus* and *Nyanzapithecus* are homoplasies.

Harrison's (1986a) argument is based on the same premise as Sarmiento's (1987) and Pilbeam's (1996), that there is a high degree of detail in the trunk and forelimb similarities of extant (and some Miocene) hominoids, and also that these detailed similarities pervade numerous anatomical regions. It has already been noted, however, that there is a lack of consensus about the extent, and degree of detail, of hominoid postcranial similarities (Larson, 1998), which makes it difficult to assess the validity of this premise. Even if similarities in the hominoid trunk and forelimb are detailed and pervasive, it does not immediately follow that they are synapomorphic. Harrison (1986a) uses his supposition about the detailed nature of similarity between hominoid genera to imply that this makes it intrinsically more likely that these traits are synapomorphic rather than homoplastic. This argument, however, is based solely on probability; synapomorphy can only be shown by reconstructing the state of expression of any given character present in a group of terminal taxa, in that group's most recent common ancestor (Lockwood and Fleagle, 1999). If the states are identical then homology (and possibly synapomorphy, depending on the state of expression in the outgroup) can be confirmed.

Other workers are more vague as to their reasoning for believing that hominoid trunk and forelimb features are synapomorphies. Benefit and McCrossin (1995:249), for example, argue that, "Aside from the possible parallel acquisition of modern hominoid-like morphologies by *Oreopithcus* . . . the hanging adaptations of the limb and vertebral column seen in living hominoids probably evolved only once." Unfortunately they do not go on to substantiate this assertion.

Hylobatid Trunk and Forelimb Homoplasy

It has long been recognised that while *Hylobates* shares many morphological similarities with hominids, it is also the most specialised member of the Hominoidea. Analyses of morphological and molecular data (e.g., Mann and Weiss, 1996; Pilbeam, 1996; Shoshani *et al.*, 1996; Ruvolo, 1997) suggest that this taxon was the first to diverge from the common hominoid lineage. These factors have led several workers (e.g., Simons, 1962, 1967a; Tuttle, 1975a; Hollihn, 1984; Begun, 1993; Larson, 1998) to suggest that *Hylobates* developed its trunk and forelimb specialisations independently of hominids.

Tuttle (1975a) has advanced this argument based on a consideration of three characters related to bimanual forelimb suspension: forelimb elongation, pollical reduction and wrist structure. Tuttle (1975a) reviews Simons's (1962, 1967a) hypothesis of independent evolution of forelimb elongation in several genera of anthropoids (see below for review). He concludes (Tuttle, 1975a:457) that, "*Ateles*, *Oreopithecus*, and, to a lesser extent, the hylobatid apes acquired forelimb elongation independently from each other and from [hominids] is fairly assured." He maintains that it is much less likely for *Pongo* and the African apes to have developed this trait independently (though he concedes that it is not implausible). He suggests (Tuttle, 1975a) that a shared behavioural adaptation to suspensory foraging on fruits and flowers in the periphery of trees may provide an explanation for the homoplastic evolution of this trait (i.e., possessing a long reach would be functionally advantageous).

Tuttle (1975a) also reviews the anatomy of several anthropoid primates with regard to pollical reduction. He concludes (Tuttle, 1975a:459) that independent reduction of pollical structures occurred at least three times, "in *Ateles*, *Colobus* (*sensu lato*), and the Pongidae [great apes, *sensu* Simpson, 1945]." Pollical reduction is interpreted as part of a manual adaptation for rapid hauling movements. He notes that the pollical long flexor tendon is reduced in both the orang-utan and chimpanzee, but maintains that whether this trait developed independently in *Pongo* and *Pan*, or was inherited from a common ancestor remains equivocal.

In his review of wrist structure, Tuttle (1975a) summarises Lewis's (1969) model that extant hominoids share a derived ulnocarpal morphology. He criticises many of Lewis's (1971a, 1972b) conclusions relating to the retreat of the ulna from the carpus and the concomitant changes in the ulnar carpal bones in various hominoid taxa, and cites several other workers who have conducted studies on the carpus of other anthropoids, which contradict Lewis's findings about the unique nature of these adaptations (e.g., Cartmill and Milton, 1974, 1977). Tuttle (1975a) concludes that some ulnar deviation may have occurred prior to the furcation of the hylobatid and hominid lineages, but that further changes in carpal structure relating to increased flexibility probably developed independently in the two lineages *pari passu* with forelimb elongation.

Overall, Tuttle's (1975a) review of these three character complexes leads him to conclude that *Hylobates* and *Ateles* evolved elongated forelimbs convergently with hominids, and that these taxa, together with *Colobus*, developed pollical reduction also through convergent evolution. Tuttle remains equivocal on whether the wrist structure evident in hominoids evolved only once or was subject to homoplasy.

Pongine and Hylobatid Trunk and Forelimb Homoplasy

Although *Hylobates* is the most morphologically divergent of extant hominoids, it is also widely recognised that *Pongo*, while exhibiting many morphological similarities with African apes, is anatomically and behaviourally distinct from African ape knuckle-walking, terrestrial specialisations, having diverged before the lineage leading to the African ape/human clade. This has led some workers (e.g., Simons, 1962, 1967a; Hollihn, 1984; Begun, 1993; Larson, 1998) to hypothesize that the orang-utan evolved its trunk and forelimb morphology independently of the African ape/human clade and to imply this is also the case for *Hylobates*.

Simons (1962:292) has argued that the character 'forelimb elongation' (functionally correlated with forelimb suspension) evolved independently "at least 3, and possibly as many as 6 times" in the Anthropoidea. The lower limit was later revised to "at least five times" (Simons, 1967a:241), in the lineages culminating in gibbons (including siamang), orang-utans, African apes, spider monkeys and *Oreopithecus*. He considers the acquisition of this character in these various groups to exemplify true parallel evolution, not convergence.

Simons's (1962) model is premised on forelimb elongation characterising the five taxa in his scheme, and although he does not present figures or references to support this (he cites the high mean values for intermembral indices evident in these taxa), it has been well documented that this is the case (e.g., Erikson, 1963; Napier, 1963; Schultz, 1973). Simons (1962) bases his hypothesis on a number of assumptions. Firstly, his claim that *Hylobates* developed forelimb elongation independently is based on the assumption that the presumed Miocene ancestors of this genus were far less specialised than their living relatives, retaining the primitive arrangement of having longer hindlimbs than forelimbs, and therefore

that the specialisations seen in modern gibbons must have emerged after the furcation of that lineage from the hominid lineage. Simons's (1962) justification for this assumption comes from specimens assigned to the Miocene taxon *Pliopithecus* that exhibit a low, mean intermembral index (approx. 95). *Pliopithecus*, along with several other early Miocene genera, was at this time interpreted to be an ancestor of modern gibbons. Since Simons's (1962) paper was published, however, the phylogenetic provenance of the gibbon lineage has become much more ambiguous. Fleagle (1984) has argued that no Miocene taxon can be linked unequivocally with extant gibbons. If this is the case, then Simons's argument is invalid, as early representatives of the gibbon lineage may have expressed similar trunk and forelimb specialisations, increasing the likelihood that these adaptations were present in the common ancestor of the Hominoidea, and are therefore synapomorphies.

Secondly, Simons's (1962:292) hypothesis that forelimb elongation in *Pongo* arose independently is based on the assumption that the orang-utan lineage evolved separately from that of the African ape/human lineage, "since early Miocene times at least." Simons (1962:292) suggests that this interpretation is supported by "combined fossil, morphological, and physiological evidence", but fails to produce any of it. Once again, in the decades since Simons's publication evidence has come to light disputing an early Miocene divergence of the orang-utan lineage. Many workers (e.g., Andrews and Cronin, 1982; Pilbeam, 1982; S. Ward and Kimbel, 1983; S. Ward and Pilbeam, 1983; S. Ward and Brown, 1986; Brown and S. Ward, 1988) now regard early relatives of *Pongo* (i.e., *Sivapithecus*) to have developed in the late Miocene. Regardless of whether *Pongo* and *Sivapithecus* are sister taxa, the argument that an early divergence of *Pongo* from the African ape/human lineage automatically means that forelimb elongation evolved in parallel in these taxa is invalid. The only valid criterion that can be used to diagnose the presence of homoplasy is to assess the state of expression of any given character in the most recent common ancestor of a group of terminal taxa, and see if this condition matches that expressed in those taxa (Lockwood and Fleagle, 1999). If the common ancestor and all descendents share the same state, then homology can be assumed, if the common ancestor expresses a different condition to that of the terminal taxa, then parallelism, convergence or reversal may be hypothesized. In this case, it is necessary to reconstruct the

condition that the common ancestor of hominids expressed for the character 'relative forelimb elongation', something Simons (1962, 1967a) does not attempt.

Thirdly, Simons's (1962:292) claim that forelimb elongation was independently acquired in *Ateles* and *Oreopithecus* is based on the premise that the:

> ancestral stocks of [*Ateles* and *Oreopithecus*] already were distinct from that which produced modern hominoids by late Eocene times – times when there is no evidence that forelimbs elongation had occurred in any primate group.

This argument is similar to the one outlined above, though here at least there is some recognition that proof of homology (and homoplasy) is contingent on assessing the expression of a trait in the common ancestry of terminal taxa. In the four decades since Simons's (1962) work, it has become apparent that the lineage leading to extant hominoids diverged from that leading to extant cercopithecoids much later than was previously thought (probably in the late Oligocene or early Miocene; Fleagle, 1983; Fleagle and Kay, 1983), and further that the oreopithecid lineage originated at the earliest in the early Miocene of East Africa (Harrison, 1985, 1986b; Benefit and McCrossin, 1997). This being the case, it is obvious that the lineage leading to *Oreopithecus* could not be distinct from that leading to crown hominoids in the Eocene epoch, since neither group can be distinguished in the fossil record until much later. Simons's (1962) claim that forelimb elongation is not evidenced in the fossil record preceding these lineages is used as a basis for the supposition that the common ancestor of these taxa did not possess this trait, and therefore that it must have evolved independently after the furcation of these groups. This conclusion needs to be reassessed in light of the fact that these lineages originated in the Miocene, rather than the Eocene. It does appear, however, that early Miocene forms retain the usual primate configuration of longer hindlimbs than forelimbs (Rose, 1997; C. Ward, 1997), and this lends some weight to Simons's (1962) argument. An accurate appraisal of his model will have to await a more rigorous reconstruction of the most recent common ancestor of these groups.

Hollihn (1984) agrees with Simons's (1962) supposition that some of the morphological specialisations relating to forelimb suspension evolved

independently in the hylobatid, pongine and African ape/human lineages. He used material from the published literature to conjecture (Hollihn, 1984:95) that:

> it seems probable that the ancestors of the Hylobatidae . . . were monkey-like animals capable of a large variety of locomotor and postural behaviours, but lacking the morphological specialisations of recent gibbons, pongids [great apes, *sensu* Simpson, 1945] and hominids [*Australopithecus* and *Homo*].

In the same chapter he claims (Hollihn, 1984:95):

> The most immediate common ancestor of [hominids] did not possess morphological features related to brachiation, knuckle-walking or bipedalism.

The implications of these statements are that *Hylobates* developed specialisations relating to brachiation only after diverging from the common ancestor of the Hominoidea, and that *Pongo* developed its suspensory related features, and *Pan* and *Gorilla* developed their knuckle-walking specialisations, after the furcation of the hominid lineage (i.e., the orang-utan evolved features relating to forelimb suspension and climbing independently from the hylobatids). Hollihn (1984) also regards the postcranial similarities in atelins and hylobatids to be homoplasies.

Pilbeam *et al.* (1990) described two humeri (GSP 30754 and GSP 30730) that are attributed to *Sivapithecus*. The morphology of these specimens presents a mosaic of primitive and derived features that has important ramifications for extant hominoid phylogeny. The proximal humerus is characterised by a medially inclined and retroflexed shaft, a flat deltoid plane, prominent deltopectoral and deltotriceps crests, and mediolateral plus anteroposterior curvatures of the shaft, all features that have been functionally correlated with quadrupedal locomotion and morphologically associated with early Miocene hominoids (e.g., *Proconsul*), and extant arboreal quadrupeds (Rose, 1989; Pilbeam *et al.*, 1990). On the other hand, the distal humerus exhibits a mediolaterally broad, spool-shaped trochlea with a prominent lateral trochlear keel and deep, narrow *zona conoidea*; these features may be functionally correlated with forelimb suspension or vertical climbing, and have been hypothesized to be shared derived for living apes (Ciochon, 1983; Harrison, 1987; Sarmiento, 1987; Rose, 1988a). *Sivapithecus* has been phyletically linked to the extant taxon *Pongo* by numerous workers (e.g.,

Andrews and Cronin, 1982; Pilbeam, 1982; S. Ward and Kimbel, 1983; S. Ward and Pilbeam, 1983; S. Ward and Brown, 1986; Brown and S. Ward, 1988) on the basis of palatal and maxillofacial similarities that they share to the exclusion of all other living and fossil hominoids, and which have been interpreted as shared derived characteristics. This combination of facial and forelimb traits presents a phylogenetic conundrum. Pilbeam *et al.* (1990:238-239, emphasis added) outline two mutually exclusive hypotheses that can account for this:

> First, that *Sivapithecus* and *Pongo* are sister taxa, in which case *a number of postcranial features shared by living large hominoids must represent convergences*. Second, that *Sivapithecus* and *Pongo* are not sister taxa, in which case their palatal and facial similarities are not shared derived features but either convergent derived or shared primitive features.

Pilbeam *et al.* (1990) concede that biologically plausible procedures may not exist for the unequivocal resolution of these alternatives. If *Pongo* and *Sivapithecus* are sister taxa, then it follows that the derived proximal humeral morphology of extant hominoids (characters such as the straight shaft and convex deltoid plane) must have evolved independently at least three times, in the hylobatid, pongine and African ape/human lineages.

Benefit and McCrossin (1995) have argued, however, that many of the facial characters linking *Sivapithecus* with *Pongo* are, in fact, primitive for catarrhines and therefore symplesiomorphic in these taxa. If true, this means that *Sivapithecus* and *Pongo* are not sister taxa, and therefore that the derived proximal humeral morphology seen in *Pongo* is a synapomorphy of the Hominoidea.

Moyà-Solà and Köhler (1996) suggest that the two Miocene hominoids *Dryopithecus* and *Sivapithecus* are linked to the *Pongo* clade. In the case of *Dryopithecus*, this supposition is based on the shared possession of numerous postcranial characteristics of the CL1 18000 skeleton that they interpret as derived; in the case of *Sivapithecus*, they argue that facial characters shared by these two lineages are derived[5]. They also argue that both these taxa retain several

[5] Moyà-Solà and Köhler (1996) argue that the genus *Sivapithecus* includes two different locomotor adaptations: climbing and suspension (*S. indicus*), and quadrupedalism (*S. parvada*). This supposition is based on the morphology of the proximal humerus in *S. parvada* (GSP 30754), which, as Pilbeam *et al.* (1990) has shown, exhibits primitive features, and the proximal humeral morphology of *S. indicus* (GSP 30730), which (according to the reconstruction of this crushed specimen by Moyà-Solà and Köhler) exhibits derived (hominoid) features (*contra* Pilbeam *et al.*,

primitive features that extant hominids share a derived condition for. They conclude (Moyà-Solà and Köhler, 1996:158-159) that, if both these suppositions are correct:

> the common ancestor of all extant great apes would have been more primitive than hitherto inferred by the analysis of extant forms. If so, then resemblances between the Asian and the African subclades in such derived features must reflect homoplasy.

Moyà-Solà and Köhler (1996) are therefore arguing that the locomotor adaptations of Asian and African hominids (and the structural complexes that underlie them) developed after their separation from a common ancestor (which they infer to be a "generalised (orthograde) climber"; Moyà-Solà and Köhler, 1996:159) that possessed the primitive condition for many postcranial features commonly inferred to be shared derived for crown hominoids.

Andrews (1992) argues that if *Sivapithecus* is linked to the pongine clade then the shared postcranial morphology of the orang-utan and the African apes must have evolved independently. Andrews (1992) does not explicitly specify which postcranial similarities he thinks are homoplasies, though he implies that the proximal humeral characters highlighted by Pilbeam *et al.* (1990; e.g., retroflexed shaft, flat deltoid plane etc.) are the most likely to have arisen independently.

Begun (1993) argues that both *Hylobates* and *Pongo* evolved forelimb similarities independently of each other and the African apes/humans, though he does not specify which postcranial similarities he thinks are homoplasies (he mentions the character complex relating to below-branch positional behaviour). He does suggest (Begun, 1993), however, that some of the similarities in the phalangeal morphology of hominoids (and other suspensory primates) may have developed independently in all lineages. Begun (1993) points out that phalanges are particularly sensitive to substrate variables and that the relationship between phalangeal morphology and locomotor behaviour is stronger than that of other factors, such as body size and phyletic affinity, though he contends that

---

1990). Thus, Moyà-Solà and Köhler (1996) suggest that the postcranial morphology of *Sivapithecus* does not contradict the proposed close relationship of this genus to *Pongo* (based on shared craniofacial features).

information relating to phylogenetic relationships can still be extracted from these features.

Trunk and Forelimb Homoplasy in all Hominoid Genera

Some workers have gone further than suggesting that trunk and forelimb features are independently derived in Asian and African apes. They contend that at least some of the postcranial similarities exhibited by hominoids evolved independently in all genera. One justification for inferring that trunk and forelimb features have been acquired independently in all hominoid genera is the argument that some of these traits may be an allometric artefact of large body size.

Harrison (1986a, 1987) has suggested that this may be the case for two forelimb characters: medial trochlear keel development and forelimb elongation. He suggests (Harrison, 1987:70) that:

> the similarity in the development of the trochlear keeling in *Proconsul* [and *Oreopithecus*] and in extant great apes [*sensu* Simpson, 1945] may have been convergent acquisitions in large-bodied primates, rather than a reflection of a close phyletic relationship.

This interpretation is based on the observation of an allometric tendency among anthropoids for the trochlea to increase in breadth with body size at a faster rate than the capitulum (Harrison, 1982). The increased relative surface area of the trochlea in large primates necessitates structural modifications (e.g., double-keels and marked waisting) to stabilize the humeroulnar joint during flexion/extension (Harrison, 1986a). Thus, Harrison (1982, 1986a, 1987) suggests that the prominence of the medial keel in all hominoids may be an independent development in these lineages, as a result of increasing body size.

Harrison (1986a, 1987) also argues that the elongation of the forelimbs in the Miocene taxon *Oreopithecus* and in extant hominoids may have evolved independently, either as a response to similar functional demands, or alternatively, as an artefact of large body size. The latter argument is based on the observation of an overall trend among non-human primates for relative forelimb length to increase with body size (Aiello, 1981b, 1984; Jungers, 1984, 1985). Harrison (1986a, 1987) suggests that this allometric trend can account for the high intermembral index of *Oreopithecus* (and extant hominoids), since this taxon

exhibited a relatively high estimated body weight (30-40 kg; Stern and Jungers, 1985; Szalay and Langdon, 1985, 1986) and would therefore be expected to have elongated forelimbs as a manifestation of this, rather than as a result of phyletic heritage.

Harrison (1986a, 1987) does not commit himself to the hypothesis that forelimb elongation and medial trochlear keel development evolved independently among Miocene and extant hominoid genera, as a result of an overall similarity in gross body size. He prefers, rather, to note it as a possibility, while suggesting that these features remain potential synapomorphies for the Hominoidea.

The hypothesis that gibbons are secondarily dwarfed (Groves, 1972; Pilbeam, 1996), having evolved from a large-bodied ancestor, would, if correct, support the assertion that some forelimb similarities in hominoids are the product of allometric tendencies rather than phyletic heritage, since these features, where present in modern gibbons, could have developed early in the gibbon lineage as a result of large body size, before the recent dwarfing.

Cartmill and Milton (1977:251) have also suggested that the trunk and forelimb similarities of hominoids may have evolved independently, possibly as a result of an increase in body size, from a "monkey-like quadruped". These workers argue that an increase in body size early in the lineages leading to extant hominoids led inescapably to rather cautious locomotor habits, where these taxa distributed their weight over several supports and crossed arboreal gaps by pulling or swinging themselves across, instead of jumping. If the lineages leading to the extant apes went through a stage of cautious, orthograde (possibly suspensory) quadrupedalism (similar to that of *Pongo*), this could account, they claim, for the suite of trunk and forelimb characters usually associated with forelimb suspension that extant hominoids share to the exclusion of other non-atelin anthropoids (e.g., transversely broad thorax, forelimb elongation, etc.; Cartmill and Milton, 1977). Since the importance of suspensory locomotion in a primate's repertoire increases as body size increases, and since a large primate will more easily suspend from a small support than balance on top of it (Napier, 1967), Cartmill and Milton (1977) argue that a cautious quadruped with long forelimbs would become increasingly suspensory if it increased in body size. Thus, these workers acknowledge the possibility that the Hominoidea diverged from a monkey-like (pronograde quadruped) ancestor and that each of the lineages leading to extant genera

developed their specialised trunk and forelimb morphology independently, as a result of the allometric effects of large body size and the concomitant locomotor parameters it bestowed.

Larson (1998) has reviewed the phylogenetic analyses of various workers in an attempt to ascertain whether some of the trunk and forelimb similarities of hominoids reflect parallel evolution. She concludes that almost half of the postcranial character states that are widely assumed to be synapomorphies for the Hominoidea[6] are in fact present in other primate taxa, and many of the remaining traits are present in a convergent condition in *Ateles*. Larson (1998) contends that this makes the notion of parallel evolution in hominoid postcranial morphology more plausible, though concedes that the absence of fossil evidence documenting the origins of most of these trunk and forelimb features precludes a definitive evaluation of the status of these characters in the Hominoidea. Larson (1998), however, does not attempt to reconstruct the ancestral hominoid morphotype (i.e., the most recent common ancestor of hominoids) based on the distribution of character states in terminal hominoid taxa; a technique that may be used effectively to distinguish between homologous and homoplastic traits in situations where relevant fossil material is absent (Maddison and Maddison, 1989; Lockwood and Fleagle, 1999).

Summary

A diversity of opinion exists concerning hominoid postcranial phylogeny. Several different types of argument have been used to suggest that hominoid trunk and forelimb adaptations either evolved once or developed independently in several lineages. Arguments based on probability, the pervasiveness of detailed similarity, or the early divergence and subsequent independent evolution of hominoid taxa are, however, inadequate; they cannot diagnose synapomorphy or homoplasy.

The only valid criterion for establishing if a given character is homologous, consists of observing the state of expression of this trait in a group of terminal taxa and assessing whether this condition matches that exhibited by

---

[6] Larson (1998) reviews thirty five different characters from the thorax, pectoral girdle, humerus, ulna, radius, and carpals.

the group's most recent common ancestor (Lockwood and Fleagle, 1999). If the common ancestor, and all descendents share the same condition then homology can be assumed, if the common ancestor expresses a different state to the terminal taxa then homoplasy (parallelism or convergence) may be hypothesized (Lockwood and Fleagle, 1999).

Hypotheses to Test

In the formulation of an evolutionary hypothesis, it is recognised that, following Hennig's (1966:121) "auxillary principle", the origin of traits by homoplasy should not be assumed *a priori*. The null hypothesis for this study, therefore, is that:

(1) The trunk and forelimb characters examined here are extant hominoid synapomorphies.

The alternative hypotheses are that:

(2) The trunk and forelimb characters examined here are extant hominid synapomorphies.

(3) The trunk and forelimb characters examined here are extant African ape/human synapomorphies.

(4) The trunk and forelimb characters examined here are homoplasies.

Within this theoretical framework, three further hypotheses, relating to the *extent* of homoplasy within the Hominoidea, are also tested:

(4a) Hylobatids evolved the trunk and forelimb characters examined here independently of hominids.

(4b) Pongines and hylobatids evolved the trunk and forelimb characters examined here independently of each other and the African ape/human clade.

(4c) The trunk and forelimb characters examined here are independently derived in all hominoid genera.

Thesis Outline

Chapter One has outlined the aims and objectives of this investigation, delineated the taxonomic classifications and systematics of the extant and fossil taxa mentioned in this study, and reviewed previously published hypotheses relating to the possibility of homoplastic evolution in the hominoid trunk and forelimb. Chapter Two provides a comparative review of the trunk and forelimb morphology and locomotor patterns of some extant anthropoid primates. Chapter Three outlines the trunk and forelimb morphology of some fossil catarrhine primates, and uses this as a basis for inferring the locomotor behaviour of these forms. Chapter Four reports the results of an analysis of character evolution in nine traits from extant anthropoid postcranial morphology and summarises the theoretical framework used in this study, providing an account of the methods of phylogenetic systematics and how these methods facilitate the diagnosis of homoplasy. Chapter Five presents the results of an analysis of character evolution in two traits from fossil catarrhine postcranial morphology. The results of the study are summarised and discussed in Chapter Six, and outlines for further research are given.

CHAPTER TWO

EXTANT ANTHROPOID TRUNK AND FORELIMB MORPHOLOGY AND LOCOMOTOR PATTERNS

Introduction

Living primates inhabit a diverse array of environments, from tropical rain forests to semi-temperate savannah and grassland (Fleagle, 1999). It is not surprising, therefore, that they have developed an equally diverse array of postural and locomotor behaviours to deal with whatever local conditions dictate. When primatology was a nascent discipline, the true diversity of primate locomotor behaviour was obscured by an over-reliance on anatomically based locomotor categorization (Day, 1979). Discrete categories such as 'slow climbers', 'leapers' and 'brachiators', and the broad definitions used to establish these categories, can be useful for descriptive purposes (e.g., Rollinson and Martin, 1981; Martin, 1990), but are hardly diagnostic of the full locomotor repertoire of any one species, never mind genera (Prost, 1965).

Such coarse behavioural groupings do not indicate with what frequency, duration, for what purpose or in what circumstance a particular locomotor method is used (Day, 1979). The categories also do not take into account the ways in which locomotor behaviour may sometimes be intermediate between two or more defined 'modes' (Rose, 1979). In the 1960s, when these categories were defined, quantitative data were not available to address these topics (Hollihn, 1984). Since the early 1970s detailed field studies have recorded a much less uniform pattern of locomotor behaviour for most primate taxa and there is now an appreciation that postural and locomotor repertoires are much more nuanced than these labels suggest (Hollihn, 1984).

Primates seldom rely on one mode of locomotion exclusively, but it is common for a species to have a preferred mode within a more varied repertoire (Fleagle, 1976; Fleagle and Mittermeier, 1980). The most frequently employed

locomotor mode is used to classify living primates into locomotor categories[7] (Prost, 1965; Rollinson and Martin, 1981; Martin, 1990; Hunt *et al.*, 1996). To assess how similar the locomotor repertoires of extant hominoids are to each other, and how they differ from non-hominoid taxa, the frequency and duration with which different locomotor behaviours are employed will be reviewed in the sample taxa, mostly at the generic level (unless there are considerable specific differences in locomotion). As noted above, however, it should be kept in mind that primates of one species or subspecies may move in a variety of ways depending on circumstance, and further, that delineating primate locomotor patterns at the generic level is far from ideal since there is so much specific variation in behavioural repertoires (Mittermeier and Fleagle, 1976; Fleagle and Mittermeier, 1980; Fleagle, 1999). The functional-anatomical basis for these locomotor behaviours will also be reviewed. Since the present study is focused on trunk and forelimb anatomy, the following review will concentrate on this area.

In most primate genera the forelimb can engage in a wider range of movement and a broader spectrum of functions than the hindlimb (Morbeck, 1979). Since most primates inhabit forest of one type or another, forelimb anatomy is shaped by phylogenetic adaptations to the irregular, three-dimensional habitat structure encountered there (Pounds, 1991). Most of the distinguishing features of the forelimb, such as pectoral girdle mobility, flexion/extension capability, pronation/supination of the forearm and grasping hand use can be accounted for on this basis (Morbeck, 1979).

---

[7] There are numerous problems with this approach. Firstly, within each locomotor group (e.g., quadruped, brachiator etc.) there is considerable variation in the movements typical of that group (Oxnard, 1967). Secondly, some taxa are in an equivocal position: e.g., *Ateles* has been classed as a semibrachiator (Napier, 1963; Oxnard, 1963, 1967; Ashton and Oxnard, 1964b), though could, on the basis of proportion of locomotion carried out by bimanual forelimb suspension, be termed a brachiator (Erikson, 1963). Thirdly, some genera are capable of, and are morphologically designed for, particular types of locomotion and yet habitually use completely different modes of progression. For example, the gorilla is essentially a terrestrial quadruped (Hunt, 1991b), but maintains the structural potential for bimanual forelimb suspension (Oxnard, 1967).

Hominoidea

Note on the Term 'Brachiation'

In the field of primatology there has been considerable debate over the last century about the definition of the terms 'brachiator' and 'brachiation' (from *brachium*, Latin for 'the arm'; specifically the upper arm from shoulder to elbow; Brown, 1993), and about which taxa engage in this form of locomotion (Tuttle, 1975a). Although initially coined in the 19th century, the term brachiator was never clearly defined (Andrews and Groves, 1976), and as a result has been loosely applied. The term originally denoted a type of locomotor activity, but since the 1960s has been consistently used as a description of an anatomical-functional complex (Andrews and Groves, 1976). This ambiguity over the correct usage of the term brachiation has led to confusion over the behaviour it describes and the adaptive complex concerned in it (Andrews and Groves, 1976; Takahashi, 1990). Some workers have applied the terms 'brachiator', 'semibrachiator', or 'brachiating primates', to gibbons, siamangs, orang-utans, chimpanzees, gorillas, humans, atelin monkeys, and alouattin monkeys (Tuttle, 1975a). In addition, a further term, 'ricochetal brachiation' has been used, chiefly to differentiate between slow, cautious brachiation and fast, free-flowing (ricochetal) brachiation.

With no rigidly definable concept of, or terminology for, suspensory behaviour in primates, the only common factor among different definitions is that the forelimbs are used in a below-branch position (Takahashi, 1990). One way to resolve this confusion is to clearly differentiate between ricochetal brachiation, brachiation, and suspension on the one hand, and between the behaviour of brachiating and the structural and functional complex that underlies it on the other. In this study, therefore, the terms ricochetal brachiation, brachiation and suspension will not be applied to a specific taxon in an attempt to categorize its locomotor behaviour, but will instead be reserved as descriptions of particular locomotor modes that can be observed within a particular taxon's broader repertoire, and of the anatomical complexes that underlie these habits.

The term ricochetal brachiator, or ricochetal brachiation, will only be used to denote the locomotor behaviour of rapid, smooth-flowing, pendular bimanual forelimb suspension (Carpenter, 1976), incorporating an aerial phase (Baldwin and Teleki, 1976), which involves extensive trunk and arm rotation (approaching

180°; Avis, 1962) between handholds, without the use of other appendages (i.e., tail or pedal), and the adaptive complex associated with this (in practice this term will therefore be reserved only for *Hylobates*). The term brachiator, or brachiation, will be used to describe pendular bimanual forelimb suspension, of a slow to moderate speed and cautious manner, involving extensive bodily rotation between hand holds, without additional support from other appendages (Avis, 1962). The term forelimb suspensory, or forelimb suspension will be applied to the behaviour of bimanual forelimb suspension that involves moderate bodily rotation and may include the use of other appendages (e.g., that seen in atelin monkeys). Note that all of these terms denote behaviours that differ from simple arm-swinging between supports, because many primate taxa can arm-swing to varying degrees (Mittermeier and Fleagle, 1976).

Trunk and Forelimb Morphology and Locomotion

Living apes share several derived craniodental features, although postcranial synapomorphies are more numerous (Rae, 1999). On the axial skeleton the lumbar spine is reduced, with only three to four vertebrae for hominids and four to six for hylobatids (Andrews and Groves, 1976; Ward, 1993). This contrasts with the pattern for quadrupedal monkeys of six to seven vertebrae (Groves, 1972). The sacrum is expanded with five to eight vertebrae instead of two to four (Groves, 1972), and the tail is lost. The thorax is short craniocaudally, broad mediolaterally and shallow dorsoventrally (breadth to depth index above 150), with a mediolaterally wide and craniocaudally short manubrium and long, S-shaped clavicle (Napier and Napier, 1967; Fleagle, 1999; Ankel-Simons, 2000). These features position the pectoral girdle more posterolaterally than in quadrupeds, and allow the scapula to ride on the shoulder dorsally (Morbeck and Zihlman, 1988; Ankel-Simons, 2000). The transversely broad thoracic cage may reflect a need for increased shoulder mobility, as it moves the glenoid sockets further apart, increasing the arm span and their range of circumduction (Cartmill and Milton, 1977). Thorax shape varies between the hylobatids and hominids. The scapula is craniocaudally elongated and positioned dorsally (Larson, 1998). It has a long vertebral border that maximises the leverage of the upper back muscles (*m. rhomboideus* and *m. serratus*), permitting fuller elevation of the forelimb, has

elongated acromion and coracoid processes, and exhibits a glenoid fossa shaped like a dished ovoid (Rose, 1997) that is redirected from facing ventrally, to face more cranially (superolaterally[8]; Ashton and Oxnard, 1964a; Larson, 1988). This contrasts with the morphology of most cercopithecoids, which have deep, narrow chests and laterally positioned scapulae; features diagnostic of quadrupedal habits (Ashton and Oxnard, 1964a; Ward, 1993; Fleagle, 1999). The functional significance of the elongated scapula, and associated musculature in apes is that it facilitates scapular rotation and glenohumeral joint movement, particularly when the forelimb is elevated (Morbeck and Zihlman, 1988; Ankel-Simons, 2000). Scapular shape also varies between the different hominoid genera. All these features indicate that extant hominoids share an orthograde[9] body structure.

The appendicular skeleton of hominoids (in contrast to other anthropoids) is characterised by long forelimbs relative to hindlimbs[10] (Oxnard, 1963; Andrews and Groves, 1976), though there are generic differences in the relative expression of this feature (Larson, 1998). The proximal humerus exhibits a relatively large, globular or hemispherical, medially orientated head, which is larger than the femoral head (Groves, 1972; Larson, 1988; Rose, 1989; Andrews, 1992; Gebo, 1996). The articular surface of the head projects above the level of the greater tubercle (Benefit and McCrossin, 1995), and is not present (or is present in a limited fashion) between the tuberosities (Rose, 1989). The lesser tuberosity is anteriorly rotated creating a deep, narrow bicipital groove (or intertubercular sulcus; Rose, 1989). The head is strongly twisted relative to the distal articular surface of the humerus, with an angle of torsion above 120° (Larson, 1988: Rose, 1994). This contrasts with the smaller, more posteriorly orientated humeral head in quadrupeds, which has a wide, shallow bicipital groove and a smaller angle of torsion (Gebo, 1996), typically between 90° and 110° (Larson, 1988). The degree of head torsion varies intergenerically within the Hominoidea. The humeral shaft is straight, in contrast to the retroflexion exhibited in the proximal shaft of most quadrupeds (Ankel-Simons, 2000).

---

[8] The glenoid fossa faces more cranially in non-human apes, but in humans faces more laterally than in most quadrupeds (Ashton and Oxnard, 1964a).

[9] Orthograde indicates that the trunk is held perpendicular to the ground/support, the opposite of pronograde, where the trunk is held parallel to the ground/support (Fleagle, 1999).

[10] Humans are the only exception within the Hominoidea, having relatively longer hindlimbs (Bilsborough, 1992; Fleagle, 1999).

The elbow region on the humerus is characterised on the medial side by a broad trochleiform, or 'spool-shaped', trochlea with prominent medial and lateral keels, separated by a deep trochlear groove[11] (McHenry and Corruccini, 1975; Rose, 1988a; White and Folkens, 2000). Both trochlear keels run distolaterally, giving the spool-shaped trochlear a screw-like appearance (Rose, 1988a). Lateral to this is the capitulum, which is large, globular in shape and articulates with a central fossa on the proximal surface of the radial head (Rose, 1983). In hominoids, the trochlea is broad relative to the capitulum (McHenry and Corruccini, 1975; Feldesman, 1982; Gebo, 1996). Separating the trochlea and capitulum is a deep, narrow depression (*zona conoidea*) at the midsection of the articular surface (Feldesman, 1982; Rose, 1988a; Aiello and Dean, 1990). The division of the trochlea from the capitulum by the lateral trochlear ridge frees the radius for motions independent from the ulna in various elbow positions (Napier and Davis, 1959). Proximal to the articular surface is the olecranon fossa, a triangular depression that is deep, wide and may be perforated (McHenry and Corruccini, 1975; Aiello and Dean, 1990). Medial to the articular surface is the medial epicondyle, which is large and projects medially, increasing the amount of torque the forearm muscles are able to exert about the radiohumeral and humeroulnar joints (Fleagle and Simons, 1978, 1982; Rose, 1988a, 1994).

The hominoid proximal ulna has a trochlear notch (sometimes referred to as the semilunar notch) that displays a pronounced keel running proximodistally along the sagittal midline of the articular surface, creating two articular surfaces and a distinctive 'saddle-shape'; this articulates with the trochlear groove on the humerus, thus forming a stable 'hinge' (Morbeck and Zihlman, 1988; Rose, 1988a; Aiello and Dean, 1990). The proximal ulna is also characterised by a short olecranon process that extends very little beyond the level of the articular surface of the trochlear notch (Andrews and Groves, 1976; Rose, 1988a). The proximal radial head is bevelled and almost circular, the proximal surface articulates with the *zona conoidea* and capitulum on the distal humerus.

The large articular surface on the lateral keel of the humeral trochlea (for the circumferential articulation of the radial head; Sarmiento, 1987) and the

---

[11] The depth of the trochlear groove is sometimes expressed as a degree of trochlear waisting. Trochlear waisting is a measurement of the depth of the trochlear groove relative to the height of the lateral keel (Rose, 1988a). In extant hominoids the trochlea is markedly waisted (Sarmiento, 1987; Rose, 1988a).

increased depth of the *zona conoidea*, provide enhanced humeroradial joint stability (McHenry and Corruccini, 1975; Rose, 1988a). The articulation of the bevelled proximal radial head with the bulbous capitulum stabilises the humeroradial joint against movements other than the spinning of the radial head that accompanies forearm pronation/supination (Rose, 1988a, 1997). The short olecranon process and deep olecranon fossa are functionally associated with the ability to hyperextend the elbow joint; these features, combined with the migration of the triceps insertion toward the joint fulcrum, promote a greater power and velocity of extension that facilitates forelimb suspension (Groves, 1972; Rose, 1988a). The broad, spool-shaped, double-keeled trochlea is a biomechanical adaptation designed to resist torques generated when the forearm is pronated and supinated during flexion and extension (McHenry and Corruccini, 1975; Rose, 1988a). It is functionally linked with increasing stability in the humeroulnar joint and the prominent lateral keel helps prevent lateral dislocation of the proximal ulna during pronation (Rose, 1988a; Aiello and Dean, 1990).

Wrist morphology also varies between hominoid genera, but is characterised by a distal ulna that has retreated from the primitive condition of articulation with the carpus (in particular the pisiform and triquetral; Lewis, 1969, 1971a). An extensive intra-articular meniscus is present in hominoid wrists between the styloid and the triquetral/pisiform (Lewis, 1972a, b; Lewis *et al.*, 1970). The facets on the triquetral and pisiform are convex (except in *Hylobates*), for articulation with the periphery of the meniscus (Lewis, 1971a, 1972b). Lewis (1972a, b) argues that liberation of the ulnar styloid process from direct articulation with the carpus is an essential prerequisite for an increased movement potential for pronation/supination. All hominoids have an increased range of movement (approx. 180°), compared with extant monkeys (approx. 90°; Lewis, 1971a). Lewis (1971a, 1972a, b) suggests this wider range of pronation/supination is functionally correlated with a capacity for brachiation (i.e., it is a prerequisite for bodily rotation during this locomotor mode), though other workers have argued that it is more likely an adaptation for knuckle-walking (Conroy and Fleagle, 1972) or cautious arboreal quadrupedalism (Cartmill and Milton, 1977). The lunate is relatively broad, compared to the long, narrow shape of this bone in cercopithecoids and ceboids (Begun, 1994; Larson, 1998). The shape of the lunate varies slightly between hominoid genera (Harrison, 1986a).

On the hand, the phalanges are curved and elongated proximodistally, the thumb and pollex are reduced (Begun, 1993). All living apes, with the exception of *Gorilla*, have elongated hands relative to their body weight or in relation to humerus length (Moyà-Solà *et al.*, 1999). This contrasts with the relatively shorter hand morphology of pronograde monkeys. Hands of orthograde anthropoids (except *Gorilla*) are considerably longer than those of pronograde anthropoids because a large friction surface is required to secure a firm grip during vertical climbing and below-branch suspension (Moyà-Solà *et al.*, 1999). Forelimb musculature, including the forearm rotators and wrist and hand flexors, is robust (Aiello and Dean, 1990). All of the above features are adaptations that emphasize forelimb strength and mobility (Morbeck and Zihlman, 1988; Ankel-Simons, 2000).

Extant apes employ varying degrees of suspensory behaviour, quadrumanous climbing and digitigrade quadrupedalism in their locomotor repertoires (Hunt 1991b). All living apes are more suspensory than extant cercopithecoids, and the gibbons and siamangs engage in suspensory locomotion with the greatest frequency; they are the only primates to use 'true' (Avis, 1962; Erikson, 1963; Napier, 1963), or 'ricochetal' brachiation (Andrews and Groves, 1976). Generic differences in trunk and forelimb morphology and locomotor behaviour will be dealt with in the relevant sections below.

Pan

The chimpanzee (genus *Pan*) is one of only two genera of extant African ape. Two species are recognised, the common chimp (*P. troglodytes*) and the bonobo (*P. paniscus*), and three subspecies of common chimp (*P. t. schweinfurthii*, *P. t. troglodytes* and *P. t. verus*; Fleagle, 1999). *Pan* exhibits a moderate level of sexual dimorphism in body size (Martin, 1990). Females range from approximately 33-45kg and males from 42-60kg, depending upon species and subspecies (Fleagle, 1999). Chimpanzees have a broad distribution across much of central Africa, from Tanzania in the east to Senegal in the west (Fleagle, 1999). Different populations have adapted at one extreme to primary rain forest conditions and at the other to relatively arid savannah areas, with most types of intermediate woodland or open forested terrain being exploited too (Doran, 1992;

Hunt, 1992). Since locomotor patterns are largely dependent upon habitat type (Rollinson and Martin, 1981; Pounds, 1991), it would be expected that individual populations of chimpanzee would differ in the duration and frequency with which they employ particular locomotor behaviours, according to the prevailing local conditions. This does not mean, however, that chimpanzees have no common basis of locomotor behaviour. The two chimpanzee species, and all three sub-species of common chimp, share large components of their postural and locomotor repertoires (Hunt, 1991b; Doran, 1993).

The locomotor behaviour of the chimpanzee varies according to its position in the environment. When terrestrial, travel comprises quadrupedal walking and, very occasionally, bipedalism and leaping, in arboreal settings quadrupedalism is combined with suspensory locomotion, climbing and feeding postures (Tuttle, 1986; Hunt, 1991a, 1992).

Chimpanzees spend approximately 40%-50% of their time on the ground (Hunt, 1991b). During quadrupedal locomotion, chimpanzees (together with gorillas) employ an unusual hand orientation called knuckle-walking (Tuttle, 1967). This mode of progression is a form of digitigrade locomotion that is unique to African apes (Tuttle, 1969). Most primates support their upper body and forelimb either on the palm of their hand, or on the palmar surface of their fingers (Rollinson and Martin, 1981; Fleagle, 1999). Chimpanzees and gorillas, in contrast, support their weight on the dorsal surface of the third and fourth middle phalanges of the hand (Tuttle, 1967, 1969). *Pan* does not employ other forms of terrestrial quadrupedalism (e.g., palmigrade quadrupedalism), and only very rarely engages in bipedalism (Susman *et al.*, 1980; Hunt, 1992; Doran, 1993). Bipedal progression is more common in juveniles than adults, though in both age groups the behaviour is of short duration (Susman, 1980; Tuttle, 1986; Hunt, 1991b). Chimpanzees also occasionally leap, either quadrupedally or bipedally, terrestrially or arboreally, to avoid obstructions such as streams, gulleys or branches (Tuttle, 1986; Hunt, 1992).

Chimpanzees spend about 50%-60% of their time in the trees (Hunt, 1991b), and their arboreal locomotor repertoire consists primarily of quadrupedalism, although suspension, leaping and bipedalism are also employed to a limited degree (Susman, 1980; Tuttle, 1986; Hunt, 1992). Arboreal quadrupedalism can be palmigrade on narrow supports, or knuckle-walking on

wide branches (Hunt, 1992). Suspensory locomotion takes the form of relatively slow (and infrequent) forelimb progression, and on the basis of the terminology outlined above can be characterised as brachiation (i.e., appendages other than the forelimbs are not employed for additional support; Hunt, 1991a, b, 1992). The proportion of time spent in suspensory activities differs interspecifically in *Pan*. *P. paniscus* spends 20% of its locomotor activity brachiating, while *P. troglodytes* brachiates for between only 0.5% and 5.3% of its locomotor behaviour (Hunt, 1991b).

Several features of the chimpanzee postcranial (trunk and forelimb) skeleton are shared by all extant hominoids, but some traits are not ubiquitous within Hominoidea, or if present do not follow the same pattern of expression. *Pan* exhibits the lowest mean intermembral index[12] of living non-human hominoids 102-107 (Napier and Napier, 1967; Gebo, 1996; Fleagle, 1999), although this figure is relatively high compared with other quadrupedal primates. As noted above, thorax shape, scapular shape, degree of humeral torsion and wrist morphology also vary intergenerically in the Hominoidea. In chimpanzees, the thorax is funnel-shaped (as it is in all non-human hominids), and the scapula narrow and triangular as in *Hylobates* (in contrast to *Gorilla*, *Pongo* and *Homo*; Gebo, 1996). The angle of medial torsion on the proximal humerus is 139°-159° (Gebo, 1996), with a mean of 153° (Ankel-Simons, 2000), second highest only to *Gorilla* among the extant hominoids. Elbow and forearm morphology is typical of that outlined for all hominoids above.

In the wrist, Lewis (1972b) argues there is quite a wide separation of the ulna from the carpus. The distal ulna has a hook-like styloid process, which has an articular facet on its external aspect for the intra-articular meniscus (Lewis, 1971a). The triquetral is very different to that found in extant monkeys and hylobatids. It is shaped like a triangular pyramid with the palmar and dorsal surfaces rounded off proximally to form a convex facet for the inferior surface of the meniscus (Lewis, 1971a, 1972b; Gebo, 1996). The pisiform has a large convex facet on the proximal end of the dorsal aspect for articulation with the periphery of the meniscus (Lewis, 1972b). Some other workers (e.g., Sarmiento, 1988; Gebo, 1996) have suggested that ulnotriquetral contact is at least partly

[12] The intermembral index, which expresses forelimb length as a percentage of hindlimb length, provides an indication of relative limb proportions (Aiello and Dean, 1990).

maintained in *Pan*, as it is in *Hylobates*. The lunate of both African apes is proximodistally short and thick with an extensive articular surface for the radius (Tuttle, 1969; Harrison, 1986a).

Knuckle-walking involves several specialised features of the bones, ligaments and muscles of the hand that together form a 'functional complex'[13] (Tuttle, 1969). When in the knuckle-walking position, the hand is subjected to a compressive force generated by the weight of the torso, which tends to promote a downwards collapse at the carpal and metacarpophalangeal joints (Tuttle, 1967, 1969). The unique morphology of the hand in African apes is largely a response to this compressive force. In the wrist, the carpal bones articulate with one another in a close-packed position. The stability of the wrist is further increased by bony ridges on the dorsal aspect of the distal articular surface of the radius and the scaphoid bone, which appose each other during extension (Tuttle, 1967, 1969). In the hand, the metacarpophalangeal joints can be hyperextended due to the dorsal extension of the distal articular surface on each metacarpal head (Tuttle, 1969). A transverse ridge at the base of this dorsal articular surface on the metacarpal heads helps to maintain integrity when the hand is engaged in the knuckle-walking posture[14]. In addition to these osteological mechanisms for coping with compressive forces, the powerful digital flexor tendons provide supplementary support during knuckle-walking progression (Tuttle, 1969).

Gorilla

The genus *Gorilla* is the largest extant primate. Only one species of gorilla is recognised (*G. gorilla*), though most workers distinguish three geographically isolated subspecies (Napier and Napier, 1967; Fleagle, 1999): the western lowland gorilla (*G. g. gorilla*), the eastern lowland gorilla (*G. g. graueri*), and the mountain gorilla (*G. g. beringei*). Some workers (e.g., Sarmiento and Oates, 2000)

---

[13] The term 'functional complex' denotes a suite of characters that are linked and so change in unison (C. Ward *et al.*, 1997).

[14] The dorsal transverse ridge aids knuckle-walking, but is not unique to African apes. Some large, terrestrial cercopithecoids, such as *Mandrillus*, also exhibit this feature. The dorsal ridge may, therefore, be diagnostic of digitigrade hand postures in the broadest sense (Benefit and McCrossin, 1995), encompassing the palmar digitigrady of some quadrupeds, as well as the dorsal digitigrady of knuckle-walking hominoids (McCrossin and Benefit, 1997).

make further distinctions, arguing for a fourth distinct subspecies (*G. g. diehli*) from the Cross River locality in West Africa.

Gorillas inhabit the tropical forests of sub-Saharan Africa. The lowland subspecies occupy a wide variety of forest, while mountain gorillas prefer secondary and herbaceous forests (Dixson, 1981; Remis, 1998; Fleagle, 1999). Compared to chimpanzees, and other non-hominoid African primates, gorillas have a very limited distribution.

Of all the primate genera, gorillas exhibit the most extreme sexual size dimorphism (Jungers, 1985; Remis, 1995, 1998). Female size ranges from 70-90kg and male size is over double that at 160-180kg, and sometimes up to 200kg (Napier and Napier, 1967; Jungers, 1985; Fleagle, 1999). This dimorphism is evident throughout the gorilla skeleton and contributes to the greater robusticity of the males (Sarmiento, 1994).

The locomotor habits of gorillas are known almost entirely from one subspecies (*G. g. beringei*), which is predominantly (80-95%) terrestrial (Napier and Napier, 1967; Tuttle, 1986; Hunt, 1991b; Fleagle, 1999). There is, however, a marked difference in the frequency of arboreal behaviour between lowland and highland forms (Remis, 1998). Mountain gorillas nest on the ground and rarely climb trees. Lowland gorillas, particularly females and juveniles, are more arboreal in both their feeding and sleeping habits (Tuttle, 1986; Remis, 1995, 1998; Fleagle, 1999). On the ground, gorillas move by quadrupedal walking and running, and rarely engage in sustained bipedal locomotion, although bipedal standing is a component of chest-beating displays (Hunt, 1991b). Their quadrupedal progression, as in chimpanzees, is characterised by knuckle-walking (Tuttle, 1969). When arboreal, gorillas are essentially quadrupedal climbers; suspensory locomotion and feeding postures are very rare (Dixson, 1981; Remis, 1995; Fleagle, 1999). When forelimb suspension is employed, it is at a slow pace and usually without additional support from other appendages (i.e., brachiation; Remis, 1995).

Postcranially, gorillas exhibit several trunk and forelimb features typical of the hominoid pattern. As mentioned above, relative forelimb length (as indicated by the intermembral index), thorax and scapular shape, and angle of humeral torsion are features that differ in degree of expression within Hominoidea. The gorilla exhibits a mean intermembral index of 115-116 (Napier and Napier, 1967;

Gebo, 1996; Fleagle, 1999), a fairly high figure compared with cercopithecoids and most other non-atelin monkeys, especially considering that the best known gorilla (*G. g. beringei*) is essentially a terrestrial quadruped (Sarmiento, 1992, 1994). The thorax is funnel-shaped (as it is in *Pan* and *Pongo*, but in contrast to *Hylobates* and *Homo*) and the scapula is broad and triangular (as it is in *Pongo* and *Homo*, but in contrast to *Pan* and *Hylobates*; Gebo, 1996). The angle of humeral torsion achieves its greatest expression in the gorilla at 154°-173° (Gebo, 1996), with a mean of 165° (Ankel-Simons, 2000). Elbow and forearm morphology follows the typical pattern for hominoids outlined above.

Wrist morphology in *Gorilla* is much the same as in *Pan* (Lewis, 1972a, b). Gorillas, however, differ from chimpanzees in some of the specifics of their hand anatomy, and its functional application (Sarmiento, 1992, 1994). The bony and ligamentous structures that are prominent in *Pan* achieve an even greater expression in *Gorilla* (Sarmiento, 1994). Gorillas consistently utilize all four (non-pollical) digits of a hand when knuckle-walking; chimpanzees, however, often flex the second and fifth digits until they are clear of the ground, maintaining contact with only the third and fourth digits (Tuttle, 1967, 1969; Sarmiento, 1994). Differences also exist in hand positioning. Gorillas fully pronate the hand during knuckle-walking; chimpanzees frequently employ only partial pronation (Tuttle, 1969). This hand position in gorillas affects the positioning of the rest of the forelimb and pectoral girdle; the elbows project laterally, and the shoulders jut forward (Tuttle, 1967, 1969; Sarmiento, 1994). The gorilla is also exceptional within the extant Hominoidea in its hand length. In contrast to other living apes, who have long hands relatively to body weight, gorillas have a relative hand length that falls close to that of hominines, and pronograde monkeys (Moyà-Solà *et al.*, 1999). The shortened hand is attributed to the gorilla's (i.e., *G. g. beringei*) primarily terrestrial quadrupedal locomotion, which does not place a premium on digital grasping (Moyà-Solà *et al.*, 1999).

Pongo

The orang-utan (genus *Pongo*) is one of only two genera of extant Asian ape. Orang-utans are distributed in the tropical forests of Sumatra and Borneo in South East Asia (MacKinnon, 1974b; Röhrer-Ertl, 1988). There is only one extant

species, though two geographically separated subspecies are usually recognised (Fleagle, 1999). The Bornean orangutan (*P. pygmaeus pygmaeus*) differs very little from its Sumatran (*P. p. abelli*) relative (Röhrer-Ertl, 1988). Both subspecies exhibit extreme sexual size dimorphism; with males (81kg) weighing approximately double that of females (37kg; Morbeck and Zihlman, 1988; Fleagle, 1999).

Orang-utans, together with the other Asian apes, the gibbons and siamangs, are much more arboreal than African apes (Tuttle and Cortright, 1988; Hunt, 1991b). Juveniles and adult females are almost wholly arboreal, while adult males are primarily arboreal but engage in terrestrial progression more frequently as they mature (MacKinnon, 1974b; Tuttle and Cortright, 1988; Hunt, 1991b; Fleagle, 1999). When on the ground, adult males move quadrupedally with their hands held in a fist (Tuttle, 1967, 1969), rather than on the second knuckle as in African apes, or on the palm as in cercopithecoids. When arboreal, orang-utans usually employ slow, cautious, quadrumanous climbing (MacKinnon, 1974a, b; Tuttle, 1986; Tuttle and Cortright, 1988; Morbeck and Zihlman, 1988; Hunt, 1991b), which accounts for 40-50% of locomotor movement (Tuttle, 1986). Orang-utans employ other modes of progression besides quadrumanous climbing, although these make up a small proportion of their total locomotor repertoire (with the exception of suspension; Tuttle and Cortright, 1988). Many of these other modes have been quantified[15], for example, tree swaying, quadrupedal walking and vertical climbing are employed by males 15%, 13% and 10% respectively, and by females 9%, 16% and 10% respectively (Tuttle, 1986).

Suspensory activity, unassisted by pedal grasps (i.e., brachiation), is infrequent compared to climbing, and occurs only over short distances (Tuttle, 1986; Tuttle and Cortright, 1988; Hunt, 1991b). This locomotor mode accounts for 21% and 18% of locomotor bouts for males and females, respectively (Tuttle, 1986). Orang-utan bimanual forelimb suspension lacks the speed and flow of the specialised ricochetal brachiation of gibbons (Baldwin and Teleki, 1976), and differs mechanically in its expression, with the forelimbs being swung overhead rather than underarm (MacKinnon, 1974b; Tuttle, 1986; Tuttle and Cortright, 1988). Although brachiation is employed infrequently, forelimb suspension with

[15] Some locomotor modes, especially tree swaying and suspension, are employed with variable frequency depending on the sex of the individual (Tuttle, 1986).

the aid of pedal grasping occurs much more often (Tuttle and Cortright, 1988; Hunt, 1991b).

Orang-utans are cranially quite distinct from African apes (Shea, 1988). In contrast, the postcranial skeleton of *Pongo* exhibits similar features to *Pan* and *Gorilla*, but to a more marked degree in some traits. Adaptations to arboreal, and frequently suspensory, locomotion are reflected in the musculoskeletal system and the increased movement capabilities of the joints, which maximize stability in the trunk and forelimb without compromising flexibility (Schultz, 1969; Morbeck and Zihlman, 1988; Schwartz, 1988; Tuttle and Cortright, 1988). As noted above, forelimbs are longer, relative to hindlimbs, in all non-human hominoids, but both Asian genera of apes (*Pongo* and *Hylobates*) exhibit relatively longer forelimbs than African apes (Erikson, 1963; Andrews and Groves, 1976; Morbeck and Zihlman, 1988). The mean intermembral index for the orang-utan is 139 (Gebo, 1986; Fleagle, 1999), a very high figure, reflecting the dominance of bimanual forelimb suspensory progression in its repertoire (MacKinnon, 1974b; Tuttle and Cortright, 1988).

The thorax (in orang-utans) is funnel-shaped, as in the African apes (Gebo, 1996), but the morphology of the pectoral girdle differs in the expression of some features compared with African apes and humans. The clavicles are relatively longer (Andrews and Groves, 1976) and straighter (Gebo, 1996) in the orang-utan than in any other extant ape. The scapula is broad and triangular (as in *Gorilla* and *Homo*) with a small supraspinous fossa (Gebo, 1996), and exhibits broader acromial and coracoid processes that form a 'roof' over the shoulder joint, and a more cranially orientated glenoid fossa than African apes and humans (Morbeck and Zihlman, 1988; Schwartz, 1988).

On the humerus, the head is relatively large and medially directed (though exhibits less torsion than in African apes; Ankel-Simons, 2000) with a range of 120°-162° (Gebo, 1996), and the articular surface extends beyond the insertion sites on the tuberosities for rotator cuff muscles (Morbeck and Zihlman, 1988). In contrast to other extant hominoids, *Pongo* exhibits a broad, shallow bicipital groove, though it is narrower and deeper than the intertubercular sulcus of habitual quadrupeds (Morbeck and Zihlman, 1988; Ankel-Simons, 2000). This suggests that a deep bicipital groove is not functionally correlated with medial torsion of the humeral head (Begun and Kordos, 1997). The twin functional

requirements of mobility and stability in the elbow and forearm are met with the suite of characteristics common to all hominoids in these regions (Morbeck and Zihlman, 1988).

In the wrist joint, the distal ulna is characterised by a very short, conical styloid process, which does not directly articulate with the carpus (Lewis, 1972b; Gebo, 1996). The triquetral is small, lacks a meniscal facet and has a small, convex facet at the distal extremity for articulation with the distally placed pisiform (Lewis, 1972b). These features permit increased flexibility in the wrist joint (Gebo, 1996). The lunate is broad in both genera of Asian ape, and lacks the proximodistal shortness of the African ape lunate (Tuttle, 1969; Harrison, 1986a).

Orang-utans exhibit the greatest hand length of all hominids, with long curved metacarpals and phalanges, and a reduced pollex (Morbeck and Zihlman, 1988; Rose, 1988b; Moyà-Solà *et al.*, 1999). Together with the large digital flexor muscles, these adaptations facilitate the grasping of a variety of differently sized arboreal supports (Tuttle and Cortright, 1988).

Hylobates

The genus *Hylobates* (gibbons and siamang) is the only other group of Asian ape. Gibbons inhabit the primary and secondary evergreen forests of South East Asia, from southern China and eastern India in the northwest to Java and Borneo in the southeast (Chivers, 1972; Preuschoft *et al.*, 1984). They typically utilize the middle to high strata of the canopy, and rarely visit levels below 20 feet, or come to ground (Tuttle, 1972a). The hylobatids are more specifically diverse than hominids, with some workers distinguishing nine species (Rumbaugh, 1972; Preuschoft *et al.*, 1984; Fleagle, 1999).

Anatomically, gibbons represent something of a paradox. They retain many primitive features and yet, in many ways, are the most specialised of the extant hominoids (Preuschoft *et al.*, 1984; Fleagle, 1999). There is little morphological variation among gibbons and their size is fairly uniform and small at 5-8kg, with the exception of *H. syndactylus*, the siamang at 10-12kg (Chivers, 1972; Groves, 1972; Fleagle, 1999). Gibbons exhibit little or no sexual size dimorphism (Jungers, 1984).

The locomotor repertoire of the hylobatids is very diverse, but almost entirely arboreal (Hunt, 1991b). Although they are often depicted as being wholly suspensory, they frequently engage in other modes of locomotion (Ellefson, 1974; Baldwin and Teleki, 1976). The hylobatid repertoire includes suspension, ricochetal brachiation, bridging, climbing, leaping, bipedalism and, very occasionally, tripedalism and quadrupedalism (Tuttle, 1972a; Ellefson, 1974; Baldwin and Teleki, 1976; Carpenter, 1976). Quadrupedal progression is employed for less than 3.5% of locomotor activity time (Gittins, 1983), can take the form of walking or running, and can be arboreal or terrestrial (Baldwin and Teleki, 1976). It is employed most frequently on flat, unobstructed terrain. Quadrupedalism in gibbons is somewhat ungainly, and is less efficient than in more committed quadrupeds (Carpenter, 1976).

Bipedal movement is also employed infrequently (<11% of locomotor behaviour; Chivers, 1972; Fleagle, 1976, 1980; Gittens, 1983; Srikosamatara, 1984) and can be performed at walking and running speeds. The torso is held at, or near, perpendicular to the substrate, and usually exhibits a waddling motion due to lateral hip sway as weight is transferred from one hindlimb to the other (Tuttle, 1972a; Baldwin and Teleki, 1976). Both hindlimbs remain flexed throughout the cycle, never locking at the knee, and the gait's length and duration vary with speed (Baldwin and Teleki, 1976). Gibbons occasionally engage in a form of tripedal progression; this mode consists of the hindlimbs employing a bipedal gait, while one forelimb provides additional support during the hindlimb swing phases (Baldwin and Teleki, 1976).

The frequency of leaping behaviour in *Hylobates* varies interspecifically. It is engaged in quite often among *H. agilis* (23.9% of locomotor behaviour; Gittins, 1983), *H. lar* (9.5%; Fleagle, 1980) and *H. pileatus* (8.7%; Srikosamatara, 1984), but less frequently in *H. syndactylus* (0%-3.2%; Chivers, 1972; Fleagle, 1976). Leaping can be employed by adopting a set position, or by following on from a locomotor sequence (Tuttle, 1972a). Supporting limbs are released and the individual launches into a glide through open space (sometimes covering more than 10-20 metres) before re-establishing contact with anything from one to four limbs, on an available structure (Baldwin and Teleki, 1976). Torso orientation, glide trajectory, and flight rate and distance all vary according to launching style, and the momentum achieved (Baldwin and Teleki, 1976).

The proportion of locomotor behaviour spent climbing also varies interspecifically in *Hylobates*. *H. lar* and *H. syndactylus* both climb relatively frequently (34.1% and 54.3% of locomotor activity, respectively; Fleagle, 1976, 1980), while *H. agilis* and *H. pileatus* (6.3% and 6%, respectively; Gittens, 1983; Srikosamatara, 1984) do not. Climbing is usually employed on vertical, or near vertical, structures (e.g., tree trunks, cliffs; Hunt, 1991b), and is characterised by quadrupedal progression, with the forelimbs extended to grip overhead structures and the hindlimbs following by walking along the substrate (Baldwin and Teleki, 1976). This locomotor mode is often executed with greater caution, and at a slower pace, than other patterns (Carpenter, 1976). Bridging occurs when an individual is supported by one or more limbs on a substrate and extends one or more free appendage(s) to reach across an open space and establish contact with another structure, without releasing the initial supports (Tuttle, 1972a; Baldwin and Teleki, 1976).

Suspensory locomotion in gibbons has a number of variations, all of which involve use of the forelimb(s) without pedal grasping and so can be classified as types of brachiation (Hunt, 1991b). The percentage of locomotor behaviour spent brachiating varies considerably among hylobatids. *H. syndactylus* and *H. lar* brachiate for 37.9%[16] and 51.2% of the time, respectively (Fleagle, 1976, 1980), while *H. agilis* and *H. pileatus* engage in this locomotor mode 66.3% and 84.4% of the time, respectively (Gittens, 1983; Srikosamatara, 1984).

Ricochetal brachiation is a specialised mode of suspension unique to gibbons (Andrews and Groves, 1976). It is characterised by bimanual suspension from the forelimbs, without the aid of the hindlimbs, and proceeds at a very fast, smooth pace by employing a pendulous movement of the torso (Tuttle, 1972a; Baldwin and Teleki, 1976; Carpenter, 1976). The forelimbs are placed alternately along a (usually horizontal) support and momentum is generated by releasing the grip of the rear hand, while swaying the torso forward, like a pendulum, underneath the one remaining fully extended suspensory forelimb; simultaneously, the free forelimb is arched past the hips and extended until contact is achieved with the support again (Baldwin and Teleki, 1976). Once contact is achieved with the free hand, the initially suspensory hand is released

[16] Chivers (1972) suggests that *H. syndactylus* brachiates for 80% and climbs for only 10% of its locomotor activity time.

and the cycle repeats itself (Baldwin and Teleki, 1976). During this gait, the hand is utilised as a hook to grip the support, while the elbow joint is flexed and the shoulder joint retracted to generate propulsion; the wrist joint acts as a fulcrum during the part of the cycle when the suspensory forelimb is fully extended (Tuttle, 1972a). Unlike hominids, which, when engaged in bimanual forelimb suspension, utilize 180° of trunk rotation, *Hylobates*, when employing ricochetal brachiation, rotates the trunk only 90° (Avis, 1962). This reduction in trunk rotation allows the gibbon to speed up considerably the time it takes to complete one cycle of brachiation, and, because less trunk rotation means the body is progressing in a more linear fashion (rather than the lateral swaying of hominids), this allows the gibbon to generate more momentum (Avis, 1962; Tuttle, 1972a; Baldwin and Teleki, 1976; Hunt, 1991b).

There are two other variations of suspensory locomotion that gibbons employ: slide, and hand-hop (Baldwin and Teleki, 1976). Sliding is accomplished in a similar manner to ricochetal brachiation, though in this mode the hands are never fully released from the structure they suspend from (Carpenter, 1976). The gait consists of loosening the grip of one hand and sliding it forward along a structure, then tightening the grip while shifting the body weight to this limb, the hand that initially supported the body is then loosened and slid forward beside the other (Baldwin and Teleki, 1976). The hand-hop is performed with only one suspensory hand. A pendulum sway is created in the torso by energetic movement of the free limbs, when forward momentum is achieved the suspensory hand is rapidly loosened, slid forward to a new suspensory point, and then re-tightened (Baldwin and Teleki, 1976).

The postcranial skeleton of *Hylobates* exhibits some of the shared derived features of hominids but is much more slender (Fleagle, 1999). Limb proportions, in particular, are highly specialised (Hollihn, 1984). The forelimbs are accentuated and are the longest, relative to hindlimbs, of any extant primate, as indicated by a very high intermembral index of 126-148 (Andrews and Groves, 1976; Gebo, 1996). Gibbons share some of the trunk and shoulder features that characterise extant hominids; there are, however, marked differences in several of these anatomical areas. In the lumbar spine, there are four to six vertebrae, compared to the three or four of hominids (Andrews and Groves, 1976; C. Ward, 1993). Gibbons, therefore, are intermediate between hominids and quadrupeds (which

have six to seven lumbar vertebrae) in this characteristic (Groves, 1972). The thorax differs from that of the non-human hominids in being barrel-shaped (as in *Homo*; Gebo, 1996). There are other, equally marked, differences in the morphology of the pectoral girdle. The scapulae are placed high on the thorax, necessitating that the clavicles slope downwards at a 45° angle towards the manubrium (Andrews and Groves, 1976; Hollihn, 1984). The scapula is narrow and triangular as in *Pan* (but in contrast to *Pongo*, *Gorilla* and *Homo*; Gebo, 1996), but is also less elongated and has a more oblique spine than in any other extant ape (Larson, 1998); the closest morphological resemblance is to *Ateles*, rather than hominids (Andrews and Groves, 1976). Correlated with this scapular shape, the glenoid fossa is much more cranially directed than in hominids and other primates (Hollihn, 1984; Takahashi, 1990). The glenoid fossa is also relatively smaller and shallower than in hominids, thus increasing the mobility, while reducing the stability of the glenohumeral articulation (Ankel-Simons, 2000).

The forelimb follows the pattern of other extant apes, though medial torsion of the humeral head appears to be less marked than in hominids (Groves, 1972); some workers (e.g., Larson, 1988; Ankel-Simons, 2000) cite a mean angle of just 120°, while others (e.g., Gebo, 1996) give a slightly higher range of 128°-145°. Medial torsion of the humeral head is a feature often linked to forelimb suspension and brachiation (Erikson, 1963; Napier, 1963; Oxnard, 1963), but the fact that the most suspensory hominoid expresses this trait the least suggests that the functional significance of this character may lie elsewhere (e.g., it may be correlated with knuckle-walking or cautious quadrupedalism; Larson, 1988; Gebo, 1996). The distal humerus is largely similar to that of hominids, although the medial and lateral trochlear keels are usually less pronounced (Harrison, 1986a; Gebo, 1996).

In the wrist joint, Lewis (1972a, b) argues that the ulnocarpal morphology is more monkey-like than ape-like. The distal ulna, however, is remodelled from the primitive monkey condition of direct ulnocarpal contact and exhibits a hook-like styloid process that has an articular surface on its distal aspect for the intra-articular meniscus (Lewis, 1969). The meniscus between the styloid and the

triquetral is ossified at the mid-section, forming a bone called *os daubentonii*[17] (Lewis, 1971a, 1972a, b; Groves, 1972). The triquetral is monkey-like in form, though flatter and more compressed (Lewis, 1971b, 1972b). Ulnotriquetral contact is partial (Gebo, 1996). The pisiform is more distally located than in extant monkeys, and orientated towards the palm so that the proximal surface articulates with the ossicle-containing meniscus (Lewis, 1972b).

Lewis (1971a, 1972b) contends that the liberation of the ulna from complete articulation with the carpus, and the concomitant increase in the range of pronation/supination, is functionally correlated with brachiation. If this interpretation is correct, then it begs the question why does *Hylobates*, the hominoid that shows the greatest behavioural specialisation for brachiation, exhibit the least derived wrist morphology? Lewis (1972a) suggests that the retention of primitive carpal features in *Hylobates* is a result of the specialised ricochetal brachiation employed in this taxon, which may require some limitation on rotation of the wrist. Other workers (e.g., Conroy and Fleagle, 1972) have suggested that the retreat of the ulna from the carpals in hominoids may be a knuckle-walking adaptation. This hypothesis was subsequently abandoned, however, when it was shown that knuckle-walking involved very little ulnar deviation at the wrist (see Jenkins and Fleagle, 1975). Cartmill and Milton (1977) argue that the enhanced wrist mobility in hominoids may initially have been an adaptation to cautious arboreal quadrupedalism early in the history of this lineage, a morphology that was maintained in the terrestrial quadrupedalism of the extant African apes (explaining why it achieves its greatest expression in these taxa) and was not fully developed in the hylobatids because the early members of this lineage already had suspensory adaptations.

In the hand, the phalanges are curved and elongated, as in *Pongo*, but are distinct in having a long muscular pollex (Tuttle, 1972a). These features modify the hand into a "suspensory hook" (Groves, 1972:4).

[17] This feature is not unique to *Hylobates*; in two to four month old human embryos a cartilaginous nodule occupies this position, and occasionally there is a bone there in human adults (Groves, 1972).

Summary

In this review, the aim has been to highlight those postcranial morphological features and locomotor behaviours that all extant hominoids share, and those that exhibit generic differences. It is clear that, although extant apes are fundamentally similar in their trunk and forelimb morphology, significant intergeneric differences remain (Larson, 1998). Hominoid locomotor behaviour exhibits even greater diversity, with many intergeneric and interspecific differences (Hunt, 1991b). In particular, there is a distinction between African and Asian apes; African apes share similar morphological traits and locomotor activities, as do the Asian apes (though *Pongo* exhibits some shared derived features with African apes, to the exclusion of hylobatids; Morbeck and Zihlman, 1988; Hunt, 1991b; Gebo, 1996). This is to be expected in light of the unique knuckle-walking adaptation[18] and frequent terrestriality of the African apes, and the highly suspensory locomotor repertoire of the Asian apes.

Hylobates is the most divergent, morphologically and behaviourally, of all the extant apes (Hollihn, 1984). The morphological differences between the hominids and hylobatids appear to be based on the specialised locomotor adaptations of gibbons, namely ricochetal brachiation (Tuttle, 1975a). It is incongruous, therefore, to suggest that the postcranial morphology of extant hominoids is an adaptation to one activity, 'brachiation' (including ricochetal brachiation), in which the hylobatids engage for between 38% and 85% of their repertoires (Fleagle, 1976; Srikosamatara, 1984), the orang-utan and chimpanzee indulge only rarely (<21%; Susman *et al.*, 1980; Sugardjito and van Hooff, 1986; Hunt, 1991b), and the gorilla employs hardly ever (Andrews and Groves, 1976; Hunt, 1991b). The phenotypic 'ground plan', or *bauplan* of the Hominoidea, however, may indeed have been shaped by suspensory behaviour patterns in ancestral forms, the morphological remnants (or relics) of which can be seen in living apes.

[18] Note that the polarity of the characters relating to the functional complex of knuckle-walking is uncertain. Some workers (e.g., Begun, 1992b) regard these characters as primitive for African apes, and therefore not indicative of close phyletic affinity.

Cercopithecoidea

Cercopithecoids (Infraorder Catarrhini, or Old World monkeys), represent the other major radiation of anthropoid primates in Africa and Asia. Though originally viewed as primitive relative to the inferred early catarrhine condition, more recently Old World monkeys have been viewed as quite specialised with respect to early catarrhines, such as *Aegyptopithecus* and *Propliopithecus* (Strasser and Delson, 1987; Disotell, 1996; Fleagle, 1999). The most distinctive synapomorphy of extant cercopithecoids centres on the dentition. The molar teeth are highly specialised with the mesial and distal pairs of cusps forming two crests/ridges, or lophs. This bilophodont molar structure contrasts with the hominoid retention of a Y-5 pattern and rounded cusps (Strasser and Delson, 1987; Fleagle, 1999). Postcranially, Old World monkeys are considered by most workers to be more primitive than living apes (Napier and Napier, 1970; Temerin and Cant, 1983; Harrison, 1986b, 1989; Gautier-Hion *et al.*, 1988; McCrossin and Benefit, 1994). Although cercopithecoids certainly do not exhibit the same level of postcranial specialisation as the apes, they may still be considered derived with respect to early catarrhines and extant platyrrhines (Strasser and Delson, 1987; Rose, 1994; Disotell, 1996).

All cercopithecoid genera share features of the postcranium, though most of these traits have been interpreted as symplesiomorphic (C. Ward, 1993; Rose, 1994). The vertebral column is long, enabling flexion/extension of the spine, and there are four to seven lumbar vertebrae (C. Ward, 1993). In contrast to hominoids, the torso is narrow mediolaterally, deep dorsoventrally and long craniocaudally (Rose, 1997; C. Ward, 1993). A transversely narrow thorax positions the scapulae in parasagittal planes[19] on the lateral aspect of the trunk with the glenoid fossa directed ventrally (Reynolds, 1985; Ankel-Simons, 2000), thus satisfying the mechanical demands of quadrupedal progression (C. Ward, 1993; Schmitt, 1998). The lateral positioning of the scapulae necessitates a shorter clavicle than in extant hominoids, due to the closer proximity of the scapula to the manubrium (Rose, 1994).

Proximal humeral morphology contrasts with that described for extant apes, with many features relating to the employment of pronograde quadrupedal

[19] Parasagittal planes run parallel to the sagittal plane, which divides the body craniocaudally (Aiello and Dean, 1990).

locomotion (Schultz, 1986; Rose, 1989). The humeral head faces posteriorly, the bicipital groove is shallow and wide, and the proximal shaft is retroflexed (Rose, 1989, 1994). This morphology is functionally associated with humeral movement in a parasagittal plane, and therefore is an adaptation for quadrupedalism (Schmitt, 1998). The articular surface of the head is flattened anteriorly, reducing mobility (especially rotation) during full protraction (Rose, 1989). The greater tuberosity exhibits anterior migration and elevation that is functionally correlated with rapid protraction of the forelimb during quadrupedalism (Rose, 1994).

The distal humerus is also distinct from that of living apes. It is characterised by a narrow and largely cylindrical trochlea, with pronounced anteromedial and posterolateral borders (Rose, 1988a). This shape contrasts with the spool-shaped trochlea of extant apes and is a specialised adaptation for resisting torques about the elbow when the forelimb is habitually pronated (Schmitt, 1998). The capitulum is small and non-globular, as in ceboids, but in contrast to extant hominoids (McHenry and Corruccini, 1975). The humeral medial epicondyle is smaller than in extant hominoids and projects more posteriorly, which reduces the amount of medial torque generated when the elbow is pronated during pronograde quadrupedalism (Rose, 1988a, 1994). The humeral olecranon fossa is shallow and narrow, and articulates with the long, anteriorly angled olecranon process on the proximal ulna (Rose, 1988a, 1994). These features suggest a limited range of flexion/extension in the forearm and are inconsistent with the ability to fully extend or hyperextend the elbow (Rose, 1988a; Schmitt, 1998).

The wrist is characterised by the basic mammalian quadrupedal type of morphology, with the ulna articulated directly with the triquetral/pisiform (Lewis, 1972b, 1974; O'Conner, 1975). The ulnar styloid process is robust and has a facet on its carpal aspect that articulates with a large, concave triquetral/pisiform facet, suggesting an adaptation for ulnocarpal stability in weight bearing palmigrade postures, rather than for flexibility (Lewis, 1972b; O'Conner, 1975). The hand is shorter, relative to body weight and humerus length, than that of any orthograde extant anthropoid except *Gorilla* (Moyà-Solà *et al.*, 1999). This suggests that a premium is not placed on grasping abilities (Etter, 1973). Overall, the trunk and forelimb morphology of Old World monkeys is characterised by a pronograde

body structure and an adaptation to pronograde/palmigrade quadrupedalism (Schultz, 1986; C. Ward, 1993; Rose, 1994; Schmitt, 1998).

The superfamily Cercopithecoidea encompasses only one extant family, Cercopithicidae (and one extinct family, Victoriapithecidae[20]), which is itself divided into two subfamilies, the Cercopithecinae and Colobinae (Strasser and Delson, 1987; Fleagle, 1999). These two subfamilies differ in several aspects of their hard and soft anatomy. Hard tissue differences are mostly confined to the cranium (Fleagle, 1999). Postcranially, the two subfamilies are less distinct (Schultz, 1970), but can be identified by relative limb size and digit size. Colobines usually have longer hindlimbs relative to forelimbs whereas cercopithecines have limbs of similar size (Delson *et al.*, 2000). Cercopithecines tend to have shorter phalanges and a longer pollex than colobines, which frequently have a reduced or absent pollex (Delson *et al.*, 2000).

The subfamilies Cercopithecinae and Colobinae also differ in geographical diversity (Simons, 1970). Cercopithecines have a relatively restricted range that is predominantly sub-Saharan African, with the exception of one genus, *Macaca*, which has the widest distribution of any non-human primate, encompassing much of Asia as well as northern Africa and Gibralter (Fleagle, 1999). Colobines have a wider range with multiple genera inhabiting the Asian continent and several genera in sub-saharan Africa (Fleagle, 1999).

Chlorocebus

The genus *Chlorocebus* (previously assigned to *Cercopithecus*), known variously as vervet monkeys, grivets, savannah monkeys, tantalus monkeys, or green monkeys, is one of the most geographically diverse and abundant groups of cercopithecine, and is the most widespread and abundant of all African monkeys (Fedigan and Fedigan, 1988). Although vervets lack the specific diversity of other cercopithecine genera (having only one assigned species, *C. aethiops*; Fleagle, 1999), they range throughout sub-Saharan Africa. Vervets are fairly small sized at 3-8kg (Schultz, 1970; Delson *et al.*, 2000), with the average adult female weighing 5.6kg and the average adult male slightly more at 7kg (Fedigan and

[20] Fleagle (1999) places *Victoriapithecus* in its own family Victoriapithecidae, though Von Koenigswald (1969) originally placed this genus in the subfamily Victoriapithecinae, which he referred to the Cercopithecidae.

Fedigan, 1988). Vervets, therefore, exhibit a moderate amount of sexual size dimorphism (Fleagle, 1999).

Morphologically, vervets are highly variable, due to their extensive distribution over a variety of different habitat types (Fedigan and Fedigan, 1988). Postcranially, they have hindlimbs that are relatively longer than the forelimbs with a mean intermembral index of 83 (Fleagle, 1999). On the forelimb, the greater tuberosity of the humerus extends slightly farther proximally than the articular surface of the head, an adaptation that enhances the action of *m. supraspinatus* in maintaining stability and effecting protraction of the arm in terrestrial quadrupedalism (Larson and Stern, 1992; Schmitt, 1998). Vervet monkeys also have very long tails (Fleagle, 1999).

Vervet monkeys are predominantly arboreal in their locomotor and postural habits, though they also engage in terrestrial progression for about 20% of their locomotion (Fedigan and Fedigan, 1988). Unlike many other Old World monkeys, vervets exhibit considerable behavioural flexibility and are able to exploit niches on the ground as well as in the trees (Fedigan and Fedigan, 1988). Vervets are primarily quadrupedal, with this type of progression accounting for 90% of their locomotor activity (Rose, 1979; Fleagle, 1999). When moving, vervets most often walk (49-67% of time spent in locomotion), though they also frequently climb (30%), due to their disposition for occupying tall trees (Rose, 1979; Isbell *et al.*, 1998). Leaping is engaged in only rarely (2-10%), and other locomotor activities, such as running, amount to less than 10% of the vervet's total repertoire (Rose, 1979; Isbell, *et al.*, 1998). Forelimb suspensory progression is never employed (Rose, 1979).

Colobus

The genus *Colobus* (or guereza) is found solely in Africa. The three black and white species, *C. guereza*, *C. polykomos* and *C. angolensis* all live in sub-Saharan Africa and occupy a variety of forest types from primary rain forests to drier, more open woodland (Fleagle, 1999). The black colobus monkey, *C. satanas*, was excluded from the present study. The guerezas are the largest and most robust of the African colobines, ranging in size from 7.5kg to 13.5kg

(Fleagle, 1999). Sexual size dimorphism is evident, with males being approximately 20-30% larger than females (Fleagle, 1999).

The postcranial morphology of the guereza is characterised by hindlimbs that are relatively much longer than the forelimbs, with a mean intermembral index of 78-79 (Fleagle, 1999). The glenohumeral joint is characterised by a functional mosaic of features. Some features, such as the posterior orientation of the humeral head and the wide, shallow bicipital groove, indicate a movement potential limited to a parasagittal plane (Morbeck, 1979; Rose, 1989). Other traits, such as proximal expansion of the humeral head, increased size of the coracoid and acromion processes and craniocaudal elongation of the scapula, suggest an increased range of movement, particularly in arm raising (Morbeck, 1979).

Elbow joint anatomy largely follows the typical cercopithecoid pattern, permitting a limited range of flexion/extension, though not full extension or hyperextension (Schultz, 1986). There are, however, two distinctive features in *Colobus*. Firstly, the presence of a large medial epicondyle, directed medioposteriorly is suggestive of the importance of forearm and hand flexor musculature; secondly, a low rounded medial trochlear keel (absent in cercopithecines) is commonly found in guerezas (Morbeck, 1979). Harrison (1986a) has argued that the development of a keel in colobines is an allometric artefact of large body size (i.e., prominence of the keel is positively correlated with increase in body mass).

The wrist also follows the typical Old World monkey pattern. The hand, however, is unique in having an extensively reduced pollex, including loss of the phalanges[21] (Morbeck, 1979). Overall, the forelimb morphology of *Colobus* suggests an adaptation for habitual arboreal quadrupedalism, but with a capability for arm-raising, although the latter may be behaviourally associated with feeding postures/strategies rather than arm swinging or forelimb suspension during locomotion (Morbeck, 1979).

Guerezas are arboreal, usually occupying mid to high canopy levels (Fleagle, 1999). Their primary mode of locomotion is quadrupedal walking and

[21] Some researchers have interpreted pollical reduction in *Colobus* to be behaviourally related to arboreal specialisations, and in particular suspensory activity. This led some workers to term *Colobus* a 'brachiator' (Straus, 1949), or 'semibrachiator' (Napier and Napier, 1967; Stern and Oxnard, 1973). This interpretation, however, appears to be erroneous in light of the many anatomical features reviewed here that suggest an adaptation to arboreal quadrupedalism.

running, though, as with all colobines, they are good leapers and they also climb more than vervet monkeys (Mittermeier and Fleagle, 1976; McGraw, 1996). Quantitative measures of the locomotor frequencies of guerezas vary considerably depending on the species studied and the observational methodology employed in field studies, though they broadly support the above outline. Quadrupedal walking accounts for 42-45%, and quadrupedal running for 32-33%, of the locomotor repertoire of *C. polykomos* (McGraw, 1996, 1998a). *C. guereza*, however, engages in quadrupedalism (walking and running) only 35-39% of the time (Mittermeier and Fleagle, 1976; Rose, 1979; Gebo and Chapman, 1995). Leaping is employed by *C. polykomos* between 9% and 18% of the time, while climbing accounts for 8-13% of locomotor activity (McGraw, 1996, 1998). *C. guereza* climbs a similar proportion of the time (11%), but leaps much more frequently (44%)[22] (Mittermeier and Fleagle, 1976; Gebo and Chapman, 1995).

Forelimb suspensory activity is virtually never exhibited in any of the colobines, and though quadrupedal suspension does occur, it does not form part of their usual repertoire (Mittermeier and Fleagle, 1976; Gebo and Chapman, 1995; McGraw, 1996). Bimanual forelimb suspension sometimes occurs over very short time periods (typically less than one second), but is only employed after the landing phase of leaping, when an animal may hang by its hands until it can climb bimanually onto a support that will facilitate quadrupedal progression (Mittermeier and Fleagle, 1976). Bipedalism is never engaged in (Fleagle, 1999).

Ceboidea

Ceboids (Infraorder Platyrrhini, or New World monkeys), represent the only other extant radiation of anthropoids, and inhabit Central and South America (Moynihan, 1976). They can be distinguished from the Old World anthropoids, or catarrhines, by a number of hard and soft anatomical features, though they also retain several primitive craniodental traits that were subsequently lost in the evolution of catarrhines (Rosenberger and Strier, 1989; Ross *et al.*, 1998).

---

[22] Rose (1979) provides very different figures for climbing (36%) and leaping (20%) in *C. guereza*. As noted above, this may be due to differences in field methods or differences between individual populations. The figures provided by Mittermeier and Fleagle (1976) and Gebo and Chapman (1995), however, appear to corroborate each other, and are therefore preferred here.

The postcranial anatomy of most ceboids is very different from that of apes, and, to a lesser extent, Old World monkeys (Oxnard, 1986; Gebo, 1996; Rose, 1996). The postcranial anatomy of one group, the atelins, however, is similar in some respects to that of extant apes and differs considerably from that described below as typical for platyrrhines (Erikson, 1963; Napier, 1963; Oxnard, 1963; Gebo, 1996). Limb proportions in most genera differ from the hominoid pattern. Values for mean intermembral indices range from approximately 70 to 100, relatively conservative figures, lacking the high or low extremities of hominoids or strepsirhines respectively (Erikson, 1963; Napier and Napier, 1967; Fleagle, 1999). Forelimbs, and particularly forearms, tend to be relatively short, with hindlimbs longer (although atelins have longer forelimbs than other ceboids; Erikson, 1963; Gebo, 1996). All platyrrhines possess a tail, but in five genera this appendage has been adapted for use as a fifth limb[23], and is characterised (except in *Cebus*) by the addition of a long, hairless grasping surface ventrally (Rosenberger and Strier, 1989).

The ceboid thorax is craniocaudally long, mediolaterally narrow and dorsoventrally deep (Gebo, 1996). The pectoral girdle is characterised by a scapula positioned on the lateral aspect of the thorax with a ventrolaterally directed glenoid fossa (Oxnard, 1963, 1986; Gebo, 1996). Most ceboids have scapulae with relatively elongated vertebral borders and robustly projecting acromion processes, as in extant hominoids, though the condition expressed in New World monkeys is less pronounced (Harrison, 1987).

Proximal humeral morphology is very similar to cercopithecoids, with a posteriorly directed head and shallow, wide bicipital groove (Rose, 1989). In cebids, the proximal articular surface is partially sandwiched between the tuberosities (Rose, 1989). The platyrrhine distal humerus has a cylindrically shaped trochlea (more so than in cercopithecoids) with a medial edge that shows only slight flare, and a lateral margin that, instead of exhibiting a keel, is bounded by a low ridge separating it from the capitulum (although in some taxa, and some individuals, even this ridge is absent; Rose, 1988a). The capitulum is small and non-globular, as in cercopithecoids, but in contrast to living apes (McHenry and

[23] The five genera are *Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix* from the Atelinae, and *Cebus* from the Cebinae. The prehensile ability of the tail appears to be synapomorphic for the atelines. *Cebus* is distinguished from the atelines by numerous other features, and it is therefore likely that this taxon evolved tail prehensility independently (Rosenberger, 1983).

Corruccini, 1975). The olecranon fossa on the distal humerus is fairly shallow and articulates with a long ulnar olecranon process (Rose, 1988a). The ulnar trochlear notch is narrow (Rose, 1996).

Platyrrhine wrist morphology follows the basic mammalian quadrupedal pattern of direct articulation of the ulna with the triquetral/pisiform (Lewis, 1971b, 1972b). The ulnar styloid process has a facet on its interior aspect that articulates with a large, concave pisotriquetral facet, suggesting an adaptation for ulnocarpal stability in weight bearing palmigrade postures, rather than for flexibility (Lewis, 1971b, 1972b). The hand is shorter, relative to body weight and humerus length, than any orthograde extant anthropoid except *Gorilla* (Moyà-Solà, *et al.*, 1999). Most taxa lack opposable thumbs (Fleagle *et al.*, 1981).

Overall, (non-atelin) ceboid trunk and forelimb morphology is consistent with a range of forelimb movement limited to a parasagittal plane, a limited range of flexion/extension in the forearm with an inability to hyperextend the elbow joint and an adaptation for stability, rather than flexibility in the wrist joint (Lewis, 1971b, 1972b; Rose, 1988a, 1996; Gebo, 1996).

The superfamily Ceboidea is usually divided into two families[24], Atelidae and Cebidae (Szalay and Delson, 1979). These families are in turn divided into six subfamilies, Aotinae, Atelinae, Callicebinae, Callitichinae, Cebinae and Pithecinae (Fleagle, 1999). In the present study, three taxa from the Atelinae subfamily (*Alouatta*, *Ateles* and *Lagothrix*) and one taxon from the Cebinae (*Saimiri*) are sampled. Since *Alouatta* exhibits several autapomorphies (Rosenberger and Strier, 1989; Gebo, 1996), it is useful to differentiate between the *Alouatta* lineage and the collaterally related monophyletic group of *Lagothrix*, *Brachyteles* and *Ateles*. This is achieved in this study by recognising the Tribe Alouattini (informally alouattins) for the former and the Tribe Atelini (atelins) for the latter (after Rosenberger and Strier, 1989).

The atelines are both behaviourally and morphologically heterogeneous (Rosenberger and Strier, 1989), though they share several synapomorphies,

[24] There are several different classification schemes of higher level taxonomy within Platyrrhini. Some classifications (e.g., Napier and Napier, 1967) group the atelines with the cebines in a single family, the Cebidae, while dividing the four largest platyrrhine genera into two subfamilies, Alouattinae, representing *Alouatta*, and atelinae, including *Lagothrix*, *Brachyteles* and *Ateles* (Rosenberger and Strier, 1989).

including a large body mass (4-12kg[25]) and a long tail that possesses prehensile qualities for utilisation as a fifth limb (Rosenberger and Strier, 1989; Fleagle, 1999). Atelins share the additional derived characteristic of frequently engaging in suspensory locomotor activities and, in the case of the *Ateles/Brachyteles* clade[26], bimanual forelimb suspension (Mittermeier, 1978; Cant, 1986; Rosenberger and Strier, 1989). This last characteristic has similarities with the behaviour of the Asian apes *Pongo* and *Hylobates*, and many workers (e.g., Erikson, 1963; Napier, 1963; Gebo, 1996) have argued that this is the result of functional convergence between these two distantly related groups.

Ateles

The genus *Ateles* (spider monkey) is distributed from southern Mexico to southern Amazonia (Moynihan, 1976). There are four allopatric species, all of which exhibit sexual monomorphism in body size, with mean body mass values of 7-9kg (Fleagle, 1999). Spider monkeys inhabit high primary rain forest where they prefer the upper main canopy and emergent substrate levels (Fleagle and Mittermeier, 1980).

The spider monkey's postcranial anatomy is characterised by long slender limbs, especially forelimbs, which are relatively longer than the hindlimbs, as illustrated by a mean intermembral index of 105-109 (depending on species; Fleagle, 1999). The thorax is mediolaterally wide and dorsoventrally shallow with a widened manubrium, as in living apes (Gebo, 1996). The shoulder region is similar to that seen in extant hominoids (Oxnard, 1967; Jenkins *et al.*, 1978), with a cranially directed, ovoid-shaped glenoid fossa, large globular humeral head, (moderate) medial torsion, and a narrow bicipital groove (Gebo, 1996). In addition, the humeral shaft is long and straight and the forearm is long, as in extant apes (Gebo, 1996).

---

[25] Atelines are in fact the largest of all platyrrhine taxa (Rosenberger and Strier, 1989; Fleagle, 1999).

[26] Recent genetic studies of atelines (e.g., Canavez *et al.*, 1999; Meireles *et al.*, 1999) suggest that *Brachyteles* is the sister group of *Lagothrix*, rather than *Ateles*. Thus, the tribe Atelini may be divided into the subtribes Atelina (*Ateles*) and Brachytelina (*Brachyteles* and *Lagothrix*; Meireles *et al.*, 1999). If correct, this suggests that the postcranial similarities of *Ateles* and *Brachyteles* are likely to be largely homoplasies (Pilbeam and Young, 2001).

Elbow joint morphology follows the typical ceboid pattern of a cylindrical trochlea and moderately deep olecranon fossa, on the distal humerus (Rose, 1988a). *Ateles* is distinctive, however, in that the olecranon process on the proximal ulna is slightly shortened when compared with non-atelin ceboids (Rose, 1994). This reduction is nothing like as extensive as that seen in extant hominoids, though it may share the same functional significance of facilitating extension of the forearm (Rose, 1988a, 1994). The trochlear notch on the ulna is broad and the radial head is circular, as in extant hominoids (Gebo, 1996).

Lewis (1971b) has argued that the wrist joint of *Ateles* retains the primitive mammalian arrangement of direct contact between the ulna and triquetral/pisiform. This interpretation has recently been challenged by Youlatos (1996), however, who argues that *Ateles* is distinct from other platyrrhines in exhibiting no ulnopisiform contact and reduced ulnotriquetral contact, indicating an adaptation for enhanced pronation/supination. In the hand, the phalanges are long and an external thumb is usually absent (Fleagle, 1999).

The spider monkey's locomotor repertoire is extremely diverse, encompassing arboreal quadrupedal walking and running, suspension, climbing and, to a much lesser extent, bipedalism and leaping (Richard, 1970; Mittermeier and Fleagle, 1976; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Fleagle, 1999; Cant, 1986; Cant *et al.*, 2001). Although spider monkeys are often described as 'suspensory' primates (e.g., Fleagle and Mittermeier, 1980) several field studies (Richard, 1970; Cant, 1986) suggest that quadrupedal progression is their most frequent locomotor mode; accounting for over 50% of their locomotor repertoire. Mittermeier (1978), Fleagle and Mittermeier (1980) and Cant *et al.* (2001), however, argue that quadrupedal walking and running accounts for only 20-26% of locomotor behaviour, with climbing or 'clambering', being more prolific at 25-40% frequency, depending upon the species. This discrepancy is likely to be due to the field studies being carried out in different locations, with different populations and, in particular, with differing methods of categorising locomotor activity[27] (Prost, 1965). Both leaping (4%) and bipedalism (1%) are relatively rare activities (Fleagle and Mittermeier, 1980).

[27] The lack of standardisation in locomotor description has hampered this area of primatology since its inception; there is rarely consistency within an individual author's publications, and the differences between the categorical schemes of different workers is sometimes extreme and

Ateles, however, is certainly much more suspensory than other platyrrhine taxa. Locomotion involving bimanual forelimb suspension, with use of the prehensile tail, accounts for approximately 23-40% of the spider monkey's repertoire (Richard, 1970; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cant, 1986), substantially more than any other New World monkey, although *Brachyteles* and *Lagothrix* both engage in suspension with less frequency (Defler, 1999). The complete lack of suspensory habits in *Alouatta* provides behavioural evidence that compliments the anatomical evidence for the widespread differences between spider and howling monkeys.

The suspensory behaviour of *Ateles* can be divided into three patterns: inverted quadrupedalism, arm-swinging and brachiation (Mittermeier and Fleagle, 1976; Mittermeier, 1978). Inverted quadrupedalism involves, as the name suggests, a form of upside-down walking. This behaviour is commonly used by juveniles, but is rare in adults (Mittermeier and Fleagle, 1976). Arm-swinging is a form of bimanual suspension without extensive arm and trunk rotation. Arm-swinging is only employed when covering short distances and frequently only used for a single swing to pass obstructions, or to cross between parallel supports (Mittermeier and Fleagle, 1976; Mittermeier, 1978). Brachiation is another form of bimanual progression, this time involving extensive trunk and arm rotation, which can approach 180° between handholds (Avis, 1962). This locomotor pattern is used to cover larger distances than arm-swinging, typically in situations in which quadrupedal locomotion would be difficult (e.g., on flexible supports in the periphery of trees, or among vines; Richard, 1970; Mittermeier and Fleagle, 1976).

In contrast to the 'true', or ricochetal brachiation of hylobatids, spider monkeys usually incorporate a tail hold into this type of progression, helping to stabilise the trunk and reducing the load on the forelimbs (Richard, 1970; Mittermeier, 1978). Occasionally, the tail is not employed and true brachiation is used (Mittermeier and Fleagle, 1976), though in one study this was recorded as occurring with a frequency of less than 1% (Richard, 1970). On very rare occasions, a form of suspension similar to the rapid ricochetal brachiation of

---

difficult to follow (see Prost, 1965). This problem has recently been addressed by Hunt *et al.* (1996), in an attempt to standardise the description and categorisation of locomotor and postural modes.

hylobatids is used (Mittermeier and Fleagle, 1976; Mittermeier, 1978); again, this tends to be employed in the periphery of trees (Cant *et al.*, 2001).

Lagothrix

The genus *Lagothrix*, or woolly monkey, is distributed in north and northwest South America, inhabiting primary rain forest and gallery forests (Moynihan, 1976). There are two species of woolly monkey, with a size range of 7-10kg; both exhibit sexual dimorphism in body size (Fleagle, 1999).

The postcranial morphology of *Lagothrix* shows the same long, slender limb pattern as *Ateles*, although the woolly monkey has forelimbs and hindlimbs of approximately equal length, as illustrated by a mean intermembral index of 98 (Fleagle, 1999). The thorax is mediolaterally wide and dorsoventrally shallow with a wide manubrium (Gebo, 1996). The scapula is positioned dorsally with a cranially orientated glenoid fossa (Gebo, 1996). The humeral head exhibits a moderate degree of medial torsion, though has a shallow, wide bicipital groove (Gebo, 1996; Fleagle, 1999). The elbow and wrist joints retain the primitive condition typical of arboreal quadrupeds (Gebo, 1996). Overall, thoracic, scapular and glenohumeral morphology resembles that of extant apes, while distal humeral and forearm anatomy is similar to most cebid arboreal quadrupeds (Rosenberger and Strier, 1989).

The locomotor habits of *Lagothrix* equal the diversity of the spider monkey's, although the woolly monkey's locomotor patterns have different emphases (Defler, 1999). The same five locomotor patterns of quadrupedal walking and running, suspension, climbing, leaping and bipedalism are employed, though the woolly monkey relies significantly more on quadrupedal progression and climbing, and less on suspension, than does *Ateles* (Defler, 1999; Cant *et al.*, 2001). In fact, suspensory activity accounts for only 9-12% of the woolly monkey's total repertoire, with quadrupedalism and climbing accounting for approximately 30-40% each[28], and leaping the remainder (Defler, 1999; Cant *et al.*, 2001). Bipedalism is very rarely seen in this taxon, and then only in captive, human-raised monkeys (Defler, 1999).

[28] 'Climbing' here includes the locomotor categories "clamber" and "ascent/decent" (Cant *et al.*, 2001:149).

The suspensory locomotion employed by *Lagothrix* consists of the same three types used by *Ateles*: inverted quadrupedalism, arm-swinging and brachiation (Cant *et al.*, 2001). Inverted quadrupedalism and arm-swinging are used in ways virtually identical to *Ateles* (Cant *et al.*, 2001). Brachiation is employed less often by *Lagothrix* than *Ateles*, but when it does occur, woolly monkeys use their tails as additional support more frequently than spider monkeys (Defler, 1999; Cant *et al.*, 2001). Aside from the reduced frequency with which suspension is employed, the major locomotor difference between woolly monkeys and spider monkeys is that the rapid ricochetal brachiation described for *Ateles* (Fleagle, 1976; Mittermeier, 1978) is never employed by *Lagothrix* (Defler, 1999).

Alouatta

The genus *Alouatta* (howling monkey) is the most distinct of the four ateline genera (Gebo, 1996). Howling monkeys have a broad distribution in Central and South America, ranging from Mexico to Argentina (Fleagle, 1999). All six species of howling monkey are sexually dimorphic and large in size (4-12kg). Howling monkeys inhabit primary and secondary rain forests, as well as deciduous, montane and secondary forests and their range includes habitats at altitudes between sea level and 3200 metres (Fleagle, 1999). Their preferred substrate levels are the upper regions of the main canopy and emergents of high forest, though some species travel terrestrially between patches of forest (Fleagle and Mittermeier, 1980; Fleagle, 1999).

The postcranial skeleton of the howling monkey is different in numerous ways to the atelin genera (Gebo, 1996). This has prompted some workers to assign *Alouatta* to a different subfamily or tribe (Rosenberger and Strier, 1989). The appendicular skeleton of the howler monkey exhibits forelimbs and hindlimbs that are of similar length, producing a mean intermembral index of 97-98 (Fleagle, 1999). The thorax, shoulder joint, elbow region and wrist all show the typical ceboid morphology (Rose, 1988a, 1989; Gebo, 1996), and contrast with the features seen in atelin monkeys (Gebo, 1996).

Howling monkeys employ a limited repertoire of locomotor behaviours, based primarily on slow, above-branch pronograde quadrupedalism (Cant, 1986).

Climbing and leaping are uncommon during travel, though climbing is used during feeding, with extensive support from the tail (Cant, 1986; Fleagle, 1999). Suspensory behaviours are very rare in this genus (Mendel, 1976; Cant, 1986). Several field studies (e.g., Mendel, 1976; Fleagle and Mittermeier, 1980; Cant, 1986) have indicated that howling monkeys are almost exclusively quadrupedal, with upwards of 80-90% of their repertoire consisting of this type of progression.

Howlers employ a slow and cautious form of quadrupedal walking, typically with the prehensile tail being engaged as a fifth support on branches other than the one on which the animal is positioned (probably to provide a 'safety' mechanism in case the primary support fails; Mendel, 1976). Climbing accounts for a small proportion of the howler locomotor repertoire (12-16%) and leaping even less (3-4%; Mendel, 1976; Fleagle and Mittermeier, 1980).

These studies (i.e., Mendel, 1976; Cant, 1986) suggest that suspensory activity is either extremely rare or non-existent in howler monkeys. Richards (1970), however, argues that *Alouatta* spends a significant amount of time (34% of its repertoire) 'swinging and grasping'. Richard's category, 'swing and grasp', is fairly ambiguous however, being defined as, "movement in the periphery of the trees" (Richards, 1970:252), suggesting that the behaviour is not true bimanual forelimb suspension.

Saimiri

The genus *Saimiri*, or squirrel monkey, is usually assigned to the subfamily Cebinae (Fleagle, 1999). *Saimiri* is distributed throughout southern Central America, Amazonia and the Guianas (Thorington, 1985). Squirrel monkeys are small, with a body mass range of 650-800g (Fleagle, 1999). They primarily occupy riverine, liane and secondary forests, though are found in all forest types (Fleagle and Mittermeier, 1980).

Squirrel monkey postcranial anatomy differs considerably from that seen in the Atelini (Gebo, 1996). The appendicular skeleton is characterised by long hindlimbs relative to forelimbs, with a mean intermembral index of 80 (Fleagle, 1999). Although the tail is long, *Saimiri*'s tail only possesses prehensile abilities in juveniles, not in mature adults, in contrast to ateline anatomy (Fleagle, 1999). Hand phalanges are short with an unopposable pollex (Fleagle, 1999). The

morphology of the thorax, shoulder region, elbow and wrist joints all show the typical ceboid morphology outlined above (Rose, 1988a, 1989).

Squirrel monkeys are primarily arboreal quadrupeds, though they also frequently leap (Fleagle, 1999). Arboreal quadrupedalism accounts for 55% of travel locomotion, leaping 42% and climbing 3% (Fleagle and Mittermeier, 1980; Fleagle *et al.*, 1981). Although quadrupedal walking or running is the typical mode of locomotion for *Saimiri*, these animals frequently engage in leaps of 1-2 metres, and sometimes adults are observed to jump 5-7 metres (Baldwin, 1985).

Juvenile squirrel monkeys frequently use their tails to gain extra support, either by wrapping it around a branch or their mother (Baldwin, 1985). The adult's tail is not prehensile, but is still used for balance; it trails behind the animal, moving from side to side and acting as a counterweight to the torso when negotiating difficult arboreal supports (Baldwin, 1985). *Saimiri*, because of its diminutive size, often moves on the smallest arboreal supports and frequents the lower strata of the forest (Fleagle *et al.*, 1981).

Summary

The above review has indicated the enormous variety of locomotor behaviour in extant anthropoids and has sought to concentrate attention on the difficulties involved in categorising such behaviour. It has also highlighted the fundamental differences in trunk and forelimb morphology that follow as a consequence of having a pronograde or orthograde body structure with a concomitant emphasis on quadrupedalism or climbing/suspension, respectively (Sarmiento, 1987; Gebo, 1996).

The superfamilies Ceboidea and Cercopithecoidea both differ from the Hominoidea in retaining the primitive condition for many postcranial traits (Martin, 1990). Most of these non-hominoid anthropoid taxa employ some variation of quadrupedal locomotion as their primary means of progression (Fleagle, 1999). A few, such as the atelin monkeys (especially *Ateles*), have converged on the hominoid condition for several trunk and forelimb characters (notably in the shoulder region; Gebo, 1996).

The extant hominoids exhibit similarities in numerous features of the trunk and forelimb (Table 1), but are dissimilar in their locomotor repertoires (Hunt,

1991b; Gebo, 1996). In the next section we will move on to the problem of reconstructing the locomotor behaviour of fossil forms.

Table 1: Trunk and Forelimb Similarities in Extant Hominoids*.

Thorax relatively deep and broad
Manubrium relatively broad
Scapulae dorsally positioned
Glenoid fossa cranially directed (except *Homo*)
Humeral head large, globular/round and medially directed
Humeral shaft strait
Humeral distal articular surface broad
Humeral medial and lateral trochlear keels well-developed
Capitulum large and globular/round
Zona conoidea deep and narrow
Ulnar olecranon process short
Ulnar trochlear notch broad and 'saddle-shaped'
Ulnar styloid process short
Triquetral/pisiform with convex articular facet
Ulnocarpal joint with intra-articular meniscus
Phalanges long and curved

*References: Lewis (1969, 1971a, 1972b), Rose (1988a, 1989, 1994), Begun (1993), Gebo (1996) and Larson (1998).

CHAPTER THREE

FOSSIL CATARRHINE TRUNK AND FORELIMB MORPHOLOGY AND LOCOMOTOR PATTERNS

Reconstructing Fossil Primate Locomotion

A fundamental tenet of palaeontological research is that the relationship between morphology and function, and therefore by implication behaviour, is constant (Lauder, 1981, 1995; Dennett, 1995). If this were not so, studies describing the morphology and behaviour of extant taxa would be of little benefit in reconstructing the morphology and behaviour of fossil forms (Lauder, 1982, 1994). The existence of this constant relationship between form and function allows inferences regarding the behavioural and morphological adaptations of fossil taxa to be grounded in knowledge of the relationship between the detailed hard-tissue morphology of living forms and their known behaviour patterns (Ashton and Oxnard, 1964a, b).

Although this constant relationship exists, it does not make the task of reconstructing the locomotor patterns of fossil forms easy. One of the problems that must first be addressed when attempting this task is ascertaining which morphological features in living taxa play a significant role in facilitating particular types of locomotion; in other words, which traits are functionally correlated with a particular locomotor pattern(s). Day (1979:245) summarises this problem as follows:

> One of the major difficulties faced by palaeontologists in the postcranial field is the recognition of those morphological features, or combination of features, that reflect in fossils the observable, expressed locomotor behaviour seen in living populations of similar primates, because it is obvious that locomotion will never be observable in fossil forms.

Research into the locomotor patterns and hard tissue morphology of extant primates has led to the recognition that numerous features of the postcranial skeleton of these animals are highly diagnostic of locomotor behaviour (Tuttle,

1972b, 1975b; Strasser *et al.*, 1998). Morphological patterns in joints and limbs, and the areas of the axial skeleton they articulate with, can be linked with particular movement capabilities (e.g., range of rotation or flexion) and/or locomotor/postural capabilities (e.g., arboreal/terrestrial quadrupedalism, forelimb suspension; Morbeck, 1983). When these features are preserved in the fossil record they can be used as a basis to formulate inferences concerning the locomotor repertoires of extinct primates (Day, 1979).

A major problem with the use of extant primates as a model for reconstructing fossil primate locomotion is the fact that the life history of individual animals can influence skeletal structure (Morbeck, 1983; Zihlman, 1992; Kelley, 1997). Locomotor behaviour observed in the field reflects both *proximate* (environment driven) influences, and *evolved* (morphology driven) tendencies (Pounds, 1991). This means that there may not be a straightforward correlation between locomotor morphology and locomotor behaviour; ecological variables play an important part in shaping locomotor behaviour exclusive of morphological adaptation (Pounds, 1991). Variation in the size, angle, flexibility, abundance and spatial distribution of supports can promote, or limit certain locomotor patterns. Anatomy imposes constraints on the possibilities of locomotor expression, but recognition of how this correlates with support use is essential for a good understanding of primate locomotor ecology (McGraw, 1996). This is why the characteristics of various supports are routinely collected in locomotor field studies of living primates. Unfortunately, this is not possible for fossil taxa, and so any reconstruction of extinct locomotor repertoires is necessarily less accurate. At best, it is possible to outline certain parameters that morphology would have imposed on locomotor expression, and give a broad indication of the type(s) of locomotion that would have been possible.

Assertions about the locomotor patterns of fossil primates are supported by observations made of various features of postcranial anatomy that are diagnostic of locomotor behaviour. These areas include: trunk (e.g., pectoral girdle and shoulder), forelimb (e.g., proximal humerus, elbow, wrist and phalanges); vertebrae and pelvis; hindlimb (e.g., femoral head, knee, ankle and foot); and various indices comparing limb lengths (e.g., forelimb/hindlimb and forearm/upper arm length). Unfortunately, not all of the features listed in Table 1 are preserved in the existing fossil record of Miocene hominoids.

The present study focuses on trunk and forelimb morphology, and so this review of fossil catarrhine postcranial morphology and locomotor patterns will concentrate on these anatomical areas to reconstruct the locomotor behaviour of relevant taxa. The analyses reported in this study are conducted at the generic level. Since there appears to be little specific variability in locomotor capabilities within these fossil taxa (C. Ward, 1997), most of the following review will also take place at the generic level.

Trunk and Forelimb Morphology and Locomotor Patterns of an Oligocene Stem Catarrhine

Introduction

The Oligocene epoch spans approximately 12 Million years from 35 Mya to 23 Mya (Conroy, 1990; Fleagle, 1999). The early Oligocene is characterised by the first appearance of anthropoid grade primates, the late Oligocene may encompass the origin of the hominoid clade (Fleagle, 1983). In the New World, only the fragmentary remains of a few platyrrhine genera are known (Conroy, 1990). In the Old World, anthropoid primates are virtually absent from the Oligocene mammalian faunas; they are well represented in only one place, the Fayum Depression of Egypt (Fleagle, 1999). In contrast to its environment in the present day, Egypt in the Oligocene was subtropical to tropical with extensive lowland coastal plains and seasonal (perhaps even monsoon-like) rainfall patterns that supported a diverse flora (including lianas, tall trees and mangrove swamps) and fauna (Conroy, 1990).

Two primate families are well represented in Oligocene deposits in the Fayum Province: the Propliopithecidae, and the Parapithecidae. The trunk and forelimb anatomy of the genus *Aegytopithecus* from the Propliopithecidae provides a morphological comparison with Miocene hominoid postcranial structure. This taxon has been interpreted as a stem catarrhine (Harrison, 1982, 1987, 1988; Andrews, 1985; Fleagle, 1999), and therefore forms the closest outgroup to the extant catarrhine primates (Rae, 1993).

Aegyptopithecus

Aegyptopithecus zeuxis is a stem catarrhine from the late Oligocene epoch (Fleagle and Kay, 1983; Harrison, 1987). It is known from an ulna and several humeri (as well as hindlimb specimens), recovered from deposits in Quarry I and M of the Jebel Qatrani Formation, in the Fayum Province of Egypt (Simons, 1965, 1967b). There are no specimens currently assigned to this genus from the thorax or pectoral girdle (Fleagle, 1999). The humeri include a complete specimen (DPC 1275), a specimen that lacks only the humeral head (CGM 40855), and two specimens that preserve only the distal end (DPC 1026; CGM 40123; Fleagle *et al.*, 1975; Fleagle and Simons, 1982). The ulna (YPM 23940) is fairly complete, preserving the trochlear notch and olecranon process at the proximal end, and most of the fragmentary shaft; the distal end, including the styloid process, is missing (Fleagle *et al.*, 1975).

Fleagle and Simons (1982) argue that the proximal humerus of *A. zeuxis* is characterised by a humeral head that is relatively narrow mediolaterally, with a head length/head width index of 108[29], which, they contend, is similar to that seen in extant quadrupeds, but narrower than the broad, globular head evident in extant hominoids or atelin monkeys. The orientation of the head, relative to the distal articular surface, appears to be a matter of contention. Fleagle and Simons (1982:177) state that the head "faces almost directly posteriorly as in quadrupedal anthropoids", but then contradict themselves later in the same paper, by accepting "the medial orientation of the humeral head" (1982:181). They do, however, go on to explain that the medial orientation of the head is not the result of torsion of the shaft, as in extant apes and atelin monkeys, but is instead accomplished by an expansion of the articular surface of the head on the medial side, and by a lateral movement and reduction in size of the lesser tuberosity (Fleagle and Simons, 1982). The bicipital groove is broad and shallow in appearance, as in most extant quadrupeds (Fleagle and Simons, 1982; Rose, 1989).

The distal humerus of *Aegyptopithecus* is characterised by the primitive retention of an entepicondylar foramen (subsequently lost before the divergence into the cercopithecoid and hominoid superfamilies; Conroy, 1990). The medial epicondyle is large, as in extant hominoids, though unlike in living apes it projects

[29] Rose's (1989) measurements for the humeral head of DPC 1275 suggest a head length/head width index of 115.2, indicating an even narrower head.

slightly posteriorly (Fleagle and Simons, 1982). The morphology of this feature in *Aegyptopithecus*, therefore, represents an intermediate condition between that of extant apes and cercopithecoids and is similar to that found in large arboreal quadrupeds such as *Alouatta* and *Lagothrix* (Fleagle and Simons, 1978).

The distal humeral articular surface of *A. zeuxis* resembles that of extant ceboids in being cylindrical, rather than spool-shaped, as in extant apes (Fleagle and Kay, 1983). The medial edge of the trochlea exhibits only slight flare, in contrast to the more prominent keel evident in extant hominoids and, to a lesser extent, cercopithecoids (Fleagle and Simons, 1982). In contrast to the prominent lateral trochlear keel evident in extant hominoids, in *Aegyptopithecus* only a low ridge bounds the distal and anterior surface of the lateral margin of the trochlea, separating it from the capitulum (Fleagle and Simons, 1978, 1982). The posterior surface of the lateral margin of the trochlea, however, is moderately flared, as seen in extant ceboids (Fleagle and Simons, 1978, 1982). Overall then, the broad, cylindrical trochlea of *Aegyptopithecus* is unlike that of any group of extant catarrhine, instead resembling New World arboreal quadrupeds such as *Alouatta* or *Chiropotes* (Fleagle and Simons, 1978).

The ulna of *A. zeuxis* is morphologically similar to the ulnae of extant ceboids, in particular habitual quadrupeds such as *Alouatta* (Fleagle, *et al.*, 1975), and lacks any derived features that would link it to any group of extant catarrhines (Fleagle and Kay, 1983). The olecranon process is very long relative to total ulna length. Fleagle *et al.*, (1975) calculate that the index of olecranon process length[30] is higher in *Aegyptopithecus* than in most extant anthropoids, falling closest to that of *Alouatta* and the quadrupedal strepsirhine *Varecia*. Proximal lengthening of the olecranon is functionally associated with increasing the leverage of the forelimb extensor muscles when the elbow is flexed (Fleagle, *et al.*, 1975), and with a reduction in the potential for forearm extension and hyperextension (Rose, 1988a).

The ulnar trochlear notch of *Aegyptopithecus* (YPM 23940) exhibits a slight crest running proximodistally along the sagittal midline of the articular surface (Fleagle, *et al.*, 1975); the same feature is evident, though more greatly

[30] The index of olecranon process length is 100 × (olecranon length/maximum ulna length; Larson, 1998). Note that, due to the ulna of *Aegyptopithecus* (YPM 23940) lacking the distal end, Fleagle *et al.*, (1975) estimated the maximum total length.

expressed, in extant hominoid ulnae (Rose, 1988a). The ulnar trochlear notch articulates with the distal humerus at the trochlear groove; therefore, the presence of these features in the *Aegyptopithecus* ulna allows inferences about the morphology of the distal humeral articular surface to be made (Rose, 1988a). The features suggest that the humerus possessed a trochlea with a deep groove and clear medial and lateral borders. This inference is supported by the morphology of the DPC 1275 humerus, and the other three partial humeri (Fleagle and Simons, 1978, 1982). The humeroulnar articulation in extant apes is very deep compared to that of *Aegyptopithecus*, which may be described as incipiently developed (Fleagle, *et al.*, 1975).

The features of the humerus and ulna in *Aegyptopithecus*, therefore, are diagnostic of an adaptation to arboreal quadrupedalism, involving a semipronated forelimb with a partially flexed elbow (Fleagle, *et al.*, 1975; Fleagle and Simons, 1982). The elbow morphology, in particular, suggests an adaptation for maintaining stability during climbing and other forms of arboreal locomotion (Fleagle, *et al.*, 1975).

Trunk and Forelimb Morphology and Locomotor Patterns of some Miocene Stem Hominoids

Introduction

The Miocene epoch (23-5 Mya) is one of the longest geological and palaeontological sequences in the Tertiary period (Conroy, 1990; Martin, 1990). The Miocene is commonly sub-divided into three 'stages': early (23-16 Mya), middle (16-10 Mya) and late (10-5 Mya; Fleagle, 1999). The diversity and abundance, and the functional and behavioural repertoires, of primate taxa differ from stage to stage (Martin, 1990; Fleagle, 1999).

Hominoids appear to have originated in the late Oligocene or early Miocene (Andrews *et al.*, 1981; Fleagle, 1983; Fleagle and Kay, 1983; Boschetto *et al.*, 1992). The Miocene epoch encompasses one of the most prolific adaptive radiations in primate evolution and is considered the high water mark of hominoid diversity and abundance (Ciochon and Corruccini, 1983; Conroy, 1990; Benefit

and McCrossin, 1995; Begun *et al.*, 1997b; Fleagle, 1999). Miocene hominoids have been recovered from sites in Africa, Asia and Europe (Begun *et al.*, 1997b).

There is currently little consensus concerning the higher-level systematics of these animals. Several workers (e.g., Begun, 1992b, c; Fleagle, 1999) argue that there are three families of Miocene hominoid: Proconsulidae (a paraphyletic group), Oreopithecidae and Hominidae; though many other researchers prefer their own schemes. The relationships of most (if not all) Miocene hominoids to extant forms remains unclear (Pilbeam, 1996, 1997), prompting some workers to suggest that none of these fossil forms can be linked unequivocally with extant taxa (McCrossin and Benefit, 1994; Benefit and McCrossin, 1995). Some of the taxa that are included in Proconsulidae are sometimes acknowledged to be of uncertain origin (*incertae sedis*) because they do not match *Proconsul sensu stricto* anatomically, but also do not conform to any other phyletic group (Fleagle, 1999).

There is even more contention at the level of generic and specific systematics, but most authorities claim there are in excess of 25 Miocene genera and possibly more than 40 species (Conroy, 1990; Martin, 1990; Begun *et al.*, 1997b; Fleagle, 1999). When dealing with the Miocene it is particularly pertinent to bear in mind the ephemeral nature of taxonomic classifications, which, due to the steady accrual of fossil finds from this epoch, are in a perpetual state of flux (Fleagle, 1983, 1999; Andrews, 1992; Begun, 1992c; Begun *et al.*, 1997b). Most Miocene taxa are known only from craniodental remains; isolated skeletal elements are known for some, and partial skeletons for a very few taxa (Ciochon and Corruccini, 1983; Begun *et al.*, 1997b; Fleagle, 1999).

Data on interspecific skeletal differences suggest that Miocene hominoids exhibited multifarious locomotor repertoires (Morbeck, 1983; Begun, 1992c; Rose, 1994, 1996, 1997; C. Ward, 1997). Studies of the postcranial hard tissue morphology of these animals suggest that the primary locomotor adaptation was arboreal quadrupedalism, with varying degrees of suspensory, climbing and terrestrial adaptations (Begun, 1992c; Rose, 1992b, 1994, 1997; C. Ward, 1997). Most fossil hominoids appear to have had a behaviourally more versatile locomotor skeleton than the comparatively more specialised extant taxa (Aiello, 1981a; Morbeck, 1983; Rose, 1983).

Early Miocene Stem Hominoids

Early Miocene hominoids are a taxonomically diverse group of animals that, for the most part, share a similar body plan and limb proportions, though differ considerably in size (Begun *et al.*, 1997b; Fleagle, 1999). There are approximately 13 genera of early Miocene hominoid, with perhaps in excess of 20 species. Higher-level systematics have proven difficult to delineate due to new finds and the inclination to group taxa, unnaturally, on the basis of size (Pilbeam, 1997; Fleagle, 1999). Most early Miocene taxa, however, can be grouped into one paraphyletic family, Proconsulidae (Fleagle, 1999). One early Miocene taxon, *Nyanzapithecus*, is commonly linked with *Oreopithecus* from the late Miocene and so is placed in the Oreopithecidae (Harrison, 1986b; Benefit and McCrossin, 1997). Another early Miocene taxon, *Morotopithecus*, is difficult to place phyletically. While cranially quite primitive, postcranially it is derived, and exhibits a body plan unlike that of any other contemporary Miocene hominoid (Gebo *et al.*, 1997; MacLatchy *et al.*, 2000).

The proconsulid fossil record is relatively rich, enhancing the accuracy of functional and phylogenetic inferences (Rae, 1993). Most fossil remains are craniodental, however, and those that are not usually comprise isolated skeletal elements unaccompanied by crania (Begun *et al.*, 1997b; Fleagle, 1999). This paucity in the number of postcranial specimens confounds the task of reconstructing locomotor activity and behaviour in general (Day, 1979). Relatively complete skeletons are available, however, for a few individuals of one early Miocene taxon, *Proconsul*. This material will now be reviewed.

Proconsul

Proconsul (Hopwood, 1933) is a stem hominoid from the early Miocene of East Africa (Le Gros Clark and Leakey, 1951; Napier and Davis, 1959; Rae, 1999). Specimens have been recovered from numerous sites in western Kenya, including Songhor, Koru, Mfwangano and Rusinga Island (Walker and Pickford, 1983; Walker, 1997). Four species are generally recognised, *P. africanus*, *P. heseloni*, *P. major* and *P. nyanzae* (Fleagle, 1999). Although *P. heseloni* was formerly included in *P. africanus* (Walker *et al.*, 1993) and some workers (e.g.,

Rae, 1993) prefer to retain this arrangement of specific systematics. The majority of postcranial specimens come from *P. heseloni* and *P. nyanzae*.

Vertebral and torso remains are particularly sparse in the fossil record. *Proconsul* is the only early Miocene taxon for which there are relatively complete specimens (Walker and Pickford, 1983; C. Ward, 1993; C. Ward *et al.*, 1993). C. Ward *et al.* (1993) have described a partial skeleton for *P. nyanzae* (KNM-MW 13142), from Mfangano Island, Kenya. This specimen exhibits one thoracic, four lumbar and one sacral vertebrae, which are craniocaudally elongated (C. Ward *et al.*, 1993). Originally, KNM-MW 13142 probably had six or seven lumbar vertebra (C. Ward, 1993), and this is indicative of a long, flexible vertebral column (i.e., 'monkey-type'[31]). The thorax is mediolaterally narrow and dorsoventrally deep, a morphology that complements the pelvic anatomy of narrow iliac blades that face dorsolaterally (i.e., also 'monkey-type'; C. Ward, 1993, 1997; Rose, 1994). C. Ward (1993, 1997) argues this morphological pattern is diagnostic of pronograde quadrupedalism, rather than forelimb-dominated arboreality or suspension, as in extant hominoids.

In *Proconsul*, the pectoral girdle and shoulder region are known only from partial and distorted specimens (Walker and Pickford, 1983; Walker *et al.*, 1986). A partial scapula and proximal humeral shaft (KNM-RU 2036CH) of *P. heseloni* are known from Rusinga Island, Kenya (Rose, 1983). In numerous features, the scapula resembles that of some extant platyrrhines (e.g., *Cebus* and *Alouatta*; Rose, 1983). For example, the angle between the glenoid fossa and the lateral border is large, and the acromion process overhangs the glenoid laterally (Rose, 1994). The long vertebral border of the scapula is similar to that of extant hominoids, though this may be a primitive anthropoid retention rather than a hominoid synapomorphy (Harrison, 1987). This morphology suggests a moderate level of mobility in the shoulder region, in that the forelimb would have been able to achieve overhead positions easily, but is inconsistent with suspensory

[31] C. Ward (1993) follows Erikson (1963) in making a distinction between two different basic patterns of torso morphology in extant anthropoids. The 'monkey-type' torso is craniocaudally long and mediolaterally narrow with four to seven lumbar vertebrae, a long, flexible, vertebral column that enhances leaping momentum through rapid flexion and extension, and narrow iliac blades that face dorsolaterally (C. Ward, 1993). The 'hominoid-type' torso has relatively short vertebral columns (with reduced flexion), craniocaudally shorter vertebral bodies, mediolaterally broader and craniocaudally shorter thoraxes, three to four lumbar vertebrae for hominids (five to six for hylobatids), and expanded iliac blades that face dorsally (C. Ward, 1993).

capabilities (Rose, 1983, 1994). Rose (1994) argues that the scapula was aligned vertically and positioned laterally on the side of the flattened thorax, thus creating an emphasis on flexion/extension movements.

The proximal humerus of *Proconsul* is not known from a complete fossil (Walker, 1997). Rose (1983, 1989, 1994, 1997) claims that the proximal shaft (KNM-RU 2036CH) is retroflexed with respect to the rest of the shaft and that humeral head torsion is either minimal or nonexistent. Two humeri (KNM-RU 3630A) from another individual are too distorted to be diagnostic of retroflexion, but Walker and Pickford (1983) argue that they indicate there was a considerable degree of medial torsion of the head. Another proximal humerus (KNM-RU 17376), tenuously assigned to *P. africanus* (but maybe *Dendropithecus macinnesi*; Rose, 1983; Gebo *et al.*, 1988), shows some expansion of the head and articular surface compared with the flattened, narrow head morphology that is indicative of parasagittal movement (Gebo *et al.*, 1988). The proximal shaft of this specimen also exhibits a moderate amount of retroflexion (Rose, 1994, 1996). Rose (1994) infers that these features suggest substantial movement of the shoulder was possible in all directions (*contra* Rose, 1983), but with an emphasis on flexion/extension in a parasagittal plane (analogous to that of non-atelin New World monkeys). Both Walker and Pickford (1983) and Gebo *et al.*, (1988) also conclude that *Proconsul* possessed an intermediate range of shoulder mobility between extant cercopithecoids and hominoids (similar to arboreal quadrupedal ceboids).

There are, however, differences of opinion. Fleagle (1983) argues that the humerus (KNM-RU 17376) is virtually identical to that of *Ateles* and suggests this taxon was probably a highly suspensory arboreal quadruped. In Rose's (1983) earlier publication, he argues the *Proconsul* pattern has similarities with that of cercopithecine morphology (in the proximal humeral region only; *contra* Rose, 1994, 1996). These differences, and changes, in opinion concerning *Proconsul* humeral head shape and degree of torsion, may be the result of individual variability in *Proconsul* specimens, the fragmentary nature of these specimens and/or an artefact of the development of new research methods.

The shape of the distal humerus and elbow of *Proconsul* also supports the contention that this taxon exhibited morphology intermediate between that of fully committed quadrupeds and forelimb-suspensory primates (Rose, 1988a, 1994).

The humeral trochlea (KNM-RU 2036AH, AK) is intermediate in form between a cylindrical or conical shape (as in platyrrhines), and a spool-shape (as in extant hominoids; Rose, 1983, 1988a, 1994, 1997). The medial edge exhibits a moderate lip that extends posteriorly and the lateral margin shows a well-defined ridge (Rose, 1983). The capitulum lacks the proximolaterally developed 'tail', common in Old and New World monkeys and *Aegyptopithecus*, and possesses a distinct, though incipient globular shape (Rose, 1988a). The humeral olecranon fossa is quite deep and articulates with the anteroproximally long olecranon process on the ulna (Rose, 1988a). The depth of the olecranon fossa suggests that the forelimb could achieve considerable extension (Rose, 1988a; Aiello and Dean, 1990). The long length of the olecranon process (compared with extant hominoids), however, indicates that the elbow probably could not achieve hyperextension (Rose, 1988a, 1997). The ulnar trochlear notch (KNM-RU 2036CF) exhibits similar morphology to quadrupedal cebid ulnae (Rose, 1983, 1994, 1996). All these features suggest an extensive pronation/supination capability in the forearm (Ankel-Simons, 2000).

Over the last four decades there has been contention over the nature of wrist morphology in *Proconsul* (McHenry and Corruccini, 1983; Walker, 1997). The wrist (KNM-RU 2036) was originally described as having the morphology of an arboreal quadruped (Napier and Davis, 1959). This position was then countered by Lewis (1972b:56), who argued that *Proconsul* was "well adapted to the changed biomechanical requirements of forelimb suspension". Lewis supported his argument by showing that the morphology of the ulnar styloid process and some of the carpal bones (hamate, triquetral, pisiform and capitate) was similar to that of extant hominoids, and inferred that *Proconsul* possessed an intra-articular meniscus, a feature unique to hominoids (Lewis, 1971a, 1972b). McHenry and Corruccini (1983) then tested this hypothesis and found that the shape of the wrist in *Proconsul* closely resembles that of some cercopithecoids, such as *Cercopithecus* and *Papio*. In particular, these workers cited the fact that the triquetral facet on the lunate in *Proconsul* is relatively large, in contrast to its small size in African apes and hylobatids (*Pongo* is similar to *Proconsul* in this feature; McHenry and Corruccini, 1983). Beard *et al.* (1986) described new carpal specimens (KNM-RU 2036C, 15100) from Rusinga Island, and concluded that clear, concave facets are present on the pisiform and triquetral, for articulation with the ulnar styloid process. This morphology contrasts with that of extant apes,

but the orientation and extent of the pisotriquetral facets also differs from that seen in extant cercopithecoids (Beard *et al.*, 1986). Beard *et al.* (1986) suggested that, although the wrist of *Proconsul* is characterised by direct ulnocarpal articulation, a greater degree of ulnar deviation would have been possible than in extant cercopithecoids. Rose (1983, 1994, 1997) has argued that most of the features in the wrist and hand of *Proconsul* resemble those of arboreal quadrupedal monkeys, and that stability in the dorsiflexed position is provided by several features on the ulnar side of the wrist. Although, in another paper, Rose (1992a) suggests that the mobility of the trapezium and first metacarpal joint in *Proconsul* is most similar to that of extant hominoids and allows a wide range of abduction/adduction, indicative of a pronounced grasping capability.

The hand of *Proconsul* is short relative to body weight and humerus length, this is similar to the state found in pronograde monkeys, hominines, *Gorilla* and *Oreopithecus*, but contrasts with the relatively elongated hand length of other crown apes and *Dryopithecus* (Moyà-Solà *et al.*, 1999). The pollex is relatively mobile, and therefore the thumb could have been utilised in grasping activities (Rose, 1983, 1997). McHenry and Corruccini (1983) argue that the morphology of *Proconsul* metacarpals suggests an adaptation to palmigrade quadrupedalism. Begun *et al.* (1994) argue, however, that the broad proximal phalangeal shafts evident in *Proconsul* are consistent with grasping quadrupedalism rather than palmigrade quadrupedalism, and are not compatible with suspensory capabilities as there is no curvature of the shaft (*contra* Napier and Davis, 1959). Broad phalanges may be related, Begun *et al.* (1994) suggest, to bending stresses experienced during climbing.

Dendropithecus

Dendropithecus macinnesi (Andrews and Simons, 1977) is a small-bodied stem hominoid (or stem catarrhine; Begun *et al.*, 1997) from the early Miocene of East Africa (Harrison, 1982; Fleagle, 1999). The known postcranial material for *Dendropithecus* is morphologically similar to several other early Miocene taxa (e.g., *Simiolus*, *Limnopithecus*, *Kalepithecus* and *Microcebus*; Le Gros Clark and Thomas, 1951; Andrews and Simons, 1977; Harrison, 1982; Leakey and Leakey, 1986; Rose *et al.*, 1992; Rose, 1994). Little is known about the pectoral girdle. A

proximal humerus (KNM-RU 17376) is sometimes assigned to this taxon, though may represent *P. africanus*, and has therefore been described above. Two humeri are known (KNM-RU 1675, 2097) preserving the shaft and distal end morphology.

Andrews and Simons (1977) argue that the distal humeral articular region of *Dendropithecus* is most similar to *Hylobates*, though Rose (1994) claims its morphology is closer to *Proconsul*. The medial epicondyle projects medially, the trochlea is wide and the olecranon fossa large, as in extant hominoids (Andrews and Simons, 1977). The capitulum, however, is small as in ceropithecoids and ceboids (McHenry and Corruccini, 1975), and unlike modern hominoids. The humeroradial joint features outlined for *Proconsul* are more strongly expressed, indicating quadrupedal habits (Rose, 1988a, 1994). A lateral lip on the proximal surface of the radial head is also present, indicating that a premium was placed on stability of the humeroradial joint during load bearing in quadrupedal locomotion (Rose, 1994). In most features of the wrist and hand *Dendropithecus* is similar to *Proconsul*, providing additional support for its suggested quadrupedal status (McHenry and Corruccini, 1975; Rose, 1994).

Morotopithecus

Morotopithecus bishopi is stem hominoid from the early Miocene of Uganda (Gebo *et al.*, 1997; MacLatchy *et al.*, 2000). It is known from the fossil localities Moroto I and II, in northeastern Uganda, and dates to at least 20.6 Mya (Gebo, *et al.*, 1997). Although postcranial material had been recovered in the early 1960s from the Moroto site (Allbrook and Bishop, 1963; Walker and Rose, 1968), it was not until Gebo and others revisited the site in 1994-1995 that postcranial specimens from the forelimb were recovered that have been of benefit in assessing the locomotor adaptation of *Morotopithecus* (Gebo, *et al.*, 1997). Taxonomic assessments of this large-bodied hominoid have tended to link it with other early Miocene hominoids (e.g., *Proconsul* or *Afropithecus*) on the basis of craniodental anatomy (Allbrook and Bishop, 1963; Leakey *et al.*, 1988). The postcranial material recently recovered by Gebo *et al.* (1997) suggests that although *Morotopithecus* is facially and dentally quite primitive, postcranially it shares several synapomorphies with extant hominoids.

The morphology of the lumbar vertebrae implies that the Moroto taxon had a shorter and stiffer spine (Walker and Rose, 1968; Filler, 1981; Ward, 1993; Sanders and Bodenbender, 1994), a mediolaterally broader and craniocaudally shorter torso, and broader, more dorsally facing iliac blades than habitual pronograde anthropoids (C. Ward, 1993, 1997). Gebo *et al.* (1997) and MacLatchy *et al.* (2000) use this evidence to make inferences about the behaviour of *Morotopithecus* and argue that this hominoid was primarily arboreal with a locomotor repertoire that included climbing, slow to moderate speed forelimb suspension and quadrupedalism.

The morphology of the pectoral girdle provides corroboration for the inference that *Morotopithecus* employed a locomotor repertoire incorporating a significant component of forelimb suspension. The glenoid fossa (MUZM 60) of a left scapula was recovered from the Moroto I site and exhibits a very derived morphology (MacLatchy *et al.*, 2000). The superior half of the articular surface is wide and shows a smooth craniocaudal curvature (Gebo, *et al.*, 1997), a morphology similar to that of extant hominoids and atelins, and contrasting with that of other primates (Ankel-Simons, 2000). This morphology is associated functionally with enhanced shoulder mobility (Ashton and Oxnard, 1964a; Oxnard, 1967) and behaviourally with primates that engage in bimanual forelimb suspension.

Morotopithecus, therefore, is a large-bodied stem hominoid that exhibits a derived scapula and lumbar morphology that distances this genus phyletically from the proconsulid family and other early Miocene taxa (MacLatchy *et al.*, 2000). If these features are synapomorphies, then *Morotopithecus* may be linked to the extant hominid clade, in which case the craniodental and proximal femoral similarities of hylobatids and hominids are homoplasies, or it may be the sister taxon of all extant hominoids (Pilbeam, 1996; Gebo, *et al.*, 1997).

Nyanzapithecus

Nyanzapithecus[32] is a stem hominoid from the middle Miocene of Maboko Island, Kenya (Harrison, 1986b). There are two species, *N. vancouveringorum*

[32] Concern has been expressed that *Nyanzapithecus* is inadequately differentiated with respect to *Mabokopithecus* (e.g., McCrossin, 1992). It remains contentious whether *Nyanzapithecus*

and *N. pickfordi*; postcranial material is known only for the latter. Before the postcranial material was recovered, *Nyanzapithecus* had been phyletically linked (on the basis of detailed dental similarity) with the late Miocene European hominoid *Oreopithecus* (Harrison, 1986b). Since *Oreopithecus* exhibits a very derived, extant hominoid-like postcranial anatomy, and since this taxon shares a marked similarity in upper molar morphology with *Nyanzapithecus*, Harrison (1986b) argues it is possible that the derived postcranial morphology of extant hominoids had its antecedents in the middle Miocene taxon from Maboko Island.

When postcranial material was finally recovered in 1989, it became evident that the morphology of the *Nyanzapithecus* proximal humeral head (KNM-MB 21206) complicates this scenario (McCrossin, 1992). In contrast to the broad, medially facing humeral head of living apes and *Oreopithecus* (which has been associated functionally with increased shoulder mobility and behaviourally with forelimb suspension and/or vertical climbing; Sarmiento, 1987; Rose, 1989), the *Nyanzapithecus* humeral head faces posteroproximally, as in arboreal quadrupeds (McCrossin, 1992; Benefit and McCrossin, 1997), and is slightly narrower mediolaterally than it is long anteroposteriorly. The bicipital groove is broad and shallow, and the deltoid plane is almost flat (McCrossin, 1992). This morphology contrasts with the deep, narrow bicipital groove of (non-pongine) living apes and is consistent with movement of the forelimb in a parasagittal plane (i.e., lacking the potential for circumduction of the forelimb), it therefore suggests a locomotor repertoire with a significant component of pronograde quadrupedalism, probably implemented in arboreal climbing (McCrossin, 1992; Rose, 1994; Ankel-Simons, 2000).

The relationship between *Nyanzapithecus* and *Oreopithecus* is thus more complicated than first thought. McCrossin (1992) argues either that *Nyanzapithecus* and *Oreopithecus* are not closely related and are therefore dentally convergent, or that the morphology required for forelimb suspension evolved independently in a lineage that includes all genera with *Oreopithecus*-like teeth. The extreme detail of the dental similarity between these two taxa (for example, aspects of molar morphology such as "protoconules and trigon-hypocone crests on mesiodistally elongated upper molars" are shared by only

(Harrison, 1986b) is valid as anything more than a junior synonym of *Mabokopithecus* (Von Koenigswald, 1969).

these two taxa among all hominoid primates; Benefit and McCrossin, 1997:74) suggests that the latter hypothesis may be correct (Benefit and McCrossin, 1997).

Middle and Late Miocene Stem Hominoids

Equatorius

Equatorius africanus[33] (formally *Kenyapithecus africanus*) is a stem hominoid from the middle Miocene of East Africa (S. Ward *et al.*, 1999). It is known from several localities in western Kenya, the Tugen Hills and Nachola in the Samburu region, and is dated to between 15.5 and 14 Mya (Leakey, 1967; Pickford, 1985; Ward *et al.*, 1999; Sherwood *et al.*, 2002). This genus is known, postcranially, from several isolated forelimb specimens, including a left humeral shaft (BMNH M 16334), two right ulnae (KNM-BG 15071, 17824; Leakey, 1967; Rose *et al.*, 1996; McCrossin, 1997; McCrossin and Benefit, 1997; Rose, 1997), and a partial skeleton with associated dentition (KNM-TH 28860), which contains a right scapula fragment, left proximal humerus, fragmentary right humerus, right proximal ulna and right distal ulna (S. Ward *et al.*, 1999; Sherwood *et al.*, 2002).

The morphology of the vertebral column, torso and pectoral girdle in *Equatorius*, in common with other middle and late Miocene hominoids, is known mostly from fragmentary remains (Sherwood *et al.*, 2002). The isolated specimens so far recovered (e.g., KNM-BG 15527 lumbar vertebra, 17826 thoracic vertebra) indicate that *Equatorius* is morphologically similar to *Proconsul* in these features (Rose *et al.*, 1996). C. Ward (1997) describes the vertebral bodies as being long, and infers that this reflects a craniocaudally elongated torso and a mediolaterally narrow thoracic cage (as in *Proconsul*; C. Ward, 1993), features that are indicative of pronograde quadrupedalism. The scapula (KNM-TH 28860-Z) is extremely fragmentary, with several of the margins and the glenoid process missing, though the overall shape resembles that of an Old World monkey (Sherwood *et al.*, 2002).

The proximal humerus of *Equatorius* (BMNH M 16334 and KNM-TH 28860-AA) exhibits a retroflexed proximal shaft and a flat deltoid plane, both

---

[33] Begun (2000) argues that '*Equatorius*' is a junior synonym of *Griphopithecus*. Benefit and McCrossin (2000) suggest that '*Equatorius*' is a combination of *Kenyapithecus* and *Nacholapithecus*. Kelley *et al.* (2000) dispute both claims, and support S. Ward *et al.*'s (1999) original diagnosis.

features that are diagnostic of quadrupedal habits (Rose, 1994, 1997; Sherwood *et al.*, 2002). The head is directed posteriorly, as in most extant quadrupedal anthropoids and in contrast to the medially directed humeral head of living apes and some atelins (Benefit and McCrossin, 1995; McCrossin and Benefit, 1997; Sherwood *et al.*, 2002). The shape of the head also contrasts with the extant hominoid pattern of a large, globular head, by having a low proximodistal height and a flat proximal end, as in terrestrial cercopithecoids (McCrossin, 1994, 1997; McCrossin and Benefit, 1997). *Equatorius* also shares with cercopithecoids and non-atelin ceboids a broad and shallow intertubercular sulcus, which differs from the deep, narrow bicipital groove found in (non-pongine) extant hominoids and spider monkeys (McCrossin and Benefit, 1997). The greater tuberosity of the *Equatorius* humerus is large, positioned anterolaterally and extends farther proximally than the articular surface of the head (Benefit and McCrossin, 1995); the lesser tuberosity is also large and is positioned anteromedially (both features resemble the morphology of terrestrial cercopithecoids such as *Papio* and *Theropithecus*; McCrossin and Benefit, 1997). In contrast, living apes and arboreal Old World monkeys exhibit humeral heads that extend above the greater tuberosity and extant hominoids have a small, anteriorly positioned lesser tuberosity (Rose, 1994; Gebo, 1996; McCrossin and Benefit, 1997).

In the elbow region of *Equatorius*, the distal humerus (BMNH M 16334 and KNM-TH 28860-G) is similar in some respects to that of early Miocene hominoids. The medial epicondyle is small and posteriorly directed, unlike that of extant hominoids, and the medial trochlear keel is well-developed. The ulna (KNM-BG 15071, 17824; KNM-TH 28860-K, O, Q) is characterised by a relatively long, retroflexed olecranon process (Sherwood *et al.*, 2002), similar to that of extant terrestrial cercopithecoids and *P. heseloni* (KNM-RU 2036CF), and contrasting with the long, straight olecranon of arboreal Old World monkeys and the greatly reduced olecranon of extant hominoids (McCrossin and Benefit, 1997). The proximal radioulnar joint has a laterally facing ulnar surface, as in extant hominoids; Rose (1997) argues this is compatible with a greater range of pronation/supination in the forearm, compared with other early and middle Miocene taxa.

The morphology of the wrist and hand of *Equatorius* is similar to that of quadrupedal non-hominoid anthropoids (Rose, 1997; Sherwood *et al.*, 2002). In

the wrist, the ulnar styloid process is long and maintains contact with the proximal row of the carpus (Sherwood *et al.*, 2002). The pisiform exhibits a distinct concave facet for articulation with the styloid process, as in *Proconsul* and extant cercopithecoids, but in contrast to living apes (Benefit and McCrossin, 1995; McCrossin and Benefit, 1997). In the hand, the 3rd metacarpal exhibits a strong dorsal transverse ridge next to the distal end (McCrossin and Benefit, 1997). This feature was once linked to knuckle-walking (Tuttle, 1967) because of its presence in *Pan* and *Gorilla* and absence in *Pongo* and *Hylobates*, but transverse dorsal ridges are also found in some terrestrial cercopithecoids (e.g., *Mandrillus*) and may, therefore, be functionally indicative of digitigrade hand postures in a broader sense (including palmar digitigrady), where the dorsal ridge prevents hyperextension at the metacarpophalangeal joint (McCrossin and Benefit, 1997).

Many of the postcranial features of *Equatorius* are closer morphologically to early Miocene proconsulids than to the derived late Miocene hominoids, or living apes (S. Ward *et al.*, 1999; Sherwood *et al.*, 2002). The locomotor adaptation of *Equatorius* was probably based on terrestrial pronograde quadrupedalism, similar to such extant cercopithecoids as *Papio* and *Theropithecus* (McCrossin, 1997; McCrossin and Benefit, 1997; Sherwood *et al.*, 2002).

Kenyapithecus

Kenyapithecus wickeri (Leakey, 1962) is a stem hominoid from the middle Miocene of East Africa (McCrossin and Benefit, 1994). It is known from the Fort Ternan locality in Kenya and dates to 15.5-14 Mya (McCrossin and Benefit, 1997). Only one postcranial specimen has been assigned to *Kenyapithecus*, a fragment of right humerus (KNM-FT 2751) preserving the distal end and articular surface (Pickford, 1985).

The distal humerus from Fort Ternan exhibits a mosaic of primitive and derived features (Pickford, 1986; McCrossin and Benefit, 1994; McCrossin and Benefit, 1997). The trochlea is broader than the capitulum and both are separated by a relatively deep *zona conoidea*, for articulation with the radial head (McCrossin and Benefit, 1997). The trochlea also has a marked lateral keel (Morbeck, 1983). These features have been interpreted as synapomorphies of the

extant hominoids (Ciochon, 1983; Andrews, 1985; Martin, 1986; Harrison, 1987), and contrast with the narrow trochlea, with weak lateral margin, and shallow *zona conoidea* of extant cercopithecoids (Rose, 1988a, 1994). The KNM-FT 2751 *zona conoidea* is slightly shallower and broader than that of *Pan* and is most comparable to *Hylobates* (Rose, 1994; McCrossin and Benefit, 1997). A deep *zona conoidea* is functionally associated with providing a secure articulation for the rim of the radial head, thus increasing the stability of the forearm during pronation/supination movements (Rose, 1988a; Aiello and Dean, 1990).

One significant difference between the *Kenyapithecus* distal humerus and that of extant apes is the orientation of the medial epicondyle. The KNM-FT 2751 specimen exhibits a strong posterior inclination (retroflexion) of the medial epicondyle, in contrast to the large, medially directed entepicondyle found in extant hominoids and some atelin monkeys (McCrossin and Benefit, 1994, 1997). The *Kenyapithecus* medial epicondyle has similarities to the abbreviated and posteromedially orientated medial epicondyle of terrestrial cercopithecoids (McCrossin and Benefit, 1994; Ankel-Simons, 2000). The morphology of the medial epicondyle is linked to the functional need for digital grasping (Aiello and Dean, 1990). The carpal and digital flexors take their origin from the medial epicondyle and their action is thus promoted or inhibited, according to the degree of elongation and medial orientation, or shortening and posterior reflection, of the entepicondyle (McCrossin, 1997; McCrossin and Benefit, 1997; Ankel-Simons, 2000).

With such a small postcranial sample, it is difficult to be conclusive about the locomotor adaptations of *K. wickeri*. Having said that, the distal humerus is one of the most informative and diagnostic areas of anatomy when it comes to reconstructing fossil primate locomotion (Rose, 1988a). The above review suggests that *Kenyapithecus* exhibits a mosaic of features, some associated with extant hominoids, and others with extant cercopithecoids (McCrossin and Benefit, 1994, 1997). The derived morphology of the distal articular surface, in particular, suggests an emphasis on pronation/supination movements of the forearm, as employed by extant hominoids in knuckle-walking, vertical climbing and forelimb suspension (Sarmiento, 1987; Rose, 1988a, 1994). The cercopithecoid-like morphology of the medial epicondyle, however, suggests a locomotor repertoire

with a significant component of terrestrial quadrupedalism (McCrossin and Benefit, 1997).

Dryopithecus

Dryopithecus is a stem hominid from the middle/late Miocene of Europe (Begun, 1992b, 1994; Begun and Kordos, 1997; Begun, 2001). This genus comprises four (Begun, 1992a) geographically isolated species: *D. fontani* from St. Gaudens in France, *D. brancoi* from Rudabánya in Hungary, and *D. laietanus* and *D. crusafonti* from Can Llobateres and Can Ponsic in Spain. Postcranial specimens are known for the first three species and include a humeral shaft (St. Gaudens), left humeral distal end (RUD 53), right proximal ulna fragment (RUD 22), lunate (IPMC 4344), hamate (CP 4340), two proximal (RUD 78, 109) and two intermediate (RUD 81, 115) phalanges and a partial skeleton (CL1 18800), which contains a humeral diaphysis, ulna shaft with partial proximal end and a triquetral (Begun, 1988a, 1994; Moyà-Solà and Köhler, 1996; Kordos and Begun, 2001).

Trunk and pectoral girdle remains currently assigned to *Dryopithecus* are limited to a few vertebral and thoracic fragments from the CL1 18800 skeleton (Moyà-Solà and Köhler, 1996; Köhler *et al.*, 2001). Humeral specimens are limited to the shaft and distal end (Begun, 1992c; Begun and Kordos, 1997). It is possible, however, to infer the degree of torsion exhibited by the humeral head from this material because torsion actually occurs along the diaphysis shaft of the humerus, rather than by twisting of the humeral head or lesser tubercle (Ankel-Simons, 2000). Begun (1992c) argues that the head of the St. Gaudens humerus might have been medially rotated (as in extant apes), based on the morphology and orientation of the bicipital groove, deltopectoral crest and other surfaces on the proximal shaft. In fact, Pilbeam and Simons (1971) have emphasised its similarity to *P. paniscus*. Rose (1994) argues, however, that the humeral head is more posteriorly orientated and therefore exhibits minimal torsion, as in *Proconsul*, *Sivapithecus* and other habitual quadrupeds. This interpretation is supported by the shallowness of the bicipital groove (Rose, 1997). Begun and Kordos (1997) claim that the bicipital groove is abraded and crushed in this specimen and therefore was probably deeper than is preserved (possibly deeper

than in *Pongo*, which combines a shallow groove with medial head torsion). The uncertainty in the interpretation of proximal humeral morphology may be due to the damage on the original specimen (Begun, 1994: Benefit and McCrossin, 1995; Begun and Kordos, 1997).

The proximal humeral shaft is anteroflexed and twisted medially relative to the distal end, in contrast to the retroflexed shaft of habitual quadrupeds (Morbeck, 1983; Begun and Kordos, 1997; Rose, 1997). Begun (1992c, 1994) argues that the anteroflexion of the shaft is similar to the form found in extant Asian apes and that the medial twist of the shaft indicates, as it does in all crown hominoids, the presence of humeral torsion. Rose (1994) suggests the proximal humeral shape is more consistent with the morphology of extant cercopithecines.

The functional significance of this morphology is therefore equivocal. If the humeral head lacks medial torsion, it suggests a forelimb adapted for movement in a parasagittal plane, but this is contradicted by the anteroflexion of the shaft, which is a feature shared with extant hominoids. If, as Begun (1994) has suggested, the head was medially orientated, then the entire proximal humerus and shaft will share affinities with living apes. Rose (1994) argues that dryopithecine shoulder morphology appears to be indicative of a locomotor repertoire that is primarily quadrupedal, while Begun (1992c, 1993, 1994) and Begun and Kordos (1997) suggest that *Dryopithecus* may have frequently employed forelimb suspension.

The dryopithecine elbow region includes a trochleiform humeroulnar joint, and humeroradial and radioulnar joints that are diagnostic of a large range of pronation/supination movement (Morbeck, 1983; Begun, 1992c, 1994; Rose, 1988a, 1994, 1997). The distal humerus (RUD 53) is characterised by a large, broad trochlea with a prominent lateral keel, only slightly smaller anteroposteriorly than the medial keel (in fact, the lateral keel is as strongly developed, relative to trochlear depth, as it is in *Pongo* and *Hylobates*; Morbeck, 1983; Begun, 1992c, 1994). Both trochlear keels run distolaterally, giving the spool-shaped trochlea a screw-like appearance (Rose, 1988a; Begun, 1992c). The capitulum is bulbous, almost spherical and projects anteriorly to the same extent as the lateral trochlear keel, from which it is separated by a deep, narrow *zona conoidea* (Begun, 1992c). As in extant hominoids, the trochlea is broad relative to the capitulum (anterior trochlear breadth is ten millimetres larger than anterior

capitular breadth; Morbeck, 1983). The olecranon fossa is deep, wide and triangular in shape, as in living apes (Morbeck, 1983; Begun, 1992c). The medial epicondyle is large and orientated medially and slightly posteriorly, but, in contrast to extant hominoids, does not project very far medially; Begun (1992c, 1994) suggests this is probably the result of damage.

The proximal ulna (RUD 22[34]) of *Dryopithecus* displays a pronounced keel (Morbeck, 1983) running proximodistally along the sagittal midline of the articular surface, creating two articular surfaces and a distinctive 'saddle-shape' (Begun, 1992c). The ridge articulates with the trochlear groove on the humerus, thus forming the stable 'hinge' typical of extant hominoid humeroulnar joints (Rose, 1988a; Begun, 1992c). This suite of features is morphologically (Rose, 1988a, 1994; Begun, 1992c, 1994) and metrically (Morbeck, 1983) most similar to that found in extant hominids, although minor differences are evident (the capitulum is relatively smaller than the trochlea, and the trochlear groove is slightly shallower). The functional significance of these traits is equivocal; the features appear to be implicated in climbing and suspensory capabilities (Sarmiento, 1987; Begun, 1992c, 1994), but may also provide stable load bearing during quadrupedal locomotion (Rose, 1988a, 1994).

Dryopithecine wrist morphology exhibits a mosaic of primitive and derived features. Moyà-Solà and Köhler (1996:158) argue that "[t]he triquetrum has a convex surface for the ulnar styloid process, suggesting a reduced stylotriquetral contact". If this is correct, then the *Dryopithecus* triquetral (CL1 18800) shares a similar morphology to extant hominoids; cercopithecoids, in contrast, retain a concave triquetral ulnar facet that facilitates the direct articulation of the ulnar styloid process to the carpus (Lewis, 1971a, 1972b). The lunate (IPMC 4344) is large and mediolaterally thick with a very large, relatively shallow articular surface for the capitate and hamate, similar to that of extant hominids (Begun, 1994). The position of the radial facet on the lunate, however, indicates that the bone must have been more mediolaterally orientated, rather than proximodistally orientated, as in living apes (Begun, 1994). These features represent a mix of hylobatid and African ape morphology, which has implications for dryopithecine phylogeny.

[34] RUD 22 is broken proximally, midway along the trochlear notch; the entire olecranon process is thus missing (Begun, 1992c).

One of the characters in the carpus that easily differentiates hylobatids from African apes is the *os centrale* (Tuttle, 1972). In hylobatids and most other non-hominoid primates, the *os centrale* is a separate bone; in African apes and humans it is fused with the scaphoid[35] (*Pongo* lacks this bone; Lewis, 1969, 1972b; Sarmiento, 1988), probably to increase midcarpal stability during wrist extension (Harrison, 1986a). The depth of the lunate-scaphoid facet in *Dryopithecus* is similar to that of hylobatids, and thus suggests the presence of a separate *os centrale*; the restricted nature of the facet suggests African ape affinities and thus a fused *os centrale*. So it remains equivocal whether *Dryopithecus* shared *os centrale* fusion with African apes and humans; other Miocene hominoids (*Proconsul*, *Oreopithecus*) do not (Begun, 1994). The hamate (CP 4340) also exhibits a mixture of primitive anthropoid and derived hominid characters (Begun, 1994). It is proximodistally elongated with a rounded head, and thus contrasts with the more longitudinally twisted morphology of the extant hominoid hamate (Begun, 1994; White and Folkens, 2000).

The dryopithecine hand is long relative to body weight and humerus length, this is similar to the state found in extant apes (except *Gorilla*) and contrasts with the state found in pronograde monkeys, hominines and *Oreopithecus* (Moyà-Solà *et al.*, 1999). This feature suggests that, like most living apes, *Dryopithecus* engaged in vertical climbing and below-branch suspension and therefore needed a larger friction surface on the hand to secure a firm hold (Moyà-Solà *et al.*, 1999). The proximal phalanges (RUD 78, 109) of *Dryopithecus* exhibit longitudinal shaft curvature, well-developed flexor sheath ridges, deep distal ends relative to breadth, marked dorsoventral extension of the articular surfaces, round condyles and well developed interphalangeal joint attachment sites (Begun, 1993), a suite of characters related to arboreal quadrupedalism (Tuttle, 1974; Susman, 1979; Sarmiento, 1987; Begun, 1988a; Hunt, 1991b). This contrasts with the features associated with the phalanges of more terrestrial primates (e.g., *Macaca* and *Papio*), such as shorter, straighter shafts, less prominent flexor sheath ridges, broader distal ends, smaller, less extensive

[35] The *os centrale* is initially separate in African apes and humans during the early stages of ontogeny. In contrast to most other primates (except a few Malagasy forms), it then fuses early in growth and development (Lewis, 1972b).

articular surfaces and broader, less round condyles with a flatter articular surface (Begun, 1993).

Many of the phalangeal characters associated with arboreal primates achieve their greatest expression in taxa that practice some form of below-branch suspension (e.g., *Hylobates*, *Ateles*; Begun, 1993). Most of these features are functionally linked with the patterns of stress sustained by the digits during flexion at the metacarpophalangeal and intercarpophalangeal joints (Begun, 1988a). Shaft curvature, for example, reduces bending stresses by bringing more of the shaft closer to curved supports (e.g., branches) and thereby mechanically transforms them into compressive forces (Begun, 1993). These features suggest, therefore, that RUD 78 and 109 were capable of very powerful digital flexion, or grasping, of the type seen in primates that engage in below-branch suspensory locomotion (e.g., *Hylobates*, *Pongo*, *Pan*, *Ateles*; Begun, 1993). This does not necessarily mean that *Dryopithecus* engaged in forelimb-dominated bimanual suspension, or brachiation, but rather may be more consistent with below-branch suspensory quadrupedalism (Begun, 1988a). The intermediate phalanges (RUD 81, 115) follow a similar morphological pattern (robust, highly curved shafts, narrow relative to height) and therefore carry the same functional connotations. Begun (1993) again suggests these features are strongly diagnostic of suspensory locomotor habits. Rose (1994, 1997), however, argues many of these proximal and intermediate phalangeal characters are also found in above-branch quadrupeds.

Thus, the forelimb morphology of *Dryopithecus* represents something of a mixture of primitive anthropoid and derived hominid characters (Begun, 1988b, 1992c, 2001). As a result, trying to elucidate the primary locomotor adaptation of this taxon is difficult. The morphology of the proximal humerus remains uncertain. The functional significance of a double-keeled humeroulnar joint and a deep, narrow *zona conoidea* is equivocal (Rose, 1988a, 1994). The carpal morphology is a mosaic of primitive and derived characters (Begun, 1994). Rose (1994, 1997) has argued that this genus is essentially a quadruped with some climbing and suspensory capabilities. Begun (1993) has suggested that only in the robust, curved phalanges of the hand is there strong evidence that below-branch suspension (though not necessarily forelimb-dominated) was an integral part of the locomotor repertoire of *Dryopithecus*. In contrast to these positions, Moyà-

Solà and Köhler (1996) suggest that this taxon engaged in habitual climbing and suspension.

Sivapithecus

Sivapithecus is a stem hominoid from the middle/late Miocene of southern Asia (S. Ward, 1997; Pilbeam and Young, 2001). It first appears in the fossil record at 12.7 Mya and disappears at 6.8 Mya (Pilbeam *et al.*, 1977a; Sankhyan, 1985; Kappelman *et al.*, 1991). The genus is known from the Siwalik Hills of Pakistan and India (Pilbeam *et al.*, 1977b; Kelley, 1988; S. Ward, 1997). The specific diversity of *Sivapithecus* has always been contentious; fluctuation between different taxonomies has led, in the past, to taxa from Europe and Africa being included in this genus. Most workers now recognise three Asian species: *S. sivalensis* (= *indicus*), *S. parvada* and *S. punjabicus* (S. Ward, 1997), though some authorities recognise *Gigantopithecus giganteus* as a species of *Sivapithecus* (Fleagle, 1999).

Sivapithecus is usually phyletically linked with *Pongo* on the basis of detailed craniofacial and dental similarities that have been interpreted as synapomorphies (Andrews and Cronin, 1982; Pilbeam, 1982; S. Ward and Kimbel, 1983; S. Ward and Pilbeam, 1983; S. Ward and Brown, 1986; Brown and S. Ward, 1988), although this close morphological similarity does not extend to the postcranial skeleton (C. Ward, 1997). Some workers argue, however, that the facial similarities shared between *Sivapithecus* and *Pongo* are symplesiomorphies (e.g., McCrossin and Benefit, 1994; Benefit and McCrossin, 1995) or homoplasies (e.g., Pilbeam, 1996), and are therefore not indicative of close phyletic affinity.

Few postcranial specimens are known for *Sivapithecus*; those that are known are largely unaccompanied by craniodental material, making specific assignment difficult (S. Ward, 1997). Specimens include GSP 12271 (partial humeral distal epiphysis), GSP 28062 (right proximal humerus) and GSP 30754 (left humeral shaft), all assigned to *S. parvada* (Rose, 1983, 1989). There is also a crushed left humerus (GSP 30730) assigned to *S. indicus*, and two other *Sivapithecus* humeri (GSP 6663, 13606) that currently have no specific attribution (Rose, 1983, 1989). There are no trunk or pectoral girdle specimens attributed to *Sivapithecus* (S. Ward, 1997).

The shape of the humeral head has been inferred from the shaft and distal end morphology (GSP 30730, 30754) by Rose (1994, 1997), who argues that the broad, flat bicipital groove indicates that the head would face posteriorly, with little torsion; a feature indicative of movement in a parasagittal plane (Rose, 1989). The humeral shaft is robust and posteriorly flattened; the proximal part is retroflexed, inclines medially and has a flat deltoid plane and a strong deltopectoral crest (Pilbeam *et al.*, 1990; S. Ward, 1997). These features are also diagnostic of quadrupedal habits (Rose, 1989). C. Ward (1997) argues that if the humeral head does indeed face posteriorly then it would have articulated with ventrally facing glenoid fossae, on narrow scapulae orientated in parasagittal planes, on a mediolaterally narrow thorax (i.e., a 'monkey-like' morphology; C. Ward, 1993); based on the correlation among these morphologies in extant taxa. If accurate, this inference would suggest that the torso anatomy of *Sivapithecus* is consistent with habitual pronograde (C. Ward, 1997).

In contrast to the proximal humerus, the distal humerus (GSP 12271) of *Sivapithecus* resembles living apes (Rose, 1983, 1988a; Pilbeam *et al.*, 1990; S. Ward, 1997). The trochlea is spool-shaped, the capitulum globular and the *zona conoidea* and olecranon fossa are deep, as in extant hominoids (Rose, 1983, 1988a, 1997); this implies an extensive pronation/supination capability in the forearm, through a wide range of flexion and extension of the elbow, indicating that a premium was placed on stability in the humeroulnar joint (S. Ward, 1997). A few characters on the *Sivapithecus* distal humerus are primitive for the extant Hominoidea. The medial trochlear keel is not as protuberant as in living apes and *Oreopithecus* (Rose, 1988a, 1997). The medial epicondyle is directed posteromedially, in contrast to the medially directed entepicondyle of extant hominoids (Rose, 1997).

The mosaic of primitive features in the proximal humerus and derived features in the distal humerus presents a problem for reconstructing the locomotor behaviour and phyletic relationships of *Sivapithecus* (Pilbeam *et al.*, 1990; Madar, 1994). This combination of features may be indicative of a locomotor repertoire in which both quadrupedalism and climbing are important (Rose, 1988a, 1994, 1997), although some workers (e.g., S. Ward, 1997) argue that there is no evidence that *Sivapithecus* was significantly orthograde in its positional behaviour.

There are no *Sivapithecus* ulnae, and so the morphology of the olecranon process and trochlear notch is uncertain, although the shape of the distal humerus suggests that these traits may resemble the extant hominoid condition (S. Ward, 1997). In the wrist, we know nothing about the ulnar styloid/pisotriquetral facet complex, or the proximal and distal radioulnar joints (Rose, 1984; S. Ward, 1997). The capitate shows features compatible with use of the hand in numerous locomotor activities, though it lacks features, such as enhanced mid-carpal rotation, linked to highly suspensory habits (Rose, 1994). The hamate indicates effective weight transmission through the ulnar side of the wrist (Spoor *et al.*, 1991; Rose, 1994, 1997). In the hand, the first metacarpal is saddle-shaped, indicating the presence of a mobile thumb (Rose, 1997). The proximal phalanges are long and most similar to quadrupedal monkeys (Rose, 1994, 1997).

The paucity of trunk and forelimb specimens attributed to *Sivapithecus* means that very important functional and phylogenetic information is lacking (S. Ward, 1997; Pilbeam and Young, 2001). It is possible, however, to make inferences from the existing specimens about the functional morphology and locomotor behaviour of this taxon. The monkey-like morphology of the trunk and pectoral girdle (as inferred from the humeral shaft) suggests an adaptation to pronograde quadrupedalism (S. Ward, 1997). This contrasts with the postcranial morphology and locomotor adaptations of other late Miocene hominoids (e.g., *Dryopithecus* and *Oreopithecus*) and *Pongo* (Sarmiento, 1987; Pilbeam, 1996; Begun, 2001). The distal humeral morphology is more derived, resembling that of extant hominoids (Rose, 1988a; Pilbeam *et al.*, 1990; S. Ward, 1997). The composite morphology of *Sivapithecus* makes it likely that modern analogues do not exist, further limiting our ability to reconstruct its locomotor repertoire (Pilbeam and Young, 2001).

Oreopithecus

Oreopithecus is a fossil primate from the middle/late Miocene of Europe (Straus, 1961, 1963). The genus consists of a single species, *O. bambolii*, from several sites in Florence and Tuscany, northern Italy (Azzaroli *et al.*, 1986; Delson, 1986). *Oreopithecus* is one of the most completely known fossil primates and is especially well represented in the postcranial skeleton. Unfortunately, a

large number of these specimens are crushed, due to their provenance in coalmines, making functional interpretation difficult (Straus, 1963). Phylogenetic interpretation is no less difficult, and since its first description the systematic position of *Oreopithecus* has been a subject of controversy (Harrison, 1986a).

The original describer of *Oreopithecus*, Gervais, and some other late 19th and early 20th Century workers, regarded this taxon as being closely related to extant cercopithecoids, and this classification is still favoured by a few (e.g., Delson, 1979; Szalay and Delson, 1979; Delson and Szalay, 1985; Rosenberger and Delson, 1985; Delson, 1986). Others have preferred to include *Oreopithecus* in a distinct superfamily, the Oreopithecoidea (Von Koenigswald, 1969; Simons, 1972), or to regard it as a *forme de passage* between cercopithecoids and hominoids. Most workers, however, from Forsyth Major and G. Schwalbe at the beginning of the 20th Century to Terry Harrison and Esteban Sarmiento at the end, have considered this taxon to be a hominoid, and this arrangement is kept here (Straus, 1961, 1963; Harrison, 1986a, 1986c, 1991b; Sarmiento, 1987; Harrison and Rook, 1997).

The relationships of *Oreopithecus* to taxa within the Hominoidea have proven more difficult to ascertain, owing to a preponderance of facial autapomorphies (Szalay and Berzi, 1973) and a lack of postcranial synapomorphies (Harrison, 1986a; Harrison and Rook, 1997) with any one particular representative of the superfamily. In light of this, *Oreopithecus* is usually included in its own family, the Oreopithecidae (Harrison, 1986a, 1986c; Sarmiento, 1987; Harrison and Rook, 1997), and this placement is followed here. Some workers, however, have suggested that *Oreopithecus* is a stem hominid (Begun and Kordos, 1997; Begun, 2001), or is closely linked with *Dryopithecus* (Harrison and Rook, 1997), others argue that this taxon is a stem hominine (on the basis of pelvic, lower limb and hand morphology; Köhler and Moyà-Solà, 1997; Moyà-Solà *et al.*, 1999; Rook *et al.*, 1999).

Although the postcranial material is crushed, most of the forelimb anatomy is represented. Specimens include: a partial skeleton (IGF 11778; also known as the '1958 skeleton') with right humerus, radius, partial carpus, metacarpals and phalanges; a right proximal ulnar fragment and proximal radius (IGF 4336); a right distal humerus, ulna, and proximal radius (MNHB 51); a right

distal humerus (MNHB 84); and a crushed hand (MNHB 34) with all rays present (Sarmiento, 1987).

The trunk and vertebral morphology of *Oreopithecus* has been deduced from thoracic, pectoral girdle, (fragmentary) vertebral and pelvic remains (the IGF 11778 skeleton, and two sacral specimens, MNHB 35, 50; Sarmiento, 1987). *Oreopithecus* exhibits broad scapulae with oval and dished glenoid fossae, a small angle between the glenoid and axillary border, long clavicles, an acute costal angle[36] and broad, laterally flaring iliac blades (Sarmiento, 1987; Harrison and Rook, 1997; C. Ward, 1997), all features shared with extant hominids. C. Ward (1997) argues that this indicates a mediolaterally broad torso (increasing the potential for forelimb abduction/adduction), as in living apes. The presence of five lumbar, five sacral vertebrae (Straus, 1961, 1963), and the absence of a tail, indicate a 'hominoid-type' orthograde habitual body posture (Harrison, 1986a), despite an additional vertebral segment compared to hominid anatomy (C. Ward, 1993). Other vertebral features (e.g., position of the transverse processes) also support the 'extant large hominoid-like' diagnosis (Sarmiento, 1987). These trunk and shoulder features are structurally associated in anthropoids with a more cranially (superolaterally) directed glenoid fossa, and medial torsion of the humeral head (Larson, 1988; Rose, 1989; Gebo, 1996). All these traits indicate that this taxon had considerable shoulder mobility and could abduct the forelimbs widely (Sarmiento, 1987). This suite of features is functionally consistent with a locomotor repertoire that involved climbing wide vertical supports (e.g., tree trunks) and with forelimb-dominated below-branch suspension (Sarmiento, 1987; Rose, 1994).

The *Oreopithecus* proximal humerus has a large, globular/hemispherical head (Sarmiento, 1987; Rose, 1994). The lesser tuberosity is anteriorly rotated, creating a deep, narrow bicipital groove (Rose, 1997). Although the head is crushed, it seems probable, based on the morphology of the thorax and pectoral girdle, that it exhibited a high degree of medial torsion (Sarmiento, 1987; Rose, 1997). All these features are shared with extant hominoids, and suggest a considerable amount of shoulder mobility in *Oreopithecus*.

[36] The costal angle is the angle of the ribs off the spine; obtuse denotes a narrow thorax, acute denotes a broad thorax (Ankel-Simons, 2000).

In the elbow region, *Oreopithecus* exhibits numerous similarities to extant hominids. The distal humerus greatly resembles *Sivapithecus*, though the entepicondyle is more medially directed and the medial trochlear keel is more markedly protuberant (Rose, 1997), as in living apes (Rose, 1988a, 1994, 1997). The trochlea is broad relative to the capitulum, has prominent lateral and medial keels and is markedly waisted (Sarmiento, 1987). The capitulum is bulbous and is separated from the trochlea by a deep, narrow *zona conoidea* (Rose, 1994). On the ulna, the trochlear notch faces anteroproximally, with a strong ridge running down the sagittal midline, giving it a 'saddle-shaped' appearance and reflecting the humeral trochlea shape (Sarmiento, 1987); this contrasts with the anteriorly facing semilunar notch of most quadrupeds (Rose, 1994, 1997). The olecranon process is abbreviated (Sarmiento, 1987). On the radius, the proximal head is almost circular and bevelled, reflecting the shape of the capitulum and *zona conoidea* on the distal humerus.

These features are functionally associated with increased mobility (particularly extension), and stability in the elbow. The double-keeled humerus and saddle-shaped ulnar trochlear notch stabilise the humeroulnar joint against movements other than flexion/extension (Harrison, 1986a; Sarmiento, 1987). The globular capitulum and deep *zona conoidea* on the humerus, together with the bevelled radial head, stabilise the humeroradial joint against movements other than the rotation of the radial head that accompanies forearm pronation/supination (Rose, 1994, 1997).

In the wrist, there is no direct evidence of the morphology of the ulnocarpal joint, since material from this area is either missing or crushed (Sarmiento, 1987). There is, however, a distorted lunate, hamate and scaphoid that can help elucidate the anatomical relations at the ulnocarpal joint. Harrison (1986a) claims that the lunate resembles that of Asian apes and humans in being relatively broad (unlike cercopithecoids and ceboids), and not proximodistally short and thick, as in the African apes (Tuttle, 1969). The hamate is elongated, the hamulus is distally orientated, and the facet for the triquetral faces laterally. Sarmiento (1987, 1988) argues that these features indicate the long axis of the pisiform is proximodistally orientated and closely positioned to the carpus (as in hylobatids), that the articular position of the pisiform, relative to the rest of the carpus, has migrated distally and that the triquetrum and ulnar styloid process

have reduced contact. Rose (1994, 1997), however, argues that in all of these features *Oreopithecus* resembles extant hominoids (particularly extant hominids) and infers that there was probably no contact between the ulna and the carpus (ulnar deviation), which would point to considerable mobility in this region. Sarmiento (1987) suggests that, though these features do indicate a *reduction* in contact between the distal ulna and the wrist, this does not necessarily mean a *loss* of contact; the ulnar styloid process may still have been elongated and had a small contact with the triquetrum, as it does in hylobatids. Harrison (1986a) suggests that the morphology of the scaphoid is similar to extant platyrrhines and hylobatids, and indicates that *Oreopithecus* retains the primitive condition of an unfused *os centrale* in the carpus.

Compared to other orthograde apes, *Oreopithecus* has unusual hand morphology. As mentioned above, all extant apes, with the exception of *Gorilla*, have long hands relative to their body weight or in relation to humerus length (Moyà-Solà *et al.*, 1999). As we have seen in this review, fossil apes that exhibit orthograde body structures (e.g., *Dryopithecus*) also have relatively elongated hands. *Oreopithecus*, however, has short hands relative to its estimated body weight (based on the IGF 11778 skeleton; Jungers, 1987; Moyà-Solà *et al.*, 1999). Its hand length is allometrically closer to that of *Gorilla*, hominines, and pronograde monkeys (Moyà-Solà *et al.*, 1999). This implies that *Oreopithecus* did not require the larger friction surface and concomitant enhanced grip that elongated hands bestow on their user, and thus it suggests that this taxon did not engage in vertical climbing and below-branch suspension (*contra* Sarmiento, 1987). Moyà-Solà *et al.* (1999) argue that the relatively shortened hand in *Oreopithecus* is attributable to the shift from a predominantly locomotor to a more manipulative use of the hands, as in fossil hominines. They further suggest that the thumb and finger proportions of the hand indicate a precision grip capability for *Oreopithecus* (Moyà-Solà *et al.*, 1999). These workers have argued in a series of papers that the short hand and precision grip capability of this taxon, together with evidence from the pelvic girdle and hindlimb suggesting a possible bipedal locomotor pattern, indicates that *Oreopithecus* is phyletically linked with fossil hominines (Köhler and Moyà-Solà, 1997; Moyà-Solà *et al.*, 1999 ; Rook *et al.*, 1999).

Oreopithecus resembles extant hominoids in having an orthograde body structure and similar body proportions, though it lacks some of the specialisations that extant genera have developed (Harrison, 1986a, c, 1987; Sarmiento, 1987). If *Oreopithecus* shares so many postcranial features with extant hominoids, then it is reasonable to infer that it shared many functional, and therefore behavioural, adaptations as well (Rose, 1994; Pilbeam, 1996). It is probable that *Oreopithecus* engaged in below-branch suspensory locomotion with particular emphasis on the forelimbs, and also vertical climbing on large diameter supports, for a significant proportion of its locomotor repertoire (Sarmiento, 1987).

Summary

The early Miocene hominoid forelimb is distinguished from the stem catarrhine forelimb by the incipient development of humeral head torsion, medial and lateral trochlear keels, a spherical capitulum, and a deeper, narrower *zona conoidea* (Rose, 1983). *Proconsul* is intermediate between Asian apes and non-hominoids in the development of these features (Begun, 1992c). Most early Miocene forms are inferred to have been adapted to some form of quadrupedalism (Rose, 1994, 1996).

In the shoulder, elbow and wrist regions, *Kenyapithecus* and late Miocene hominoids are distinguished from *Equatorius* and early Miocene hominoids by an increased potential for joint movements (circumduction of the forelimb over the head, full extension and hyperextension in the elbow, greater range of pronation/supination in the forearm; Rose, 1994), stability at the extremes of joint position (double-keeled humeroulnar joint, deep *zona conoidea*), and a broader axis of limb movements (rounded shafts that respond to stresses in non-parasagittal planes), as in extant hominoids (Begun, 1992c). This pattern of forelimb morphology, which implies the use of habitually suspended locomotor behaviour, is not evident in any early Miocene form, although this forelimb morphology has been implied for *Morotopithecus*, from the scapula (MacLatchy *et al.*, 2000). *Equatorius* and *Kenyapithecus* are intermediate between non-hominoids and Asian apes in the development of many distal humeral features.

The functional significance of most of these features is equivocal. Most workers argue that the features are implicated in climbing and, particularly,

suspensory capabilities (e.g., Morbeck, 1983; Begun, 1992c), but some workers (e.g., Rose, 1994) maintain that these features also provide stable load bearing during quadrupedalism. The latter argument appears to be strengthened by the fact that humeral head torsion and the development of the medial and lateral trochlear keels achieve their greatest expression in the predominantly terrestrial African apes (Gebo, 1996), implying that this morphology may be functionally associated with maintaining parasagittal movement capabilities in the forelimb and resisting torques generated through pronation of the forearm during knuckle-walking (Larson, 1988; Rose, 1988a).

CHAPTER FOUR

CHARACTER ANALYSIS OF NEONTOLOGICAL ANTHROPOID TRUNK AND FORELIMB MORPHOLOGY

Introduction

The analysis of extant taxa is a necessary prelude to an analysis of fossil forms because it is important to ascertain whether the characters examined can be relied upon to sort extant taxa into known phyletic groups (Rae, 1993). Character analysis of fossil taxa can only proceed from the basis of a reliable extant phylogeny (Wiley *et al.*, 1991).

It was noted earlier that homoplasy can manifest itself in one of three different forms: convergence, parallelism or reversal (Wake, 1991, 1996; Cartmill, 1994; Moore and Willmer, 1997). In an effort to distinguish between parallelism and convergence, the former is defined here as homoplasy in two sister groups, and the latter as all other homoplasy (after Eldredge and Cracraft, 1980). Under this definition, parallelism becomes impossible to detect in an extant-only analysis because the autapomorphies that develop independently in sister taxa that exhibit parallelism are always interpreted, on the grounds of parsimony, to be synapomorphies (Lockwood and Fleagle, 1999). In this analysis of extant taxa, therefore, the diagnosis of homoplasy is limited to the detection of convergence and reversal.

Materials

Taxa

Although the author recognises that the species is the proper unit of phylogenetic analysis (Hennig, 1965, 1966) and that variation may occur even within species, this study focuses on generic differences. Aside from the practical problems of obtaining an adequate sample for analysis at the specific level, the

genus has long been regarded by many workers (e.g., Simpson, 1945, 1961) as the taxonomic unit that best reflects the range of morphological characteristics common to a group. Analysis at the generic level therefore highlights large-scale similarities and differences between taxa (Sarmiento, 1987).

The ingroup consists of four extant genera from the families Hominidae (*Pan*, *Gorilla* and *Pongo*) and Hylobatidae (*Hylobates*), within Hominoidea. Two outgroups are used, comprising six extant genera, from the subfamilies Cercopithecinae (*Cercopithecus*) and Colobinae (*Colobus*), within Cercopithecoidea and from the families Atelidae (*Alouatta*, *Ateles*, *Lagothrix*) and Cebidae (*Saimiri*), within Ceboidea.

A total of one hundred and eighty two osteological specimens of extant primates were examined for the present study, representing ten genera (Table 2). This material came from the collections of the American Museum of Natural History (AMNH), New York, and the National Museum of Natural History (NMNH), at the Smithsonian Institute, Washington D.C. All specimens were adult, wildshot, with no apparent deformities. The extant samples included, where possible, approximately equal numbers of male and female individuals, though the data are always combined.

Table 2: Osteological Specimens from the AMNH and NMNH.

Taxa	Male	Female	Indeterminate	Total
Pan troglodytes	9	7	5	21
Gorilla gorilla	6	4	7	17
Pongo pygmaeus	4	6	7	17
*Hylobates**	10	10	4	24
Chlorocebus aethiops	9	5	0	14
*Colobus**	9	6	1	16
Saimiri sciureus	6	6	0	12
*Alouatta**	11	7	5	23
Lagothrix lagothrichca	7	8	2	17
*Ateles**	8	12	1	21

*For *Alouatta*, *Ateles*, *Colobus* and *Hylobates*, the samples were made up of specimens from several species of each genus. Samples for other genera were made up from a single species.

Characters

Nine metric characters were chosen for this study. Characteristics that have been interpreted as synapomorphic for extant hominoids and have been implicated in forelimb-dominated arboreal activities were chosen specifically to test their hypothesized shared derived status and their functional significance. Traits were taken from a variety of areas on the thorax and forelimb to avoid the inclusion of several traits in one 'functional complex', as this might confound the analysis[37].

Measurements for metric traits were taken to the nearest 0.01 mm with Mitutoyo Absolute Digimatic digital calipers. All measurements are given in millimeters. Angles were recorded using a protractor to the nearest 0.5 degree. A total of seventeen linear measurements and two angles were taken on the postcranial specimens. Raw measurements for metric traits were converted into 10 indices to control for allometric size differences between taxa. Characters, measurements and indices were taken from Larson (1998) and references therein. Some measurements and indices were modified.

1: Manubrium Breadth

Index 1: 100 × (manubrium breadth/manubrium length).

This index was taken from Schultz (1930). The length of the manubrium was measured from the most superior edges of the clavicular notches to the most inferior margin, where the manubrium articulates with the corpus sterni. The breadth of the manubrium was measured between the most lateral projections of the costal notches (Figure 1).

Extant hominoids have previously been characterised as possessing relatively broad manubria compared with other anthropoids (Erikson, 1963, Goodman, 1963; Napier and Napier, 1967). This contrasts with the craniocaudally

[37] If characters chosen for analysis are all from one anatomical region they may form a 'functional complex' (i.e., all the characters may be linked and so might change states in unison; C. Ward *et al.*, 1997). It is less likely that complete convergence, or parallelism, will be found across all characters if traits are sampled from different anatomical areas. Using traits from only one region, therefore, may bias the analysis, since it increases the probability of getting a result that indicates homoplasy (C. Ward *et al.*, 1997).

elongated and mediolaterally narrow manubria of most non-hominoid anthropoids (Ankel-Simons, 2000). The shared possession of a broad manubrium by living apes has been interpreted as a synapomorphy (Goodman, 1963; Tuttle, 1974; Ciochon, 1983; Andrews, 1985; Martin, 1986; Harrison, 1987).

Most workers (e.g., Goodman, 1963; Cartmill and Milton, 1977; Sarmiento, 1987; Gebo, 1996) have related the need for wide manubria in hominoids to the functional requirements of forelimb-dominated arboreal locomotion; the manubrium, together with the thorax as a whole, widens mediolaterally, reflecting a need for increased shoulder mobility, as the glenoid sockets are moved further apart increasing the arm span and their range of circumduction. It has been suggested that some of the New World atelin monkeys (in particular *Ateles*) have converged on the hominoid condition for this trait as a result of engaging in (superficially) similar locomotor modes (i.e., forelimb suspension; Gebo, 1996).

2: Glenoid Fossa Angle

Angle 1: Angle of glenoid fossa relative to scapular vertebral (axillary) border.

This angle was taken from Oxnard (1968). The glenoid fossa angle was measured as the angle between the glenoid cavity (taken as a linear projection between the supraglenoid tubercle and the infraglenoid tubercle) and the lateral (axillary) border (taken as a linear projection between the infraglenoid tubercle and the inferior margin of the infraspinous fossa; Figure 2).

The glenoid fossa has been described as being cranially directed in non-human hominoids compared to the more ventrally and laterally orientated fossae of most other anthropoids (Ashton and Oxnard, 1964a; Larson, 1988). The cranial orientation of the glenoid fossa in living non-human apes has been interpreted as diagnostic for this group (Le Gros Clark, 1959; Ciochon, 1983; Martin, 1986; Harrsion, 1987). Humans are an exception to the other apes in having a laterally facing glenoid fossa (Ashton and Oxnard, 1964a). The angle of the glenoid fossa provides an indication of the orientation of the glenoid cavity relative to the scapula as a whole. A small angle denotes a more cranially directed fossa; a larger angle signifies a more laterally or ventrally (depending on whether the scapula is

positioned dorsally, as in hominoids, or laterally, as in most other anthropoids) orientated fossa (Ashton and Oxnard, 1964a).

3: Humeral Head Size

Index 2: (Humeral head ML diameter x humeral head PD diameter)/geometric mean of all variables.

This index was taken from Larson (1995). The confounding effect of differences in body size between taxa was minimised by dividing each value by the geometric mean of all values for each specimen (after Mosimann and James, 1979; Jungers *et al.*, 1995). The mediolateral (ML) diameter of the humeral head was measured from the most medial projection of the articular surface of the head to the most lateral margin of the head (excluding the greater tubercle). The proximodistal (PD) diameter of the head was measured from the most proximal aspect of the articular surface (excluding the greater tubercle) to the most distal aspect where the head joins the surgical neck. The mediolateral width of the humeral distal articular surface was measured from the medial aspect of the trochlea, to the lateral margin of the capitulum (Figure 3).

Extant hominoids have been described as possessing a relatively large humeral head compared with other anthropoid taxa (Le Gros Clark, 1959; Groves, 1972; Corruccini and Ciochon, 1976; Larson, 1988; Rose, 1989; Andrews, 1992). The increased relative size of the humeral head in living apes has been interpreted as a synapomorphy (Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). The larger relative size of the hominoid humeral head may be a morphological adaptation designed to cope with the increased stresses and torques that accompany forelimb-dominated arboreal (or terrestrial, in the case of knuckle-walking) locomotion (Harrison, 1987; Rose, 1989).

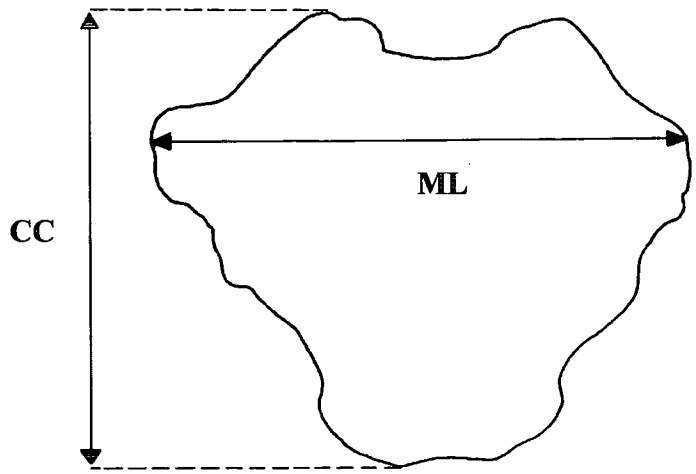

Figure 1: Measurements for Relative Manubrium Breadth.

Anterior view of a *Homo sapiens* manubrium, indicating mediolateral (ML) breadth relative to craniocaudal (CC) length (after White and Folkens, 2000).

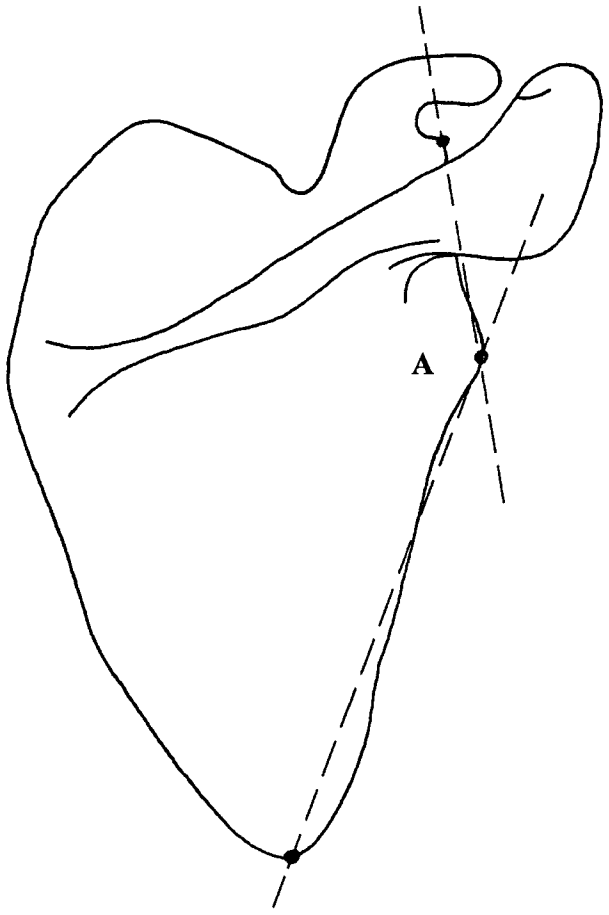

Figure 2: Measurements for Glenoid Fossa Angle.

Dorsal view of a *Homo sapiens* right scapula, showing (A) the angle of the glenoid fossa relative to the vertebral (axillary) border (after Oxnard 1963).

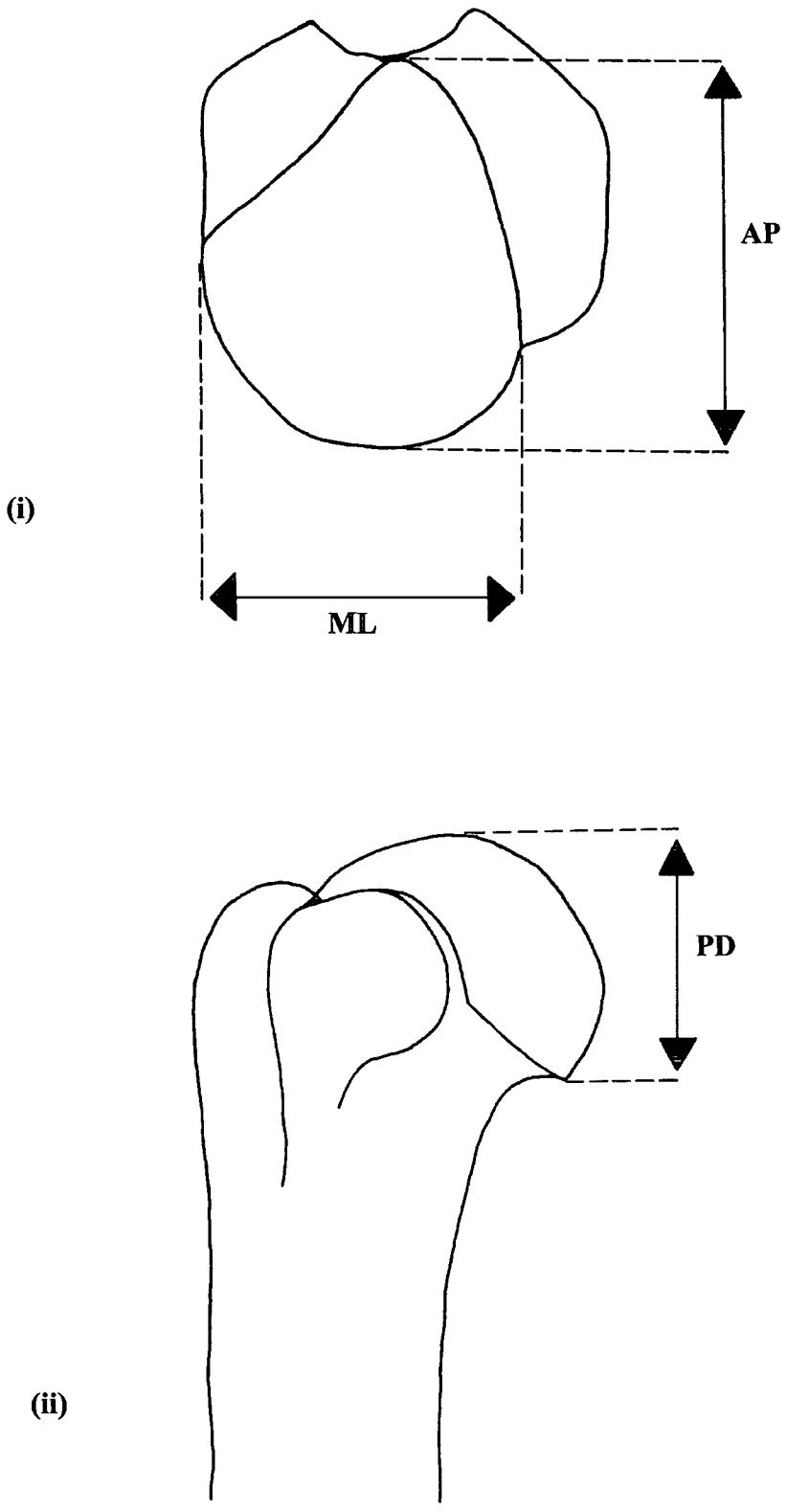

Figure 3: Measurements for Humeral Head Size and Shape.

Right humeral head of *Colobus guereza* in (i) superior view, showing mediolateral (ML) width and anteroposterior (AP) length, and (ii) medial view, showing proximodistal (PD) depth (after Rose, 1989).

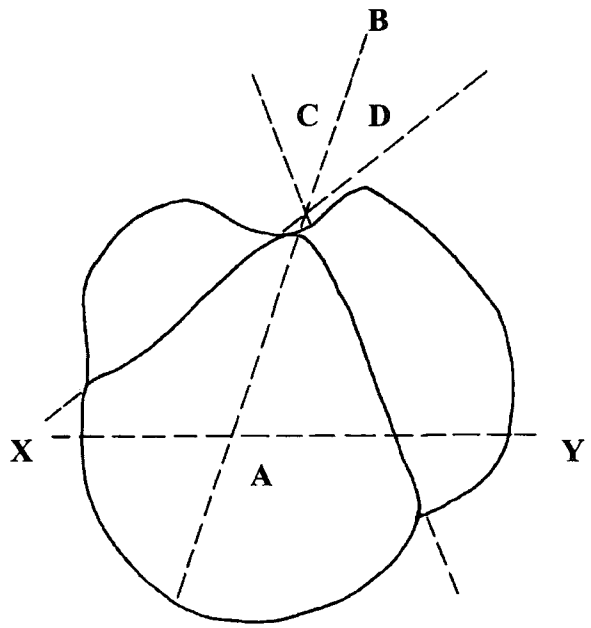

Figure 4: Measurements for Humeral Head Torsion Angle.

Right humeral head of *Colobus guereza* in superior view, showing (A) the angle of the humeral head relative to the axis of the distal articular surface (X-Y). Line B is the bisector of the intertuberosity angle (the sum of angles C and D; after Rose, 1989).

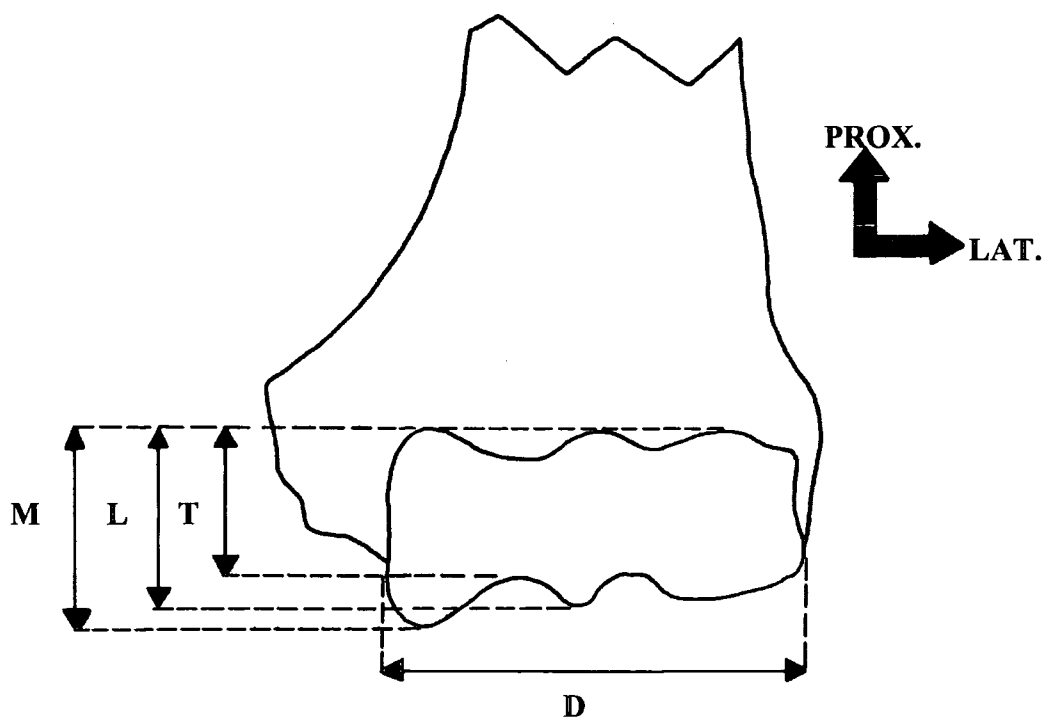

Figure 5: Measurements for Medial and Lateral Trochlear Keel Development.

Anterior view of a *Pan troglodytes* left distal humerus, showing (M) medial trochlear ridge height, (L) lateral trochlear ridge height, (T) trochlear groove height and (D) distal articular surface width (used as part of a size surrogate in Index 2; after Rose, 1988a).

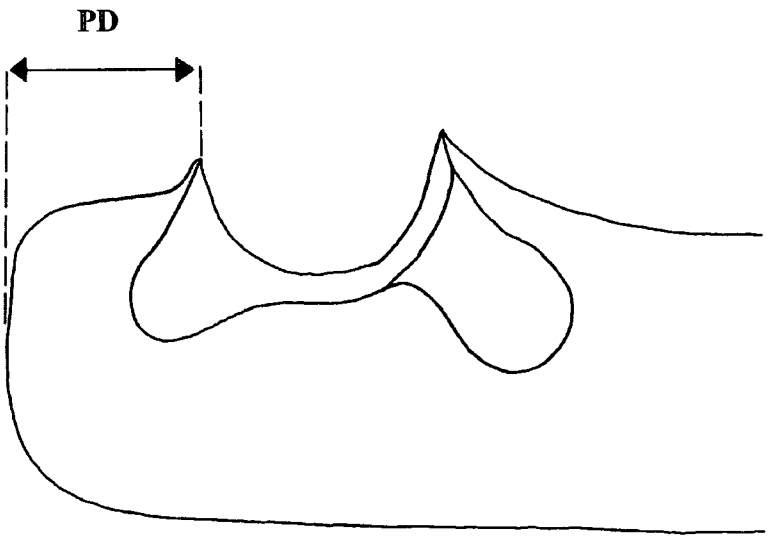

Figure 6: Measurements for Olecranon Process Length.

Lateral view of a proximal ulna, showing proximodistal (PD) length of the olecranon process (after Harrison, 1982).

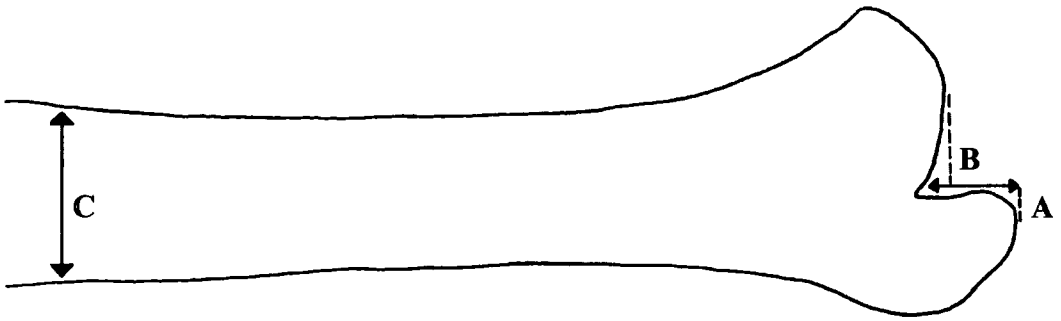

Figure 7: Measurements for Ulnar Styloid Process Length.

Lateral view of a *Pan troglodytes* distal ulna, showing (A) ulnar styloid process length, (B) ulnar head height, and (C) indicating the mid-shaft where AP and ML diameters were taken (original drawing from NMNH specimen).

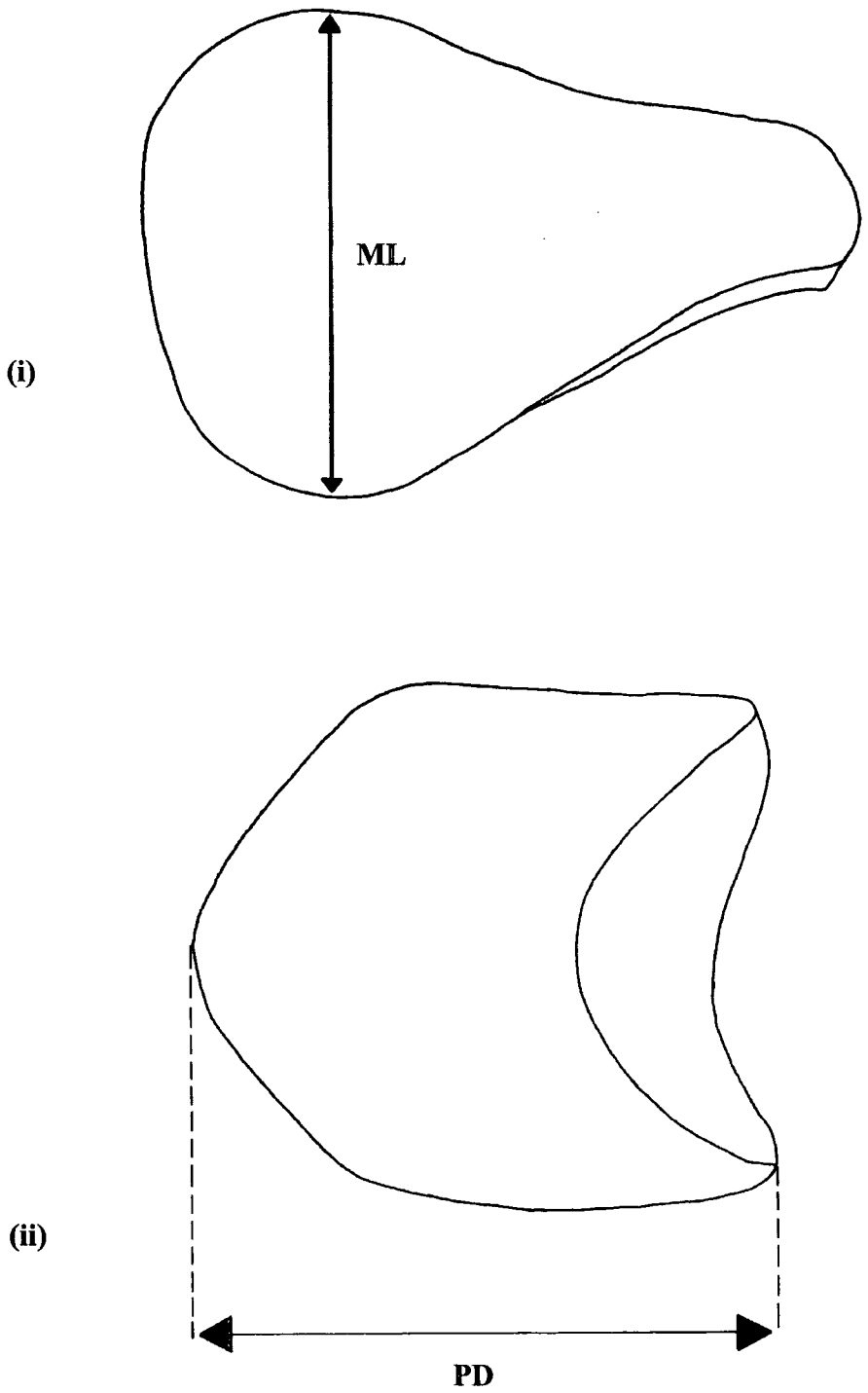

Figure 8: Measurements for Relative Lunate Breadth.

(i) Dorsal view of lunate, showing mediolateral (ML) breadth, and (ii) medial view of lunate, showing proximodistal (PD) depth (after Harrison, 1982).

4: Humeral Head Shape

Index 3: 100 × (humeral head PD diameter/humeral head ML diameter).

Index 4: 100 × (humeral head AP diameter/humeral head ML diameter).

Index 5: 100 × (humeral head AP diameter/humeral head PD diameter).

Three indices were used (from Rose, 1989) to quantify this character, due to its three dimensional nature. One or two sets of measurements cannot diagnose whether a humeral head is globular/round; three sets of measurements can detect a globular shape according to the degree to which taxon means approximate the value 100 (i.e., if a taxon displays a mean of 100 for all three indices, values for AP length, ML width and PD depth, will be identical; thus, humeral head shape will be globular). The anteroposterior (AP) diameter of the humeral head was measured from the most anterior aspect of the articular surface of the head (excluding the lesser and greater tubercles) to the most posterior aspect (Figure 3).

Living apes have been described as possessing a relatively globular (hemispherical or rounded) and symmetrical humeral head (Le Gros Clark, 1959; Goodman, 1963; Groves, 1972; Corruccini and Ciochon, 1976; Larson, 1988; Rose, 1989; Andrews, 1992; Gebo, 1996). This means that the values exhibited for anteroposterior head length, mediolateral head width and proximodistal head depth should be similar. The shared possession of a globular humeral head by extant hominoids has been interpreted as a synapomorphy of the clade (Goodman, 1963; Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). Most other anthropoids (especially quadrupeds) have been characterised as having proximodistally longer and mediolaterally narrower humeral heads (Rose, 1989). The globular-like humeral head of living apes has been functionally linked with the ability to circumduct the forelimb above the head and with an increase in the circumferal movement of the shoulder joint as a whole, as utilised in forelimb-dominated arboreal activities (Rose, 1989).

5: Humeral Head Torsion Angle

Angle 2: Angle of humeral head relative to axis of distal articular surface.

This angle was taken from Larson (1996). Humeral head torsion was measured as the orientation of the bisector of the intertuberosity angle in relation to the axis of the distal humeral articular surface (Figure 4).

The living genera of apes are said to be characterised by a medially orientated humeral head with an angle of torsion above 120° (Larson, 1988; Rose, 1994; Ankel-Simons, 2000). The medial torsion of the humeral head has been interpreted as a synapomorphy of the extant hominoid clade (Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). The medially directed hominoid humeral head contrasts with the more posteriorly orientated head of most other anthropoids, which typically exhibit a smaller angle of torsion of between 90°-110° (Larson, 1988; Gebo, 1996).

6: Humeral Medial and Lateral Trochlear Keel Development

Index 6: 100 × height trochlear groove/0.5 × (height medial + height lateral trochlear ridge).

Index 7: 100 × (height lateral trochlear ridge/height trochlear groove).

Two indices were used (from Rose, 1988a), to give an indication of the development of the medial and lateral trochlear keels relative to each other (Index 6), and to gauge the prominence of the lateral trochlear keel independently (Index 7). Three distal humeral measurements were taken, all from the most proximal aspect of the distal articular surface to various points on the distal end of this surface. Humeral lateral trochlear ridge height was measured to the most distal aspect of the lateral ridge of the trochlea. Medial trochlear ridge height was taken to the most distal aspect of the medial ridge of the trochlea. Trochlear groove height was measured to the most proximal aspect of the distal end surface of the trochlear depression (Figure 5).

Extant hominoids have been described as having prominent medial and lateral trochlear keels, separated by a deep trochlear groove (Goodman, 1963; Rose, 1988a, 1994). This broad, spool-shaped (trochleiform), double-keeled

trochlea has been interpreted, variously, as a synapomorphy of the extant Hominoidea (Goodman, 1963; Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987) and of extant hominids (Martin, 1986). Harrison (1986a, 1987), however, has argued that the development of a prominent medial trochlear keel in living apes may be the result of convergence, due to increases in body size in these lineages.

The development of the double-keeled trochlea has been interpreted as an adaptation designed to resist the torques generated when the forearm is pronated and supinated during flexion/extension (Harrison, 1982, 1986a; Morbeck, 1983; Rose, 1988a; Begun, 1992c). The prominence of the keels is functionally linked with increased stability in the humeroulnar joint (Rose, 1988a). The prominence of the lateral trochlear keel, in particular, may be linked with preventing lateral dislocation of the proximal ulna during pronation (Rose, 1988a; Aiello and Dean, 1990).

7: Ulnar Olecranon Process Length

Index 8: 100 × (olecranon length/ulnar length).

This index was taken from Feldesman (1976). Maximum length of the ulna was measured from the most proximal aspect of the olecranon process to the most distal aspect of the styloid process. Olecranon length was taken from the most proximal margin of the olecranon process to the tip of the olecranon beak (Figure 6).

Living apes have been described as having a short olecranon process (Goodman, 1963; Tuttle, 1975a; Andrews and Groves, 1976; Rose, 1988a) that extends very little beyond the level of the articular surface of the trochlear notch. This contrasts with the proximally extended, anteriorly angled process of most other anthropoids (Rose, 1988a, 1994). The abbreviated olecranon process of extant hominoids has been interpreted as a synapomorphy of the clade (Goodman, 1963; Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987; Harrison, 1987), and has been functionally associated with an increased range of flexion/extension in the elbow joint (including hyperextension; Rose, 1988a; 1994).

8: Ulnar Styloid Process Length

Index 9: 100 × ulnar styloid process length/(ulnar mid-shaft AP diameter x ulnar mid-shaft ML diameter).

This index was modified from Harrison (1982). Ulnar styloid process length was taken from the most distal aspect of the ulnar head to the most distal projection of the styloid process (except in hominids where it was taken from the most proximal aspect of the notch separating the styloid process from the ulnar head, to the distal end of the styloid process). Ulnar head height was taken for hominids only; it was measured from the most proximal aspect of the notch separating the styloid process from the ulnar head, to the most distal aspect of the ulnar head. For hominids, ulnar head height was subtracted from styloid process length to give a more accurate measurement of the projection of the styloid process. Mid-shaft anteroposterior diameter was taken from the most anterior aspect of the mid-shaft (measured as the mid-point between the proximal extremity of the olecranon process and the distal extremity of the styloid process) to the most posterior aspect. Mid-shaft mediolateral diameter was measured from the most medial aspect of the mid-shaft to the most lateral aspect (Figure 7).

Extant hominoids have been characterised by some workers (e.g., Goodman, 1963; Lewis, 1969, 1971a, b, 1972a, b; Corruccini, 1978a; Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987; Harrison, 1987) as having a synapomorphic wrist morphology, although Martin (1986), has suggested that this morphology may be shared derived for hominids only. The hominoid wrist adaptation consists of a retreat of the distal ulna from its primitive articulation with the carpus, leaving a greatly reduced styloid process, an intra-articular cartilaginous meniscus and a concomitant change in carpal morphology (Lewis, 1969, 1972b). The length of the styloid process provides an indication of the degree to which ulnocarpal contact is maintained; a longer process will achieve greater contact than a shorter one. Thus, a short ulnar styloid process indicates a loss of contact between the distal ulna and wrist (i.e., ulnar deviation; Harrison, 1982). *Hylobates* has been described as being closer in wrist morphology to monkeys than to hominids (Lewis, 1971a, 1972b), with a long, hook-like styloid process and a primitive triquetral, which exhibits a concave facet on its proximal surface for articulation with the intra-articular meniscus (Sarmiento, 1988).

9: Lunate Breadth

Index 10: 100 × (lunate ML breadth/lunate PD depth).

This index was taken from Harrison (1982). Lunate mediolateral breadth was measured from the most medial aspect of the lunate to its most lateral aspect. Proximodistal depth was taken from the most dorsal aspect of the lunate to the most ventral (palmar) aspect (Figure 8).

Extant hominoids have previously been described as possessing a relatively broad lunate (Harrison, 1982, 1986a; Sarmiento, 1988) and this trait has been interpreted as a synapomorphy of the clade (Harrison, 1987). The broad lunate of the living apes has been attributed to the expansion of the radial articular facet (Harrison, 1982, 1987). A broad lunate has been interpreted as part of a suite of carpal adaptations to suspensory behaviour (Harrison, 1982; Sarmiento, 1988).

Methods

Cladistics

The assessment of phyletic relationships in this study is based on the methodology of Hennig (1965, 1966). When Hennig first published his work on systematics in 1950 (in German) he sought to establish a more objective method[38] of ascertaining phyletic relationships and a pattern of classification that was not dictated by the subjective approach of individual taxonomists (Quicke, 1993). The former was achieved by explicitly stating the protocol used to diagnose phyletic relationships and by making a new distinction between different kinds of homologous traits. The latter was achieved by making classification reflect phylogenetic patterns as closely as possible (Schoch, 1986). The new system is referred to as phylogenetic systematics, or cladistics.

The most important insight of cladistics is that if you take *all* the traits shared by a number of organisms into account you will not necessarily get a classification that reflects actual evolutionary relationships. This is because not all

[38] The objective methodology of cladistics was in part a response to the shortcomings of other systematic schemes (Mayr, 1981). Evolutionary systematics employs a more subjective methodology than cladistics, while phenetic systematics assumes that similarity is solely correlated with common descent (instead of the product of both homology and homoplasy; Mayr, 1981).

traits possess the same amount of phyletic information (Schoch, 1986). Cladistic methodology focuses on those traits with the greatest information potential for elucidating evolutionary relationships. Before Hennig devised his method, it was known that similarity could manifest itself in two different forms. Homologous similarity is based on close phyletic affinity; analogous (or homoplastic) similarity is a response to similar functional demands (Lockwood and Fleagle, 1999). Hennig's (1966) innovation was to make a further distinction between two different types of homologous similarity.

Using Hennig's (1965, 1966) method, homologous traits are differentiated into those that are primitive (plesiomorphic) and those that are derived (apomorphic). This distinction is based on the logic that two groups of organisms may share numerous common attributes, but only those attributes that are specialised (i.e., derived) relative to other more distantly related groups demonstrate close relationship (Schoch, 1986). Primitive traits shared between different taxonomic groups (symplesiomorphies) reflect common ancestry at some distant point, and are therefore not diagnostic of close phyletic relationship (Hennig, 1965). Shared derived traits (synapomorphies) are specialisations shared by two taxonomic groups and their last common ancestor; they are diagnostic of degree of phyletic affinity (Hennig, 1966). Hennig also recognised a third state for homologous traits, autapomorphic. This kind of trait is a specialisation that is unique to one taxonomic group, and thus has no value in establishing relationships with other groups that lack this trait (Hennig, 1966). It is important, when using this methodology, to recognise that individual traits are not primitive or derived *per se*, but only become so with reference to particular groups of taxa (Schoch, 1986; Bilsborough, 1992). It is therefore necessary to define the above terms in relation to a particular taxonomic level (or a particular node on a cladogram).

One of the major tenets of cladistics is that taxonomic groups should only be composed of species that share a common ancestor. Such groups are termed 'monophyletic' and comprise an evolutionary 'clade' (Hennig, 1965, 1966). Though higher-level taxonomic groups must have evolved from speciation events involving individual species, it is rarely possible to demonstrate this. In the absence of species that can be reliably identified as common ancestors, cladistic systematists rely on the presence of derived characters to identify monophyletic

groups (Schoch, 1986). Paraphyletic and polyphyletic[39] groups are avoided in cladistics if possible, though if an assortment of taxa displays uncertain affinity these types of group are sometimes recognised to avoid placing the taxa in a group labelled *incertae sedis*[40].

The term 'sister group' or 'sister taxon' was used by Hennig (1965, 1966) to describe the closest relative to a monophyletic group (determined by one or more synapomorphies uniting the groups). Cladistic methodology allows such pairs of groups to form the basis of an entire system of classification (Mayr, 1981). This is dependent on both sister groups inheriting derived characters from their last common ancestor. The term sister group can apply to any taxonomic level, and is not restricted to groups that share the same taxonomic rank; a species or genus may be identified as the sister group of a larger taxonomic assemblage such as a superfamily or order (Quicke, 1993).

In evolutionary biology the term 'character' is often used synonymously with the terms 'feature' or 'trait' to denote any recognisable attribute of an organism. In normal parlance, the term is used to identify the minutiae of individual anatomical features; large anatomical features, such as joints and limbs, are usually referred to as being composed of a group, or suite of characters (Quicke, 1993). There are no objective criteria governing the choice of phenotypic characters (in contrast to genetic traits; Poe and Wiens, 2000), nor is there any objective measure of independence between traits (Pilbeam and Young, 2001). The atomisation of complex shapes into discrete characters, therefore, is largely a subjective pursuit (Cartmill, 1982, 1994; Wiens, 2000). Thus, the same taxa may be formally described (as discrete characters) differently, by different workers (Zelditch *et al.*, 2000; Pilbeam and Young, 2001). This can confound phylogenetic analysis, as morphological differences within a particular anatomical region can be 'weighted' differently by individual workers, thus producing different results (Pilbeam and Young, 2001). Watrous and Wheeler (1981:4) have defined a character as, "an original form plus all of its subsequent modifications". In other words, the term character is taken implicitly to mean an attribute of an organism that can take more than one form, or state. The term 'character state' is

---

[39] Paraphyletic groups consist of some, but not all of the taxa that are descended from a common ancestor. Polyphyletic groups consist of taxa that have evolved from two or more distinct ancestors (Fleagle, 1999).

[40] *Incertae sedis* is Latin for 'uncertain affinity' (Brown, 1993); it is an admission of ignorance.

used to refer to the presence or absence of a particular feature, or to a series of alternative ways in which an attribute may be expressed. As Rae (1998:223) summarises:

> a character state is an observable property of the individual organisms that belong to a particular taxon (e.g., blue), while a character is a collection of character states presumed to be homologous (e.g., colour).

The term 'morphocline' is applied to characters that do not divide into dichotomous, binary states, and thus form a transformation series (Quicke, 1993). Taxonomists are concerned only with those characters that exhibit variation among the taxa being studied.

One frequently cited limitation of cladistic methods and analysis is that they cannot determine the presence of ancestor-descendent relationships (Eldredge, 1979). This does not mean, however, that no taxon can be ancestral to another (i.e., that all taxa must be terminal taxa). Cladistics is consistent with the concept of a 'stem' species, from which other taxa diverge (Begun, 1994). A stem species is one that exhibits some, but not all, of the shared derived characters of a particular terminal taxon (Ax, 1985). Stem species are established on the basis of the distribution of synapomorphic characters in extant and fossil terminal taxa (Ax, 1985).

The results of cladistic analysis may be depicted graphically in a hierarchical branching diagram or 'cladogram', which comprises a series of nested taxa that define relationships in a relative way (Wiley, 1979; Schoch, 1986). Synapomorphies are used to recognise monophyletic clades (monophyletic groups of organisms of any taxonomic rank), arranged in a hierarchical manner. A cladogram represents an hypothesis of the history of character evolution and possible phyletic relationships between taxa (based on the distribution of synapomorphic and homoplastic character states); it does not make any statements about the theory of evolution (tempo or mode) and does not present an absolute temporal framework[41] (Quicke, 1993; Rae, 1993).

[41] Cladograms do represent the *relative* timing of cladogenetic events (Brooks and McLennon, 1991).

Parsimony

Integral to phylogenetic methodology is a principle that acts as the final arbitrator, determining, in any situation with more than one possible solution, which solution should be favoured. Parsimony[42] is a principle that stresses the need for simplicity (Eldredge, 1979). Its use in phylogenetic reconstruction amounts to that of a methodological rule: if a given problem has multiple conflicting solutions, the simplest solution (involving the smallest number of logical steps or auxiliary conditions) should always be chosen, if all other factors are equal (Gaffney, 1979).

Parsimony is not only a key tenet of methodology, but also of analysis. Parsimony analysis is always used in cladistics; once cladograms have been generated, it ascertains, out of several possible tree topologies, which requires the least number of evolutionary steps, measured as the fewest character transitions (Farris, 1983). Computer algorithms are nearly always used when performing this kind of analysis, as the number of possible trees generated escalates exponentially with increased numbers of characters and taxa.

A fundamental assumption of parsimony analysis (and its use as a methodological principle) is that character state transitions are intrinsically unlikely events (Quicke, 1993). This does not mean, however, as has sometimes been stated, that parsimony implicitly assumes that most characters evolve only once, and therefore that homoplasy is a rare phenomenon in evolution (Farris, 1983). The use of the parsimony principle is not linked to any wider claim about evolution itself being a parsimonious process. As Rae (1993:158, original emphasis) points out, "The principle simply states that descent from a common ancestor is a better explanation of similarity in the *absence* of evidence for homoplasy." In the present study, a parsimony analysis is not carried out, although the methodological principle is still used to differentiate between conflicting solutions in the reconstruction of character evolution across a given topology.

[42] The concept of parsimony is synonymous with that of Ockham's razor, a principle originally stated by William of Ockham, a Catholic philosopher of the Middle Ages, who wrote, "Plurality is not to be posited without need" (Harrison and Weiner, 1963:77).

Synapomorphy and Homoplasy

If characters are to be used in establishing monophyletic groups, or relationships between these groups, it must first be demonstrated that the characters are the product of common ancestry (Hennig, 1966). One of the major problems in reconstructing phylogenetic relationships is distinguishing characters that are synapomorphic from those that have arisen as a result of homoplasy (C. Ward *et al.*, 1997). For hard tissue traits that can undergo fossilisation, the final arbiter in determining whether characters are synapomorphic is phylogenetic analysis. The criterion for establishing the synapomorphy of a character state shared by two groups is the presence of this character state in the group's immediate common ancestor (Hennig, 1965, 1966). If the common ancestor can be recognised through its possession of other derived traits, but lacks this character state, then the character state may be assumed to be homoplastic (Lockwood and Fleagle, 1999).

Homoplasy can occur in one of three different forms: parallelism, convergence and reversal (Wake, 1991, 1996; Cartmill, 1994; Moore and Willmer, 1997). There is a general consensus that parallelism involves some component of common ancestry, while convergence does not (Lockwood and Fleagle, 1999). This observation, however, does not provide the rigorous distinction that is necessary when performing character analysis. In an effort to achieve an operational distinction between parallelism and convergence, Eldredge and Cracraft (1980) have distinguished these processes in terms of the degree of relatedness of taxa that exhibit homoplasy. They define parallelism as homoplasy in two sister groups, and convergence as all other homoplasy (Eldredge and Cracraft, 1980). This definition is successful in making the distinction objective, although it makes parallelism impossible to detect when reconstructing the character evolution of extant taxa, as parsimony would suggest that the node where the sister groups diverge should be reconstructed as having expressed the same condition as the terminal taxa; i.e., parsimony would identify the traits as synapomorphic in this case (Lockwood and Fleagle, 1999).

Often, in palaeontological research, a common ancestor may not be known, but synapomorphy and homoplasy can still be distinguished from knowledge of the immediate ancestors of either group. The distribution of synapomorphic characters in the study group (ingroup) can be compared with that

in an outgroup (more distantly related group), to determine which character state it is most parsimonious for the hypothetical common ancestor to have expressed (Watrous and Wheeler, 1981; Farris, 1982; Maddison *et al.*, 1984). Once the ancestral morphotype(s) has been reconstructed, it is possible to compare the character states expressed in terminal taxa with those expressed in this hypothetical common ancestor. If the states are identical then synapomorphy is assumed, although a further comparison with the states expressed in the outgroup is necessary to distinguish plesiomorphic from apomorphic character states (Lockwood and Fleagle, 1999). If the common ancestor expresses a more primitive condition than the terminal taxa for any character, then that character state may be presumed to have evolved independently in each terminal taxon after the split from the last common ancestor (Hennig, 1965, 1966; Lockwood and Fleagle, 1999).

It should be noted that the 'common ancestors' referred to here are simply collections of character states that are hypothesized to be present in the last common ancestor of terminal taxa, given their distributions in those taxa. These ancestral morphotypes are not named; they are hypothetical (Begun, 1994).

Polarity

Phylogenetic systematics differs from other schools of systematics in its recognition of two distinct kinds of homology. Homologous character states are polarised into two classes, ancestral and derived, and taxa are grouped using only the latter (Hennig, 1966). Three different methods can be used to determine the polarity of a character: ontogenetic, palaeontological (phylogenetic), and comparative (ingroup and outgroup; Watrous and Wheeler, 1981; Rae, 1993).

The ontogenetic method is based on the concept that specialised characters develop from more general characters (Rae, 1993). This method is not particularly useful for evolutionary studies, as the complex nature of development in phylogeny, and the fact that ontogenetic data are only sparsely available for many vertebrate groups, both limit this method's utility for determining polarity (Rae, 1993).

The palaeontological (phylogenetic) method is based on the logical premise that ancestral states must predate derived states (Cracraft, 1979; Rae,

1993). Character states that are seen early in a group's history are therefore more likely to be primitive than those that appear later. Equating early with primitive, however, is erroneous (Eldredge, 1979; Stevens, 1980). It is perfectly possible for derived traits to be acquired by some taxa early in the history of a group, while other, collateral taxa retain a primitive condition (Rae, 1993).

The comparative method is sometimes erroneously formulated as 'common equals primitive' (the so-called 'commonality principle'; Eldredge, 1979), but determining character polarity based on the frequency of occurrence of a particular character state in an ingroup can yield misleading results. The outgroup method (as used in the present study) is a special case of the comparative method, which states that, for a given character that exhibits multiple states in the ingroup, the character state found to occur in a related group (sister group) is most likely the plesiomorphic state (Watrous and Wheeler, 1981). If the character in question exhibits only two states, the alternative state found only in the ingroup is apomorphic (Watrous and Wheeler, 1981; Rae, 1993).

Cladistics is a school characterised by relatively objective methods for reconstructing phylogeny. There is, however, one potentially subjective link in this method, the choice of outgroup (Farris, 1982; Maddison *et al.*, 1984). Choosing a taxon to use as an outgroup is at the discretion of individual workers. In practice, however, there are guidelines that serve to inform the choosing process. The comparative method is, by definition, based on the comparison of character states between taxa, and so for the method to be applied at all the outgroup must share many of the characters present within the ingroup (Watrous and Wheeler, 1981). This often means that the sister group is the preferred taxon for comparison. Outgroups composed of fossil taxa are sometimes used if the relevant characters are preserved in the fossils. In some cases, fossil taxa may even prove to be a more reliable outgroup than the nearest extant taxon (e.g., the nearest outgroup to the extant catarrhines are the fossil stem catarrhine taxa *Aegyptopithecus* and *Pliopithecus*, rather than the extant platyrrhines; Rae, 1993).

Coding

In phylogenetic analysis, characters are divided into character states. States can either form part of a binary dichotomy (e.g., 0, 1; present/absent) or part of a morphocline (a series of evolutionary transformations) that can be polarised into primitive and derived conditions (Wiley *et al.*, 1991). Discrete characters, presented as binary presence/absence statements, are easily coded. The use of metric data, however, is more complex, and the use of continuously distributed data, in particular, has been criticised by some workers as inappropriate for phylogenetic analysis (e.g., Pimentel and Riggins, 1987).

Continuously distributed data, such as metric data, have been characterised by Pimentel and Riggins (1987:201) as unsuitable for cladistic analysis because "there is no justifiable basis for recognising discrete states among them." Statistical tests of significance and procedures for transforming quantitative variables into ordinal variables are rejected by these authors as tantamount to "'data massaging' to the point of inventing data" (Pimentel and Riggins, 1987:207). This suggests that discrete characters converted from continuous ones have no basis in reality (Chappill, 1989), a view rejected by some workers (e.g., Rae, 1993, 1998). Rae (1993, 1998) argues that statistical procedures, involving the calculation of means, standard deviations and tests of significance, do have a justifiable basis in deriving character states. He suggests that the means of continuous characters can, and do, change as a result of evolution (Rae, 1998). Successive populations will display these changes, which can then be analysed by statistical significance tests in a repeatable manner. Thus, continuous data can be transformed, non-arbitrarily into discrete data (Rae, 1998).

In the present study, before a character analysis could be performed, metric measurements were taken of various trunk and forelimb characters that were hypothesized to be hominoid synapomorphies and deemed to be implicated in forelimb-dominated arboreal activity. Once collected, the raw data were converted into indices to provide a rough correction for body size differences between taxa. The extant taxa were numerically coded for each index to show the distribution of character states among these primates. In order to achieve this, an analysis of variance (ANOVA) was performed (using the SPSS computer package) with two *post hoc* tests: Games - Howell and Hochberg's GT2 (Sokal and Rohlf, 1995).

Characters are numerically coded using homogeneous subset coding or HSC (Simon, 1983), a procedure used to convert continuous (metric) data into discrete codes for use in character analysis. The numerical coding of character states is accomplished by a comparison of all taxon means to one another. Means that exhibit no significant difference are grouped in a homogeneous subset (Simon, 1983). Taxa may occasionally belong to more than one subset, but only those taxa that belong to the same subsets are coded as identical (Simon, 1983; Rae, 1993). This method delivers a numerical value (code) for each index, representing the character state that a particular taxon possesses. These codes are pooled into a table to form a data matrix with which character analysis is performed.

A variety of other coding methods have been advocated for continuous characters, such as simple gap-coding, generalised gap coding, scaling by among-group variability, and scaling by within-group variability (Archie, 1985). Some of these methods (especially generalised gap-coding) have been championed for increasing resolution among character states and eliminating potential distortions (e.g., Chappill, 1989), but were not used here because they often allow taxa to be separated that are not statistically distinct, and because they are based on arbitrary critical values (Farris, 1990; Rae, 1993, 1998).

Characters that exhibit more than two states can be treated as either ordered or unordered (Slowinski, 1993). Characters designated as ordered express states that are expected to change to those immediately surrounding them; those designated unordered express states that may change randomly into any other state (Slowinski, 1993). The designation of characters as ordered is an implicit character state weighting function (Wiley *et al.*, 1991). The reconstruction of ancestral nodes within a topology and the cladogram statistics can be altered dramatically, therefore, depending on whether characters are treated as ordered or unordered. In practise, non-metric characters are frequently designated as unordered since these characters often exhibit states that have an equal likelihood of changing into any other state (though there are exceptions, e.g., the non-metric morphocline flat - blunt - sharp; Slowinski, 1993). Metric characters have a demonstrable order to states, therefore ordering is recommended (Slowinski, 1993). This is because adjacent character states are more similar to one another than to those at the extremes of the range, and are therefore more likely to change

into one another (Rae, 1997). In the present study, all character states form a straight-forward additive sequence and are therefore treated as ordered.

Computer Program

In the analyses reported in this thesis, a computer program called MacClade (version 3.04; Maddison and Maddison, 1992) was used to reconstruct the history of character evolution. MacClade is a Macintosh-based program, designed to analyse character evolution through the manipulation of computer graphics. Alpha-numeric data, relating to character states expressed by various taxa, were entered into the program in the form of a data matrix. The data matrix was used to generate a series of character trees for each index; trees were sorted based on best estimate phylogenetic relationships (after Fleagle, 1999). The graphical depiction of the trees in this program eases the direct manipulation of topologies on the screen with a variety of different tools. These tools allow a user to change the topology of a tree to test different assumptions about character evolution or different arrangements of the phyletic relationships between taxa (Maddison and Maddison, 1989). Once changes are made, the character state positions and cladogram statistics are recalculated automatically. MacClade incorporates several different statistical measures of homoplasy. One of which, the consistency index (CI), was used in the following analyses to provide a measure of the consistency, or fit of the characters examined to a given topology (Kluge and Farris, 1969). For the purposes of this study, the distribution of character states between different taxa was observed and evidence of homology/homoplasy was sought.

Results

Table 3: Data Matrix for Extant Anthropoids.

TAXA	INDICES											
	1	2	3	4	5	6	7	8	9	10	A1	A2
Alouatta	1	2	5	7	3	4	1	4	2	0	5	2
Ateles	5	3	4	3	1	6	1	2	2	0	3	2
Chlorocebus	0	1	1	4	3	2	1	3	2	0	5	0
Colobus	1	2	2	3	2	4	1	3	2	0	5	1
Gorilla	2	5	0	2	2	1	3	0	0	3	4	3
Hylobates	2	3	3	0	0	2	3	1	2	1	0	2
Lagothrix	5	2	5	6	2	3	2	3	2	0	4	2
Pan	4	4	1	1	1	0	3	0	1	4	1	3
Pongo	3	4	3	3	2	0	3	0	0	2	2	2
Saimiri	0	0	5	5	1	5	0	3	3	0	4	2

Character 1: Manubrium Breadth

Index 1:

The results (Figures 9 and 11) show that a moderately wide manubrium is synapomorphic in Hominoidea, although *Pan* and *Pongo* have subsequently independently developed wider manubria than *Hylobates* and *Gorilla*. Homoplasy, in the form of convergence, is evident between *Chlorocebus* and *Saimiri* in their possession of the narrowest manubria of the sampled taxa. Atelin monkeys are synapomorphic in exhibiting the widest manubria of the sampled taxa. *Alouatta* and *Colobus* retain the primitive condition of having a relatively narrow manubrium.

These results support the hypothesis, put forward by Goodman (1963), Tuttle (1974), Ciochon (1983), Andrews (1985), Martin (1986) and Harrison (1987), that extant hominoids exhibit mediolaterally broad manubria compared with most other (non-atelin) anthropoid taxa and that this trait is a synapomorphy of the clade.

Character 2: Glenoid Fossa Angle

Angle 1:

The results (Figures 10 and 12) show that homoplasy, in the form of character reversal and convergence is evident in this character. *Gorilla* has undergone reversal to a more primitive condition than the other apes, possessing a moderately large glenoid fossa angle (GFA) similar to that of *Lagothrix* and *Saimiri*. Hominoidea is synapomorphic, with all genera (except *Gorilla*) having a smaller GFA than other anthropoid taxa. *Hylobates*, *Pan*, and *Pongo* all exhibit slightly different conditions of GFA, from moderately small to very small. *Chlorocebus* and *Colobus* are linked by synapomorphy, and are convergent on *Alouatta*, in possessing the largest GFA of the sampled taxa. *Lagothrix* and *Saimiri* retain the primitive condition of a relatively large GFA. *Ateles* is autapomorphic in having a medium sized (compared to the other sampled taxa) GFA.

These results support the hypothesis, put forward by Le Gros Clark (1959), Ciochon (1983), Martin (1986) and Harrison (1987), that the cranial orientation of the glenoid fossa is a synapomorphy of the extant Hominoidea. *Gorilla* exhibits character reversal to the primitive state of having a laterally orientated glenoid fossa (similar to the condition found in *Lagothrix* and *Saimiri*). The other apes all possess more cranially directed glenoids, though they do not share an identical condition for this trait.

Character 3: Humeral Head Size

Index 2:

The results (Figures 13 and 15) show that homoplasy, in the form of convergence, is evident between *Hylobates* and *Ateles* in their possession of a moderately large humeral head. Hominoidea is synapomorphic. *Hylobates* is the most primitive member of the clade. The humeral head of *Hylobates* is significantly smaller than that of hominids, falling within the cluster of other anthropoid taxa. Hominidae is synapomorphic, with *Pongo* and *Pan* exhibiting large humeral heads and *Gorilla* possessing the largest humeral head of all sampled taxa. *Chlorocebus* and *Saimiri* are autapomorphic in having small and

very small humeral heads, respectively. *Alouatta*, *Lagothrix* and *Colobus* retain the primitive condition of having a moderately small humeral head.

These results ostensibly support the hypothesis, put forward by Ciochon (1983), Andrews (1985), Martin (1986), Andrews and Martin (1987) and Harrison (1987), that all extant hominoids are linked by synapomorphy in their possession of a relatively large humeral head. The distribution of character states for this trait, however, suggests that absolute, rather than relative humeral head size has been quantified here (see Chapter Six).

Character 4: Humeral Head Shape

Index 3 (PD/ML):

The results (Figures 14 and 16) show that homoplasy (convergence) is evident in this index. *Pan* is convergent on *Chlorocebus* in having a head that is very wide relative to proximodistal depth. *Gorilla* is autapomorphic with a humeral head that is the widest of the sampled taxa. *Hylobates* and *Pongo* retain a primitive condition for the Hominoidea of having a humeral head that is only slightly wider than it is deep. *Colobus* and *Ateles* are both autapomorphic, the former with a moderately wide head and the latter with a head that is only marginally wider than it is deep. *Lagothrix*, *Alouatta* and *Saimiri* all share the same condition of having a head that is approximately equally deep as it is wide, although the polarity of their shared condition is uncertain.

Index 4 (AP/ML):

The results (Figures 17 and 19) show that homoplasy, in the form of convergence, is evident in this index. *Pongo* is convergent on *Ateles*, and is either convergent on *Colobus* or retains the primitive condition of having a humeral head that is moderately wider than it is long, depending upon the reconstruction of the ancestral catarrhine, hominoid and hominid nodes. *Hylobates*, *Gorilla*, and *Pan* are autapomorphic, and all possess heads that are relatively very wide. *Chlorocebus* is autapomorphic in having a head that is slightly wider than it is long. *Lagothrix* and *Saimiri* are autapomorphic, and possess heads that are approximately equally long as they are wide. *Alouatta* is autapomorphic in having a head that is longer than it is wide.

Index 5 (AP/PD):

The results (Figures 18 and 20) show that homoplasy, in the form of convergence, is evident in this index. *Pan* is convergent on *Ateles* and *Saimiri* in having a humeral head that is marginally deeper than it is long. *Hylobates* is autapomorphic in possessing a head that is much deeper than it is long. *Chlorocebus* is convergent on *Alouatta* in having a head that is much longer than it is deep. *Pongo*, *Gorilla*, *Colobus* and *Lagothrix* retain the primitive condition of having a head that is marginally longer than it is deep.

Summary of Character 4:

These results suggest that the extant hominoid genera do not have even remotely globular (hemispherical/rounded/symmetrical) humeral heads, and therefore that this trait is not a synapomorphy of the clade (*contra* Goodman, 1963; Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987). In particular, *Hylobates* exhibits an anteroposteriorly deep, proximodistally long and mediolaterally narrow head, which is the least globular of all the sampled taxa. *Pan* has a similar morphology to *Hylobates*. Of all the extant hominoids, *Pongo* exhibits the most globular-like head, though this is still relatively deeper (PD) and longer (AP) than it is wide (ML). The results indicate that homoplasy is evident in all three ratios of this character. The taxa exhibiting homoplasy differ from index to index. Of the living apes, *Pan* shows the most convergence (two of the three indices), though only with non-hominoid taxa.

Three genera from the Ceboidea appear to possess hemispherical-like humeral heads. *Lagothrix*, (a predominantly arboreal quadrupedal walker and climber; Defler, 1999; Cant *et al.*, 2001), exhibits the most globular-like head of the sampled taxa, followed closely by *Saimiri* (a predominantly arboreal quadrupedal walker and leaper; Fleagle and Mittermeier, 1980; Fleagle *et al.*, 1981). *Alouatta* also follows this trend, though the head is shorter (AP) than in the other two platyrrhine genera. These results indicate that the presence of a hemispherical humeral head does not correlate with forelimb-dominated arboreal locomotor habits. The taxa that exhibit the greatest expression of this trait engage primarily in arboreal quadrupedal walking/running and climbing/leaping.

Index 1

Relative Manubrium Breadth

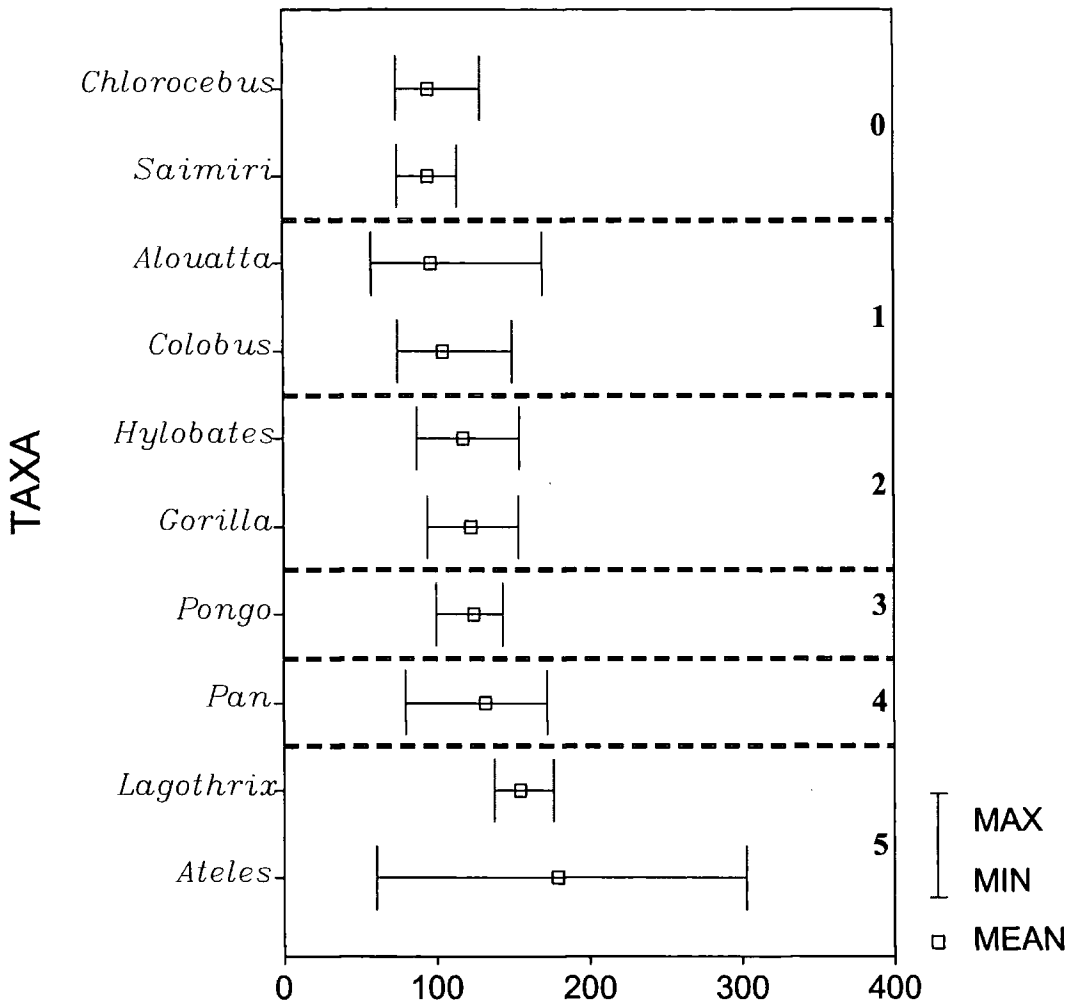

Figure 9: Univariate Chart for Relative Manubrium Breadth.

Results and coding for relative manubrium breadth (Character 1; Index 1). In this and all subsequent univariate charts, the square is the mean value and the solid horizontal line is the range of values for each taxon. The dashed horizontal lines divide groups coded as identical. Codes are given to the right. Summary data tables, giving sample sizes, arithmetic means, standard deviations and ranges are given in the Appendix.

Angle 1

Glenoid Fossa

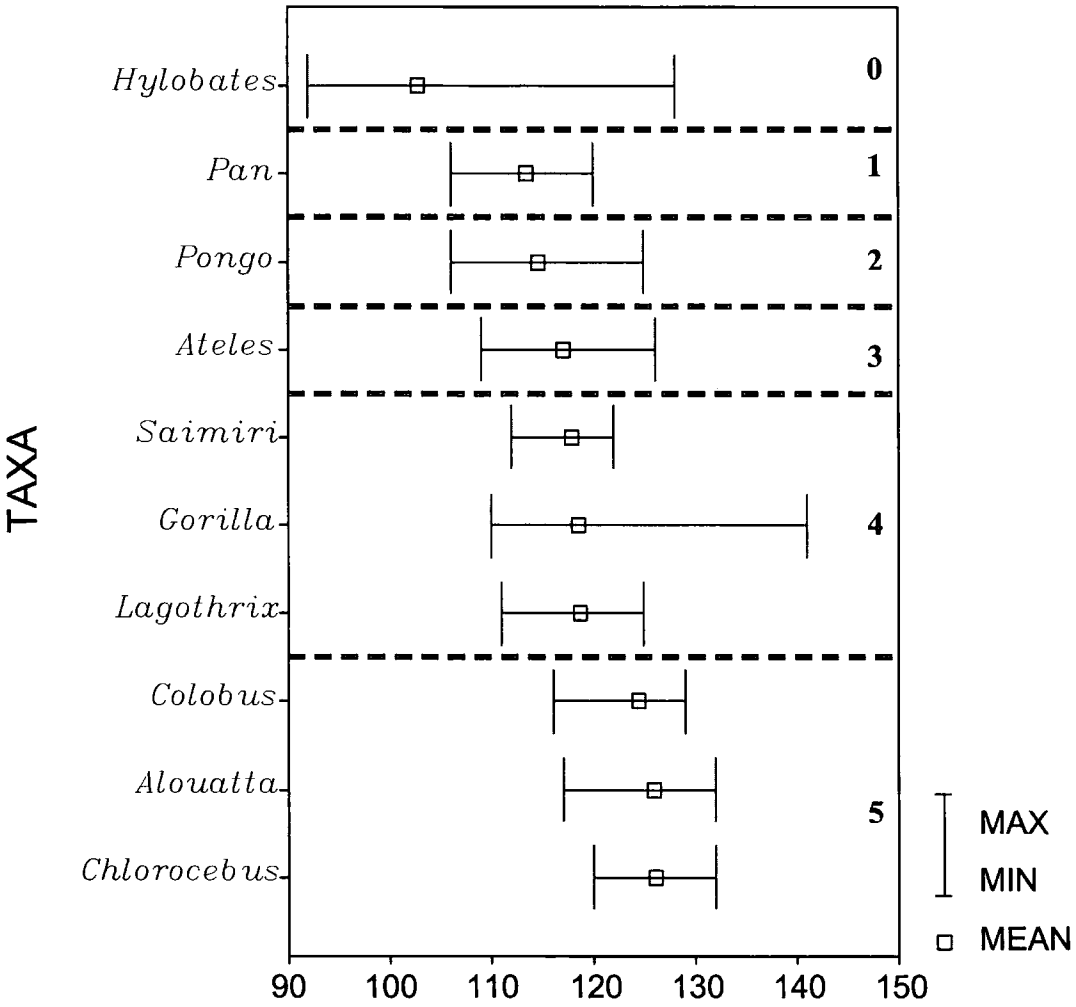

Figure 10: Univariate Chart for Glenoid Fossa Angle.

Results and coding for angle of glenoid fossa (Character 2; Angle 1).

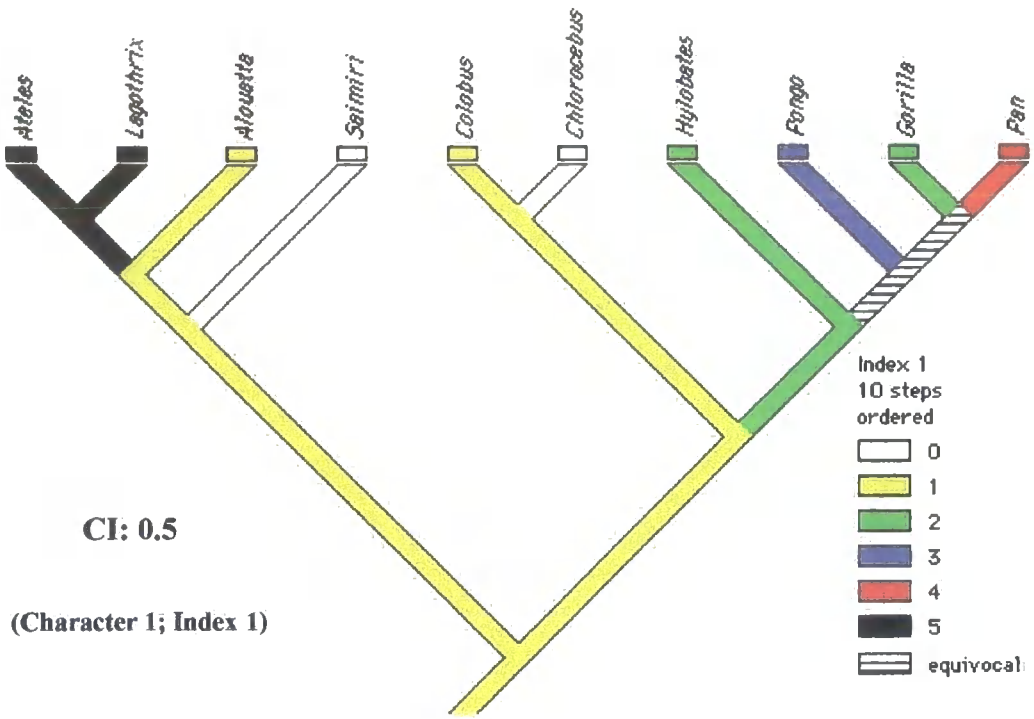

Figure 11: Relative Manbrium Breadth.

State 0 = relatively narrow / State 5 = relatively broad
States 1 and 2 = approximately square

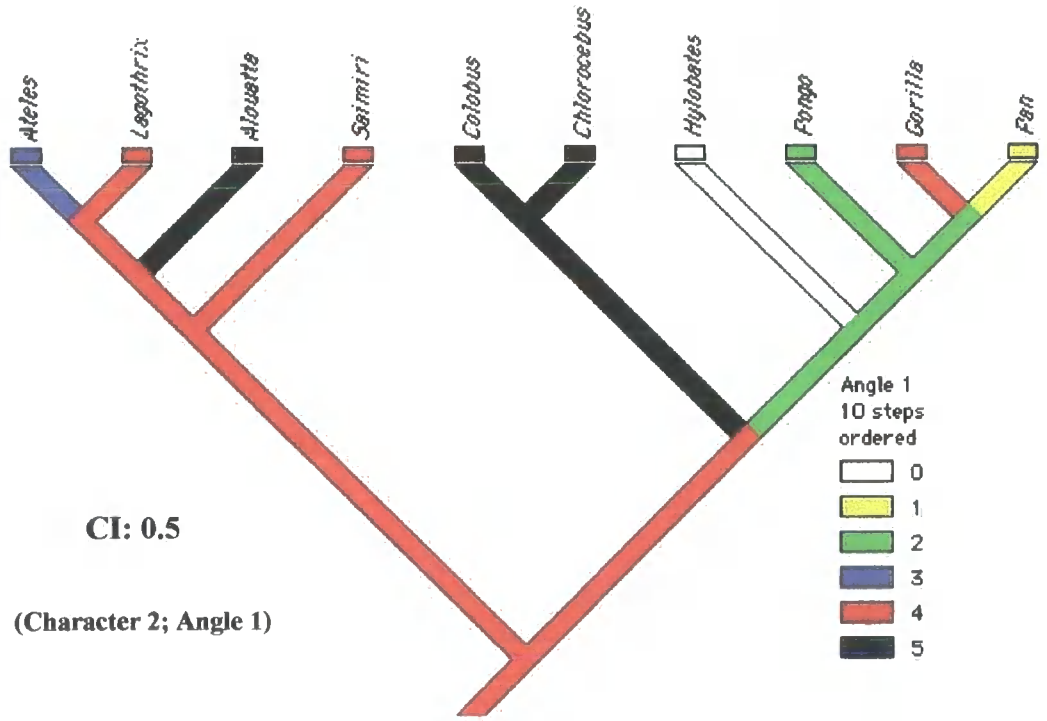

Figure 12: Glenoid Fossa Angle.

State 0 = small / State 5 = large

Index 2

Relative Humeral Head Size

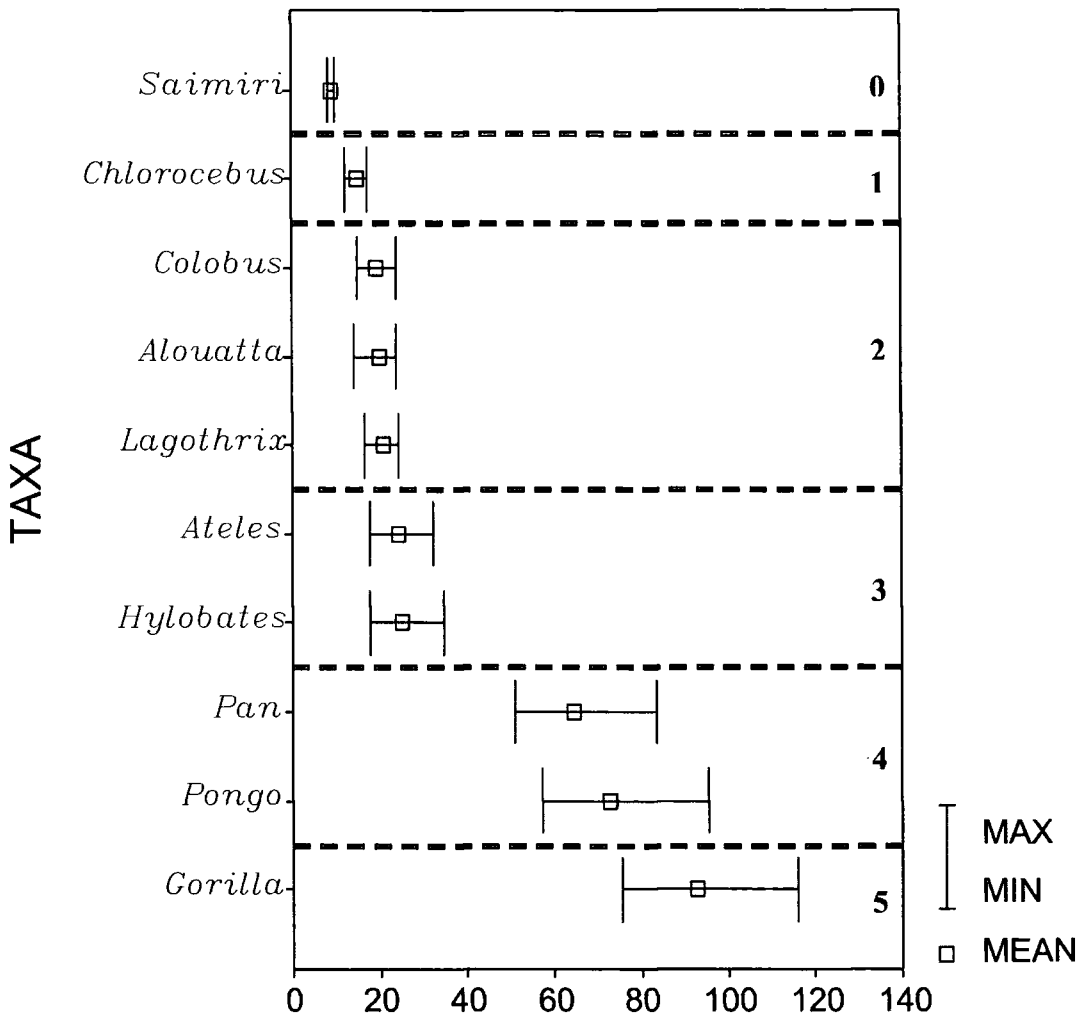

Figure 13: **Univariate Chart for Relative Humeral Head Size.**

Results and coding for relative humeral head size (Character 3; Index 2).

Index 3

Humeral Head Shape PD/ML

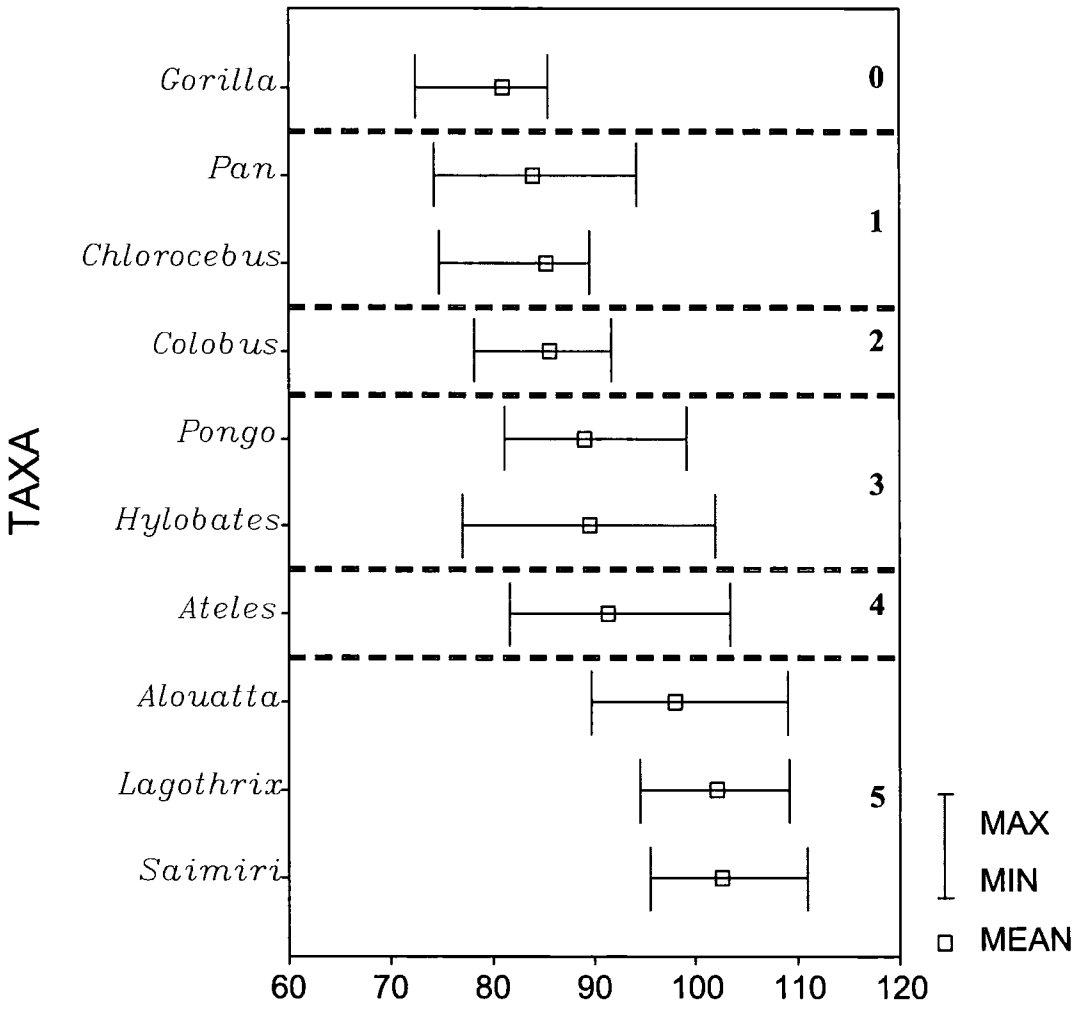

Figure 14: Univariate Chart for Humeral Head Shape PD/ML.

Results and coding for humeral head shape PD/ML (Character 4; Index 3).

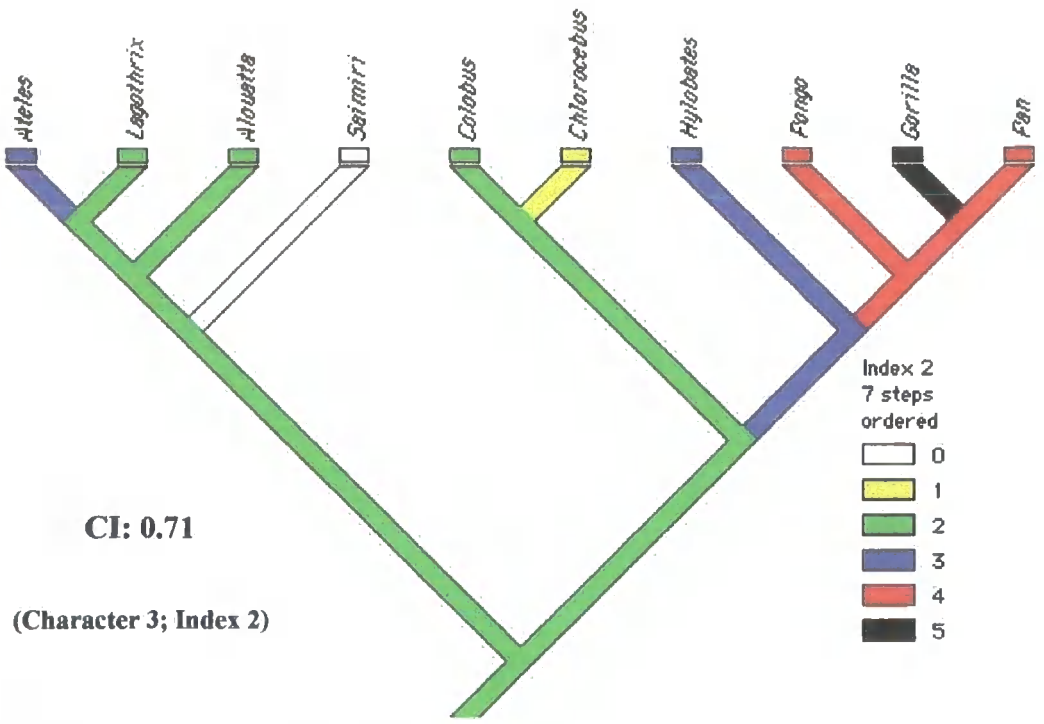

Figure 15: Relative Humeral Head Size.

State 0 = relatively small / State 5 = relatively large

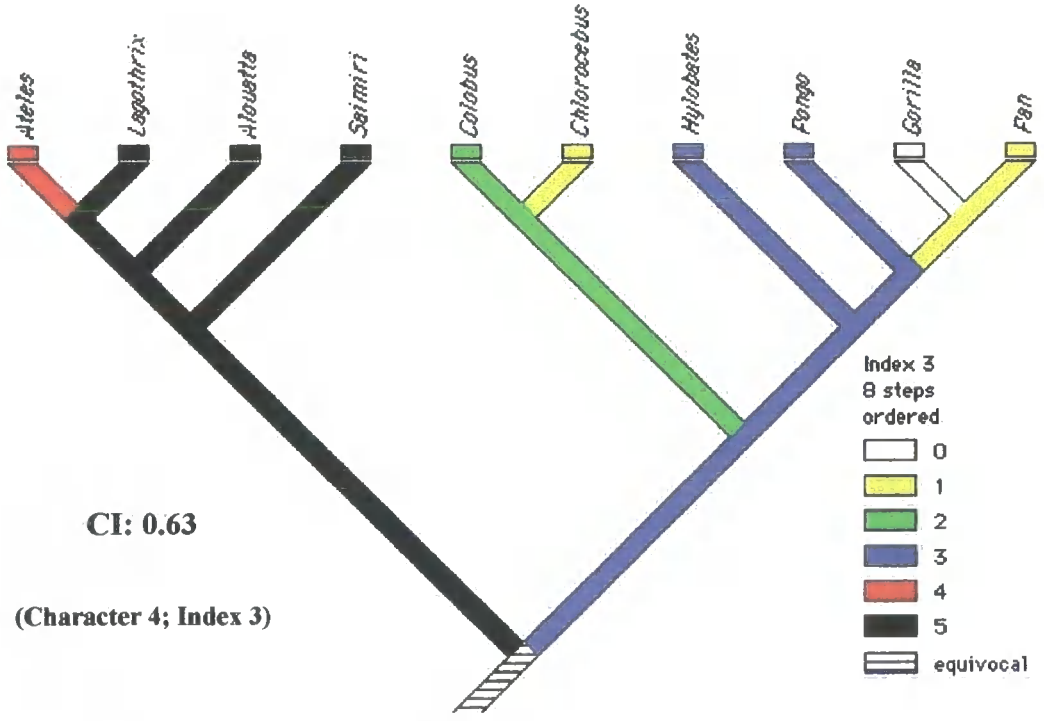

Figure 16: Humeral Head Shape PD/ML.

State 0 = wider ML than deep PD
State 5 = approximately equal values for PD depth and ML width

Index 4

Humeral Head Shape AP/ML

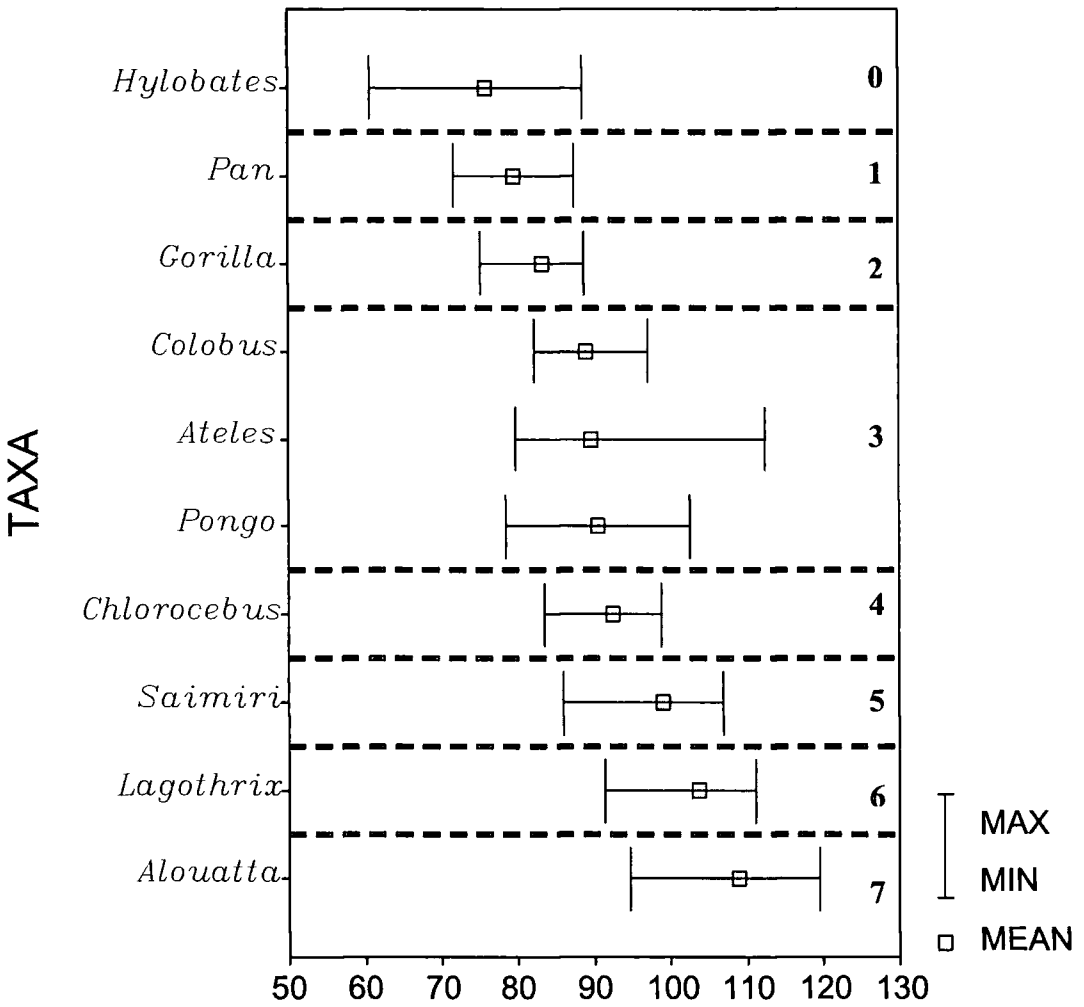

Figure 17: <u>**Univariate Chart for Humeral Head Shape AP/ML**</u>.

Results and coding for humeral head shape AP/ML (Character 4; Index 4).

Index 5

Humeral Head Shape AP/PD

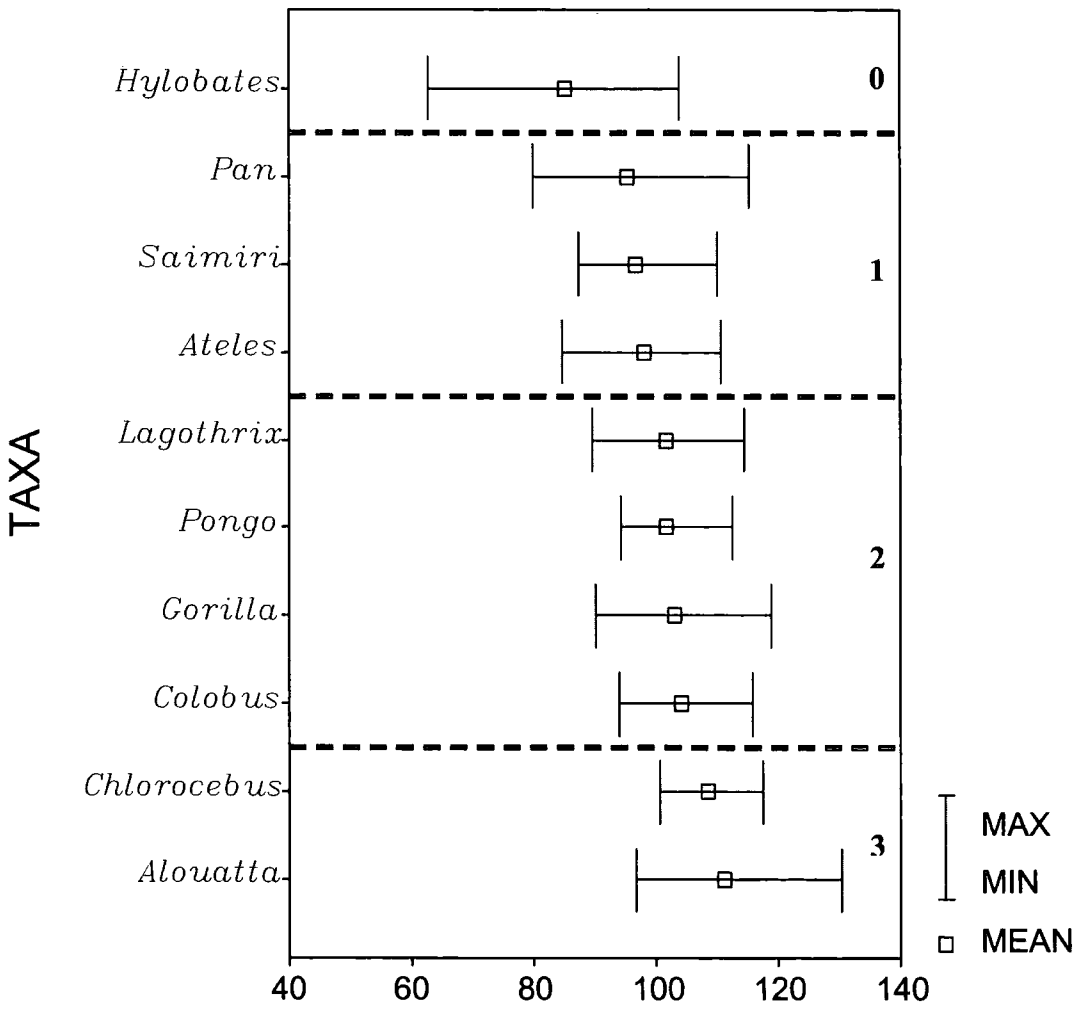

Figure 18: **Univariate Chart for Humeral Head Shape AP/PD.**

Results and coding for humeral head shape AP/PD (Character 4; Index 5).

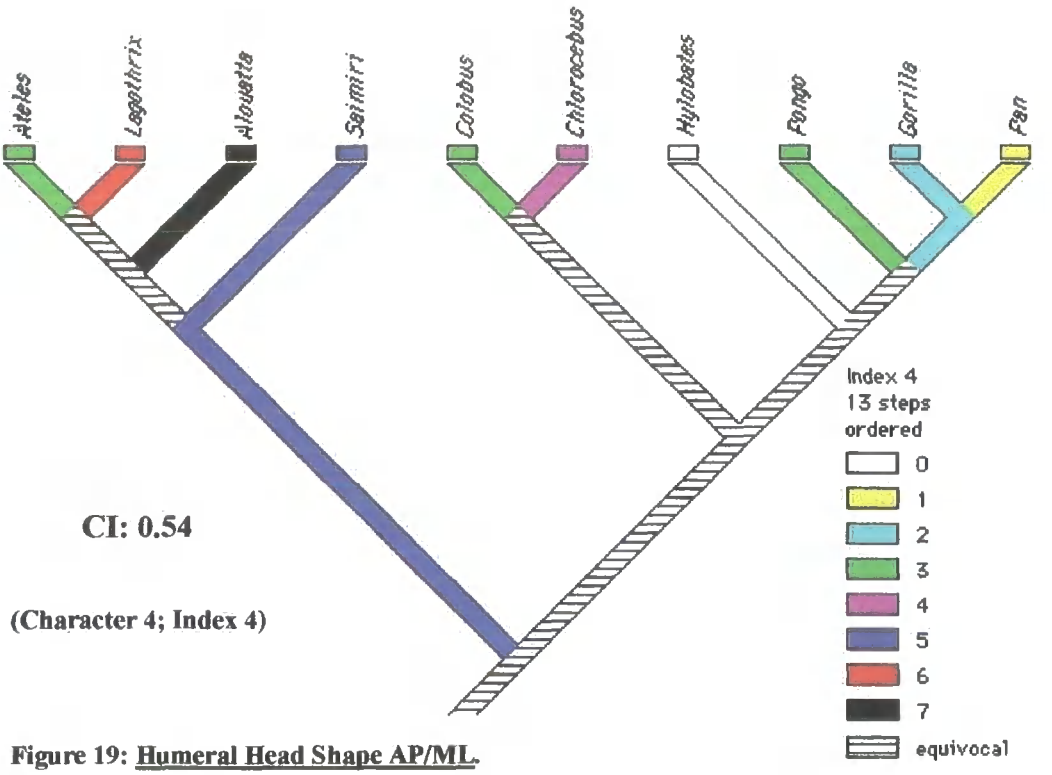

Figure 19: Humeral Head Shape AP/ML.

State 0 = wider ML than long AP
States 5 and 6 = approximately equal values for ML width and AP length
State 7 = longer AP than wide ML

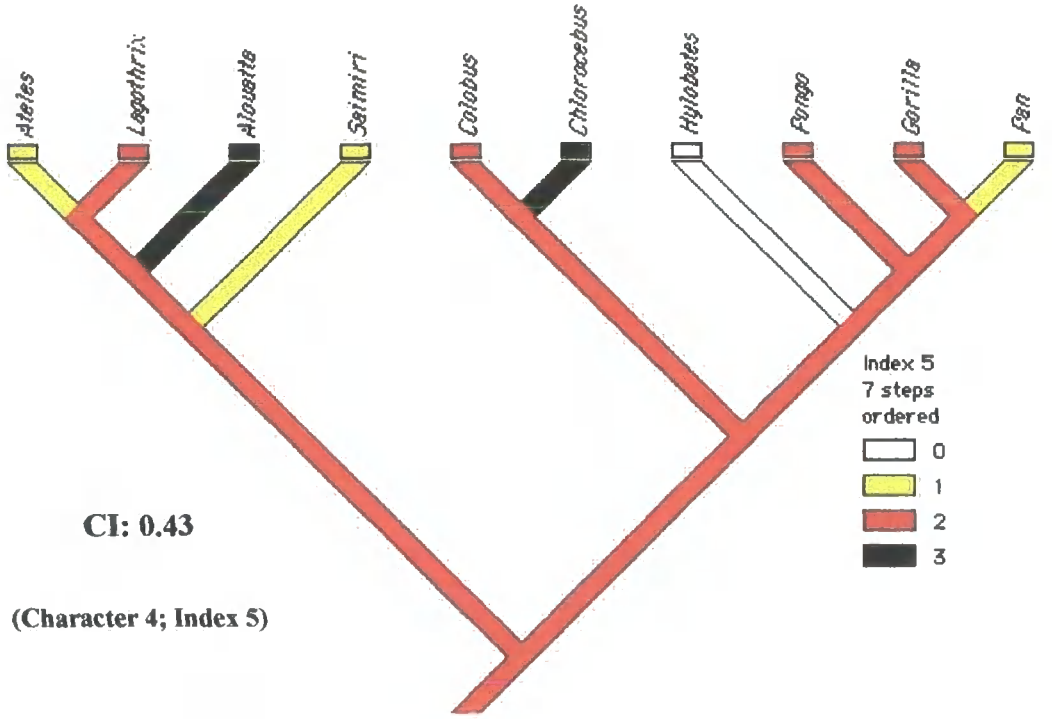

Figure 20: Humeral Head Shape AP/PD.

State 0 = deeper PD than long AP
States 1 and 2 = approximately equal values for PD depth and AP length
State 3 = longer AP than deep PD

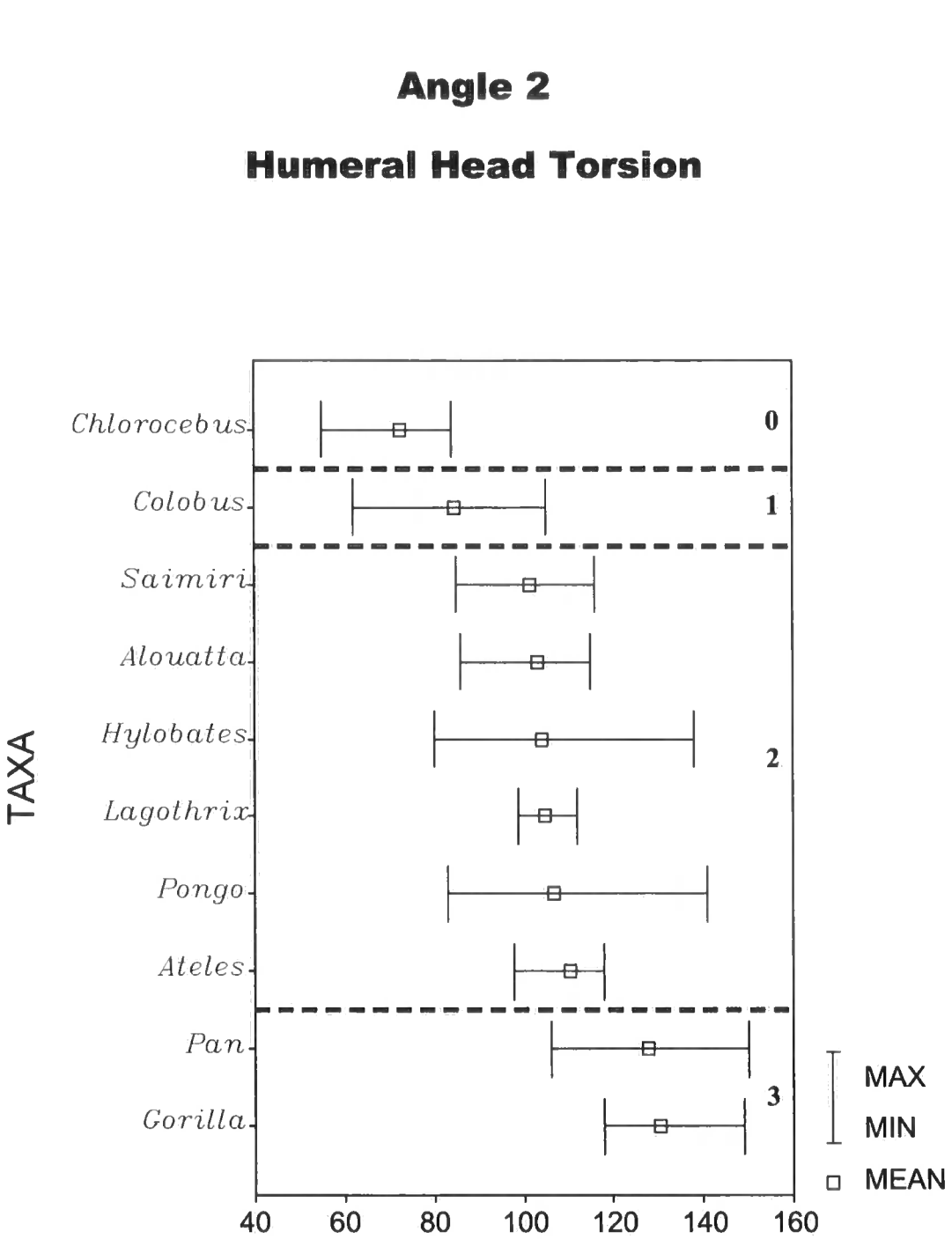

Figure 21: Univariate Chart for Humeral Head Torsion Angle.

Results and coding for humeral head torsion angle (Character 5; Angle 2).

Index 6

Medial & Lateral Trochlear Keel Development

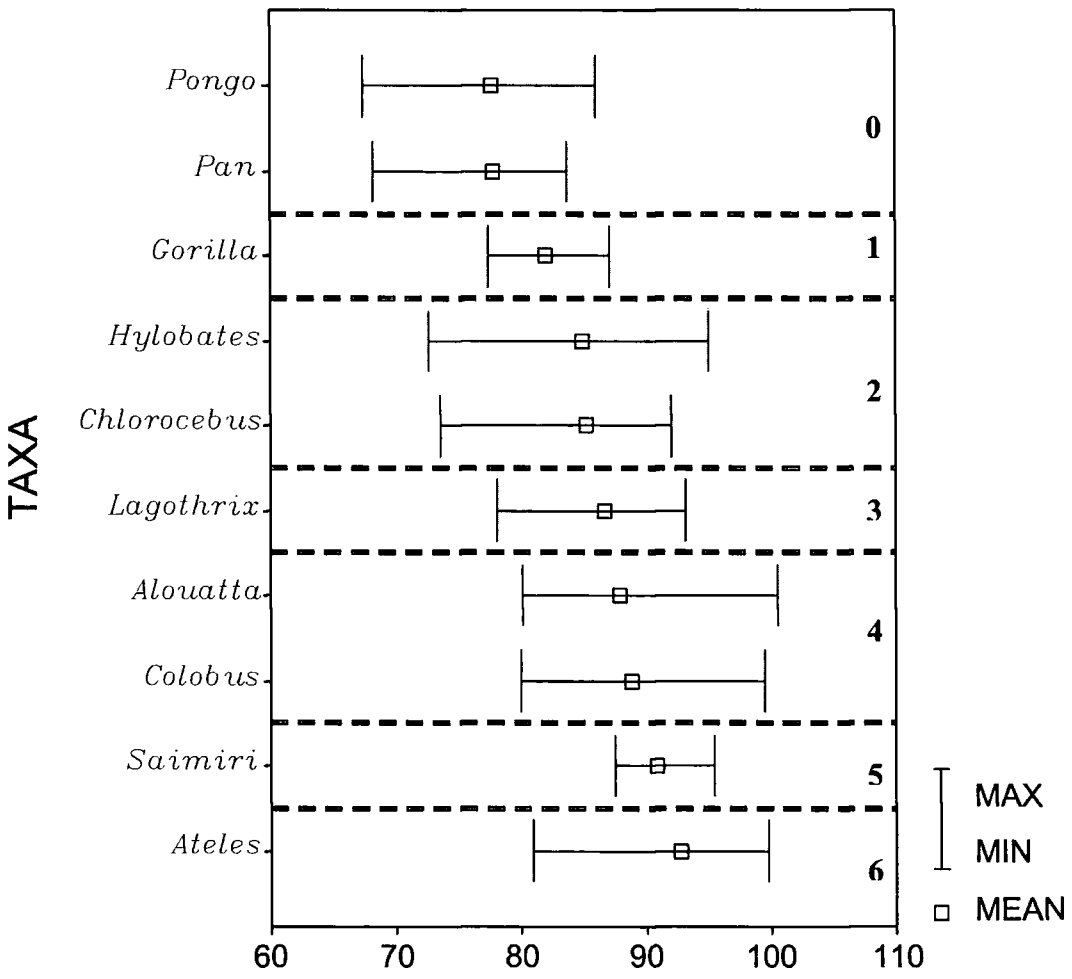

Figure 22: Univariate Chart for Medial and Lateral Trochlear Keel Development.

Results and coding for medial and lateral trochlear keel development (Character 6; Index 6).

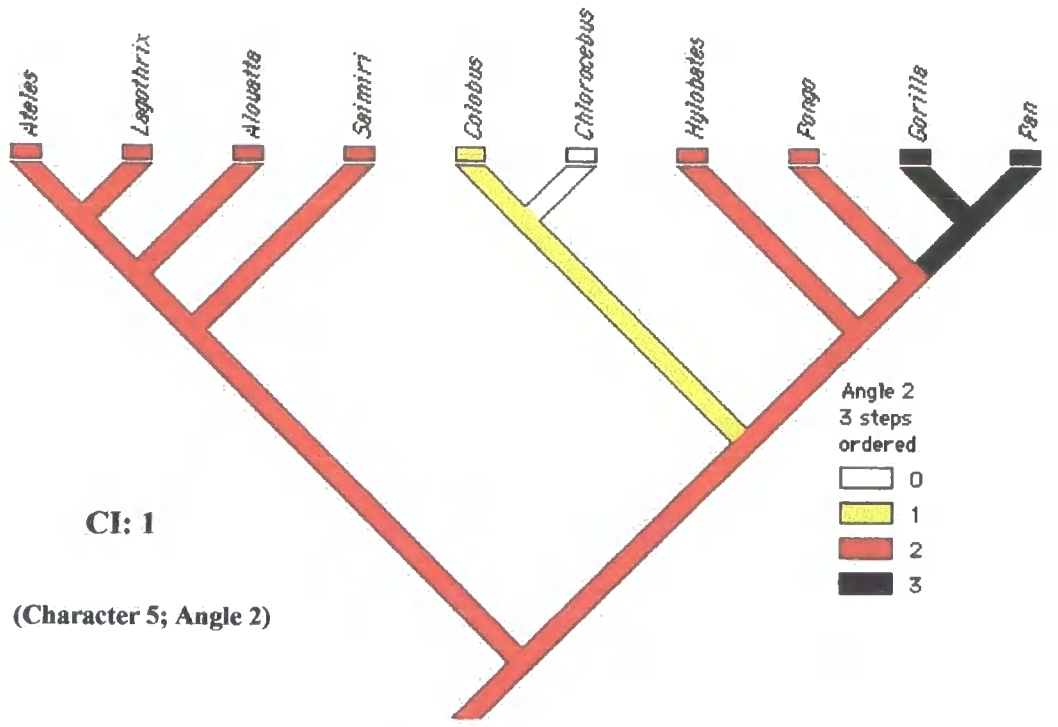

Figure 23: Humeral Head Torsion Angle.

State 0 = least torsion / State 3 = most torsion

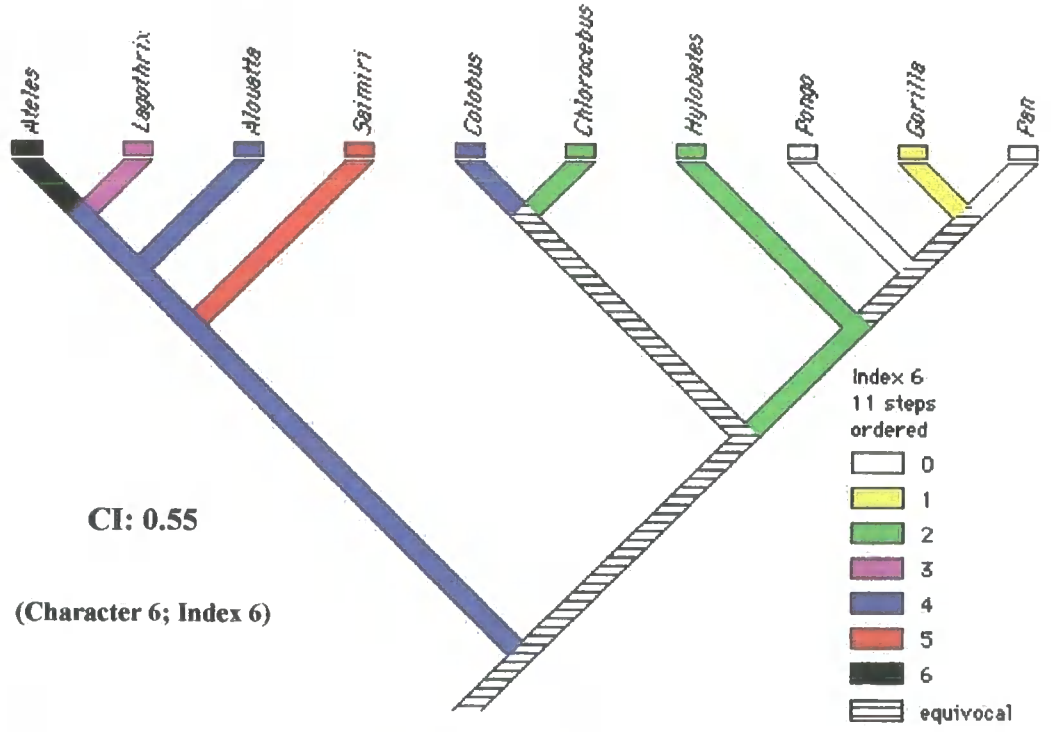

Figure 24: Medial and Lateral Trochlear Keel Development.

State 0 = very well-developed / State 6 = least developed

Index 7

Trochlear Waisting

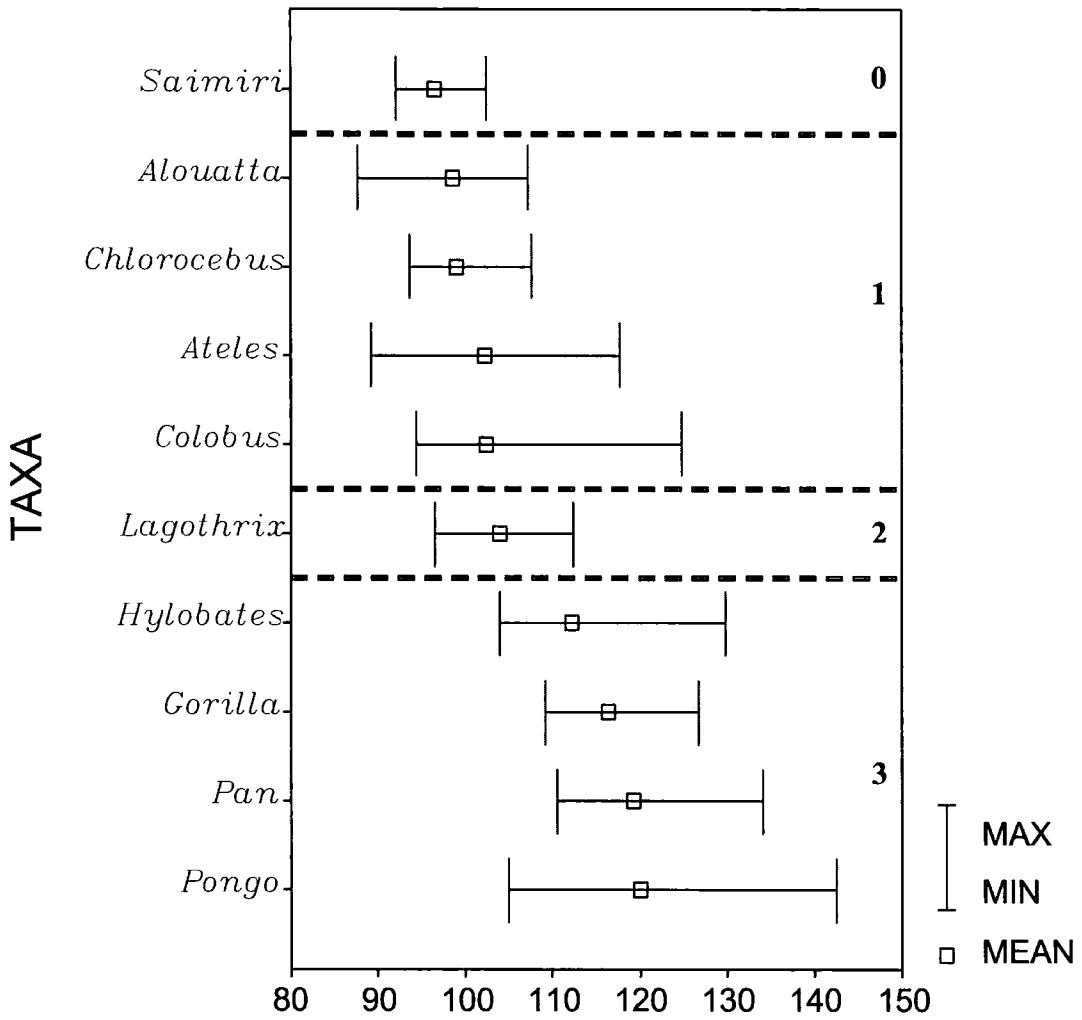

Figure 25: Univariate Chart for Trochlear Waisting.

Results and coding for trochlear waisting (Character 6; Index 7).

Index 8

Ulnar Olecranon Process Length

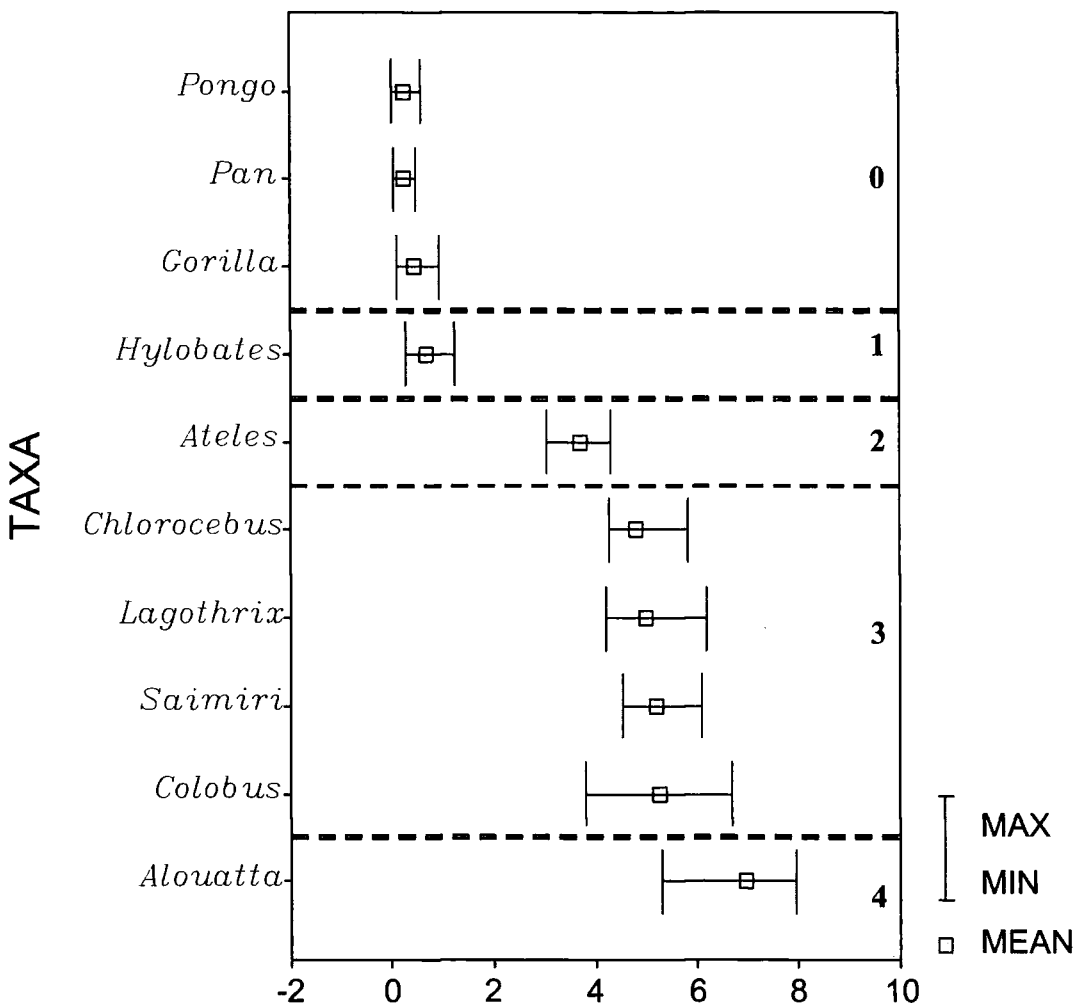

Figure 26: Univariate Chart for Ulnar Olecranon Process Length.

Results and coding for ulnar olecranon process length (Character 7; Index 8).

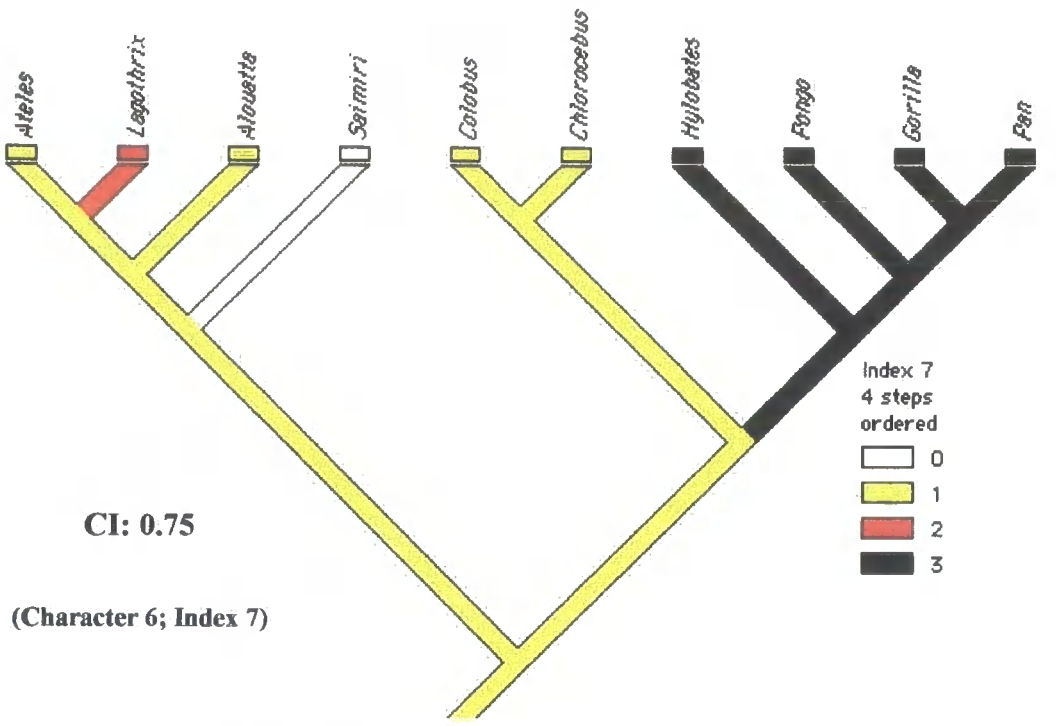

Figure 27: Trochlear Waisting.

State 0 = least waisted / State 3 = most waisted

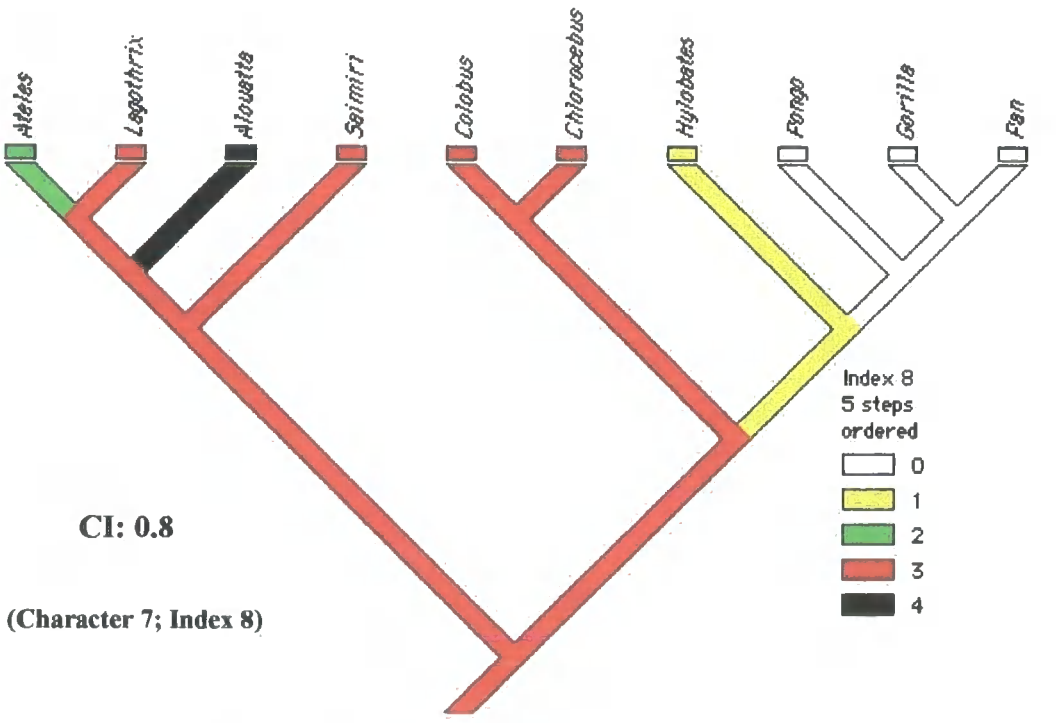

Figure 28: Ulnar Olecranon Process Length.

State 0 = short / State 4 = long

Index 9

Ulnar Styloid Process Length

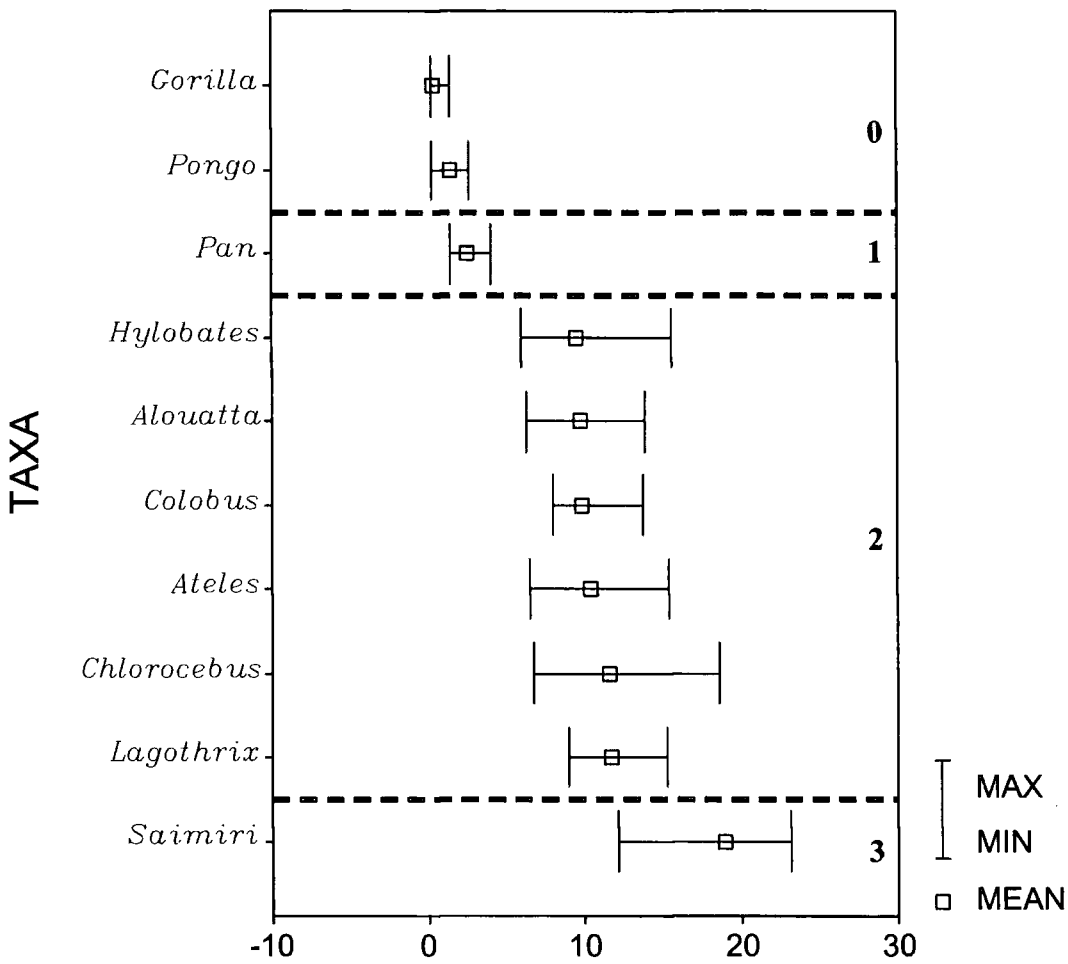

Figure 29: Univariate Chart for Ulnar Styloid Process Length.

Results and coding for ulnar styloid process length (Character 8; Index 9).

Index 10

Relative Lunate Breadth

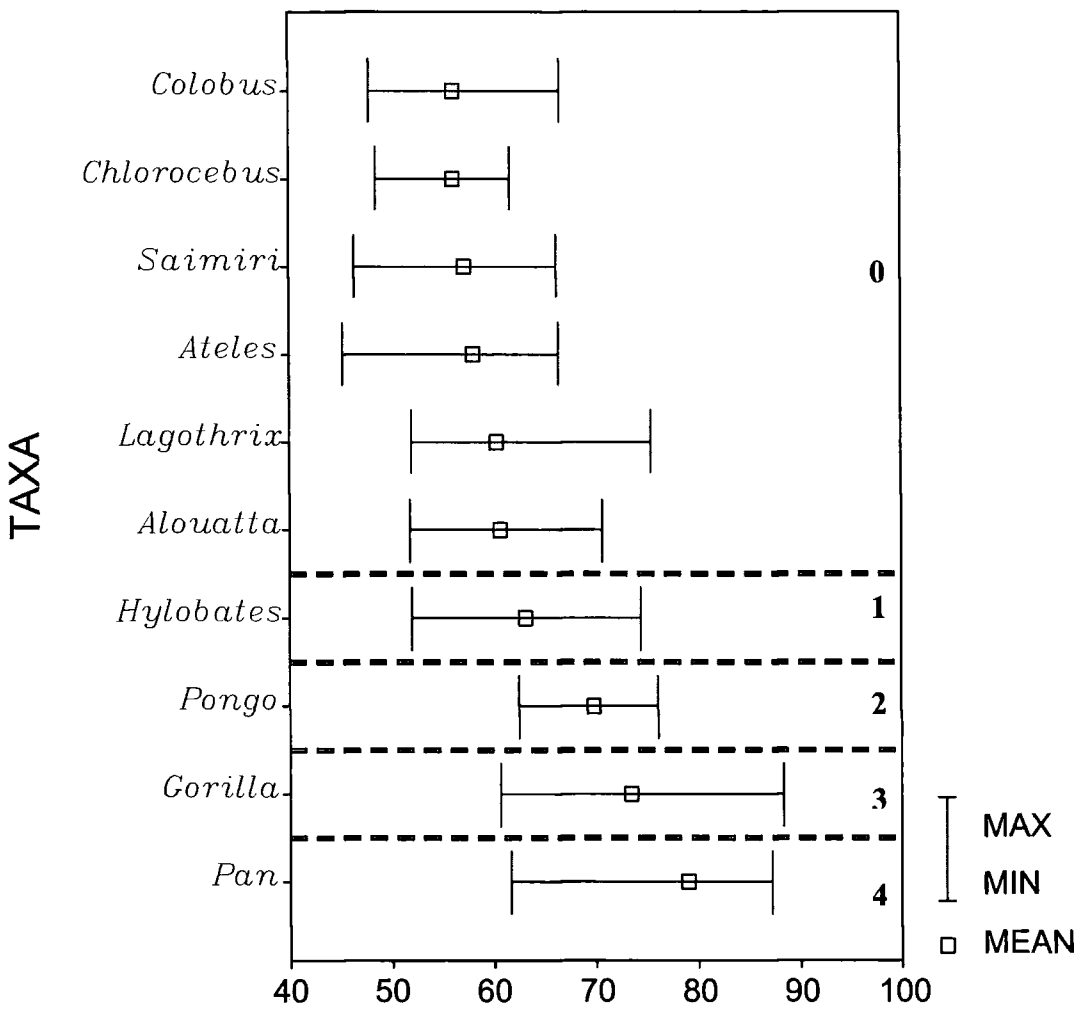

Figure 30: Univariate Chart for Relative Lunate Breadth.

Results and coding for relative lunate breadth (Character 9; Index 10).

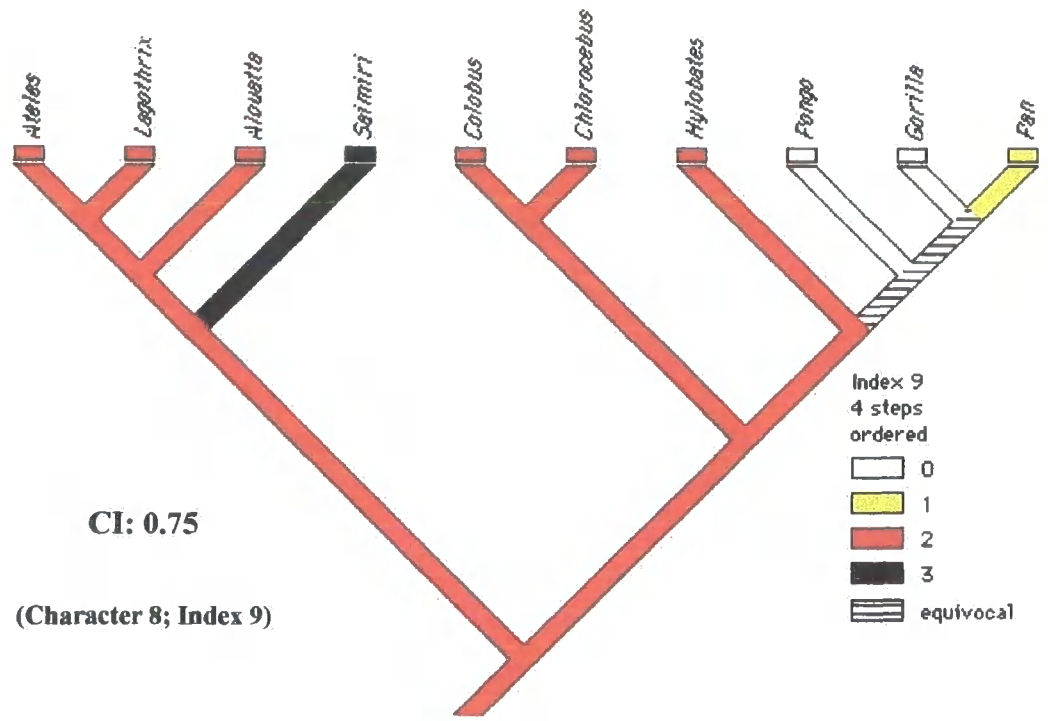

Figure 31: Ulnar Styloid Process Length.

State 0 = short / State 3 = long

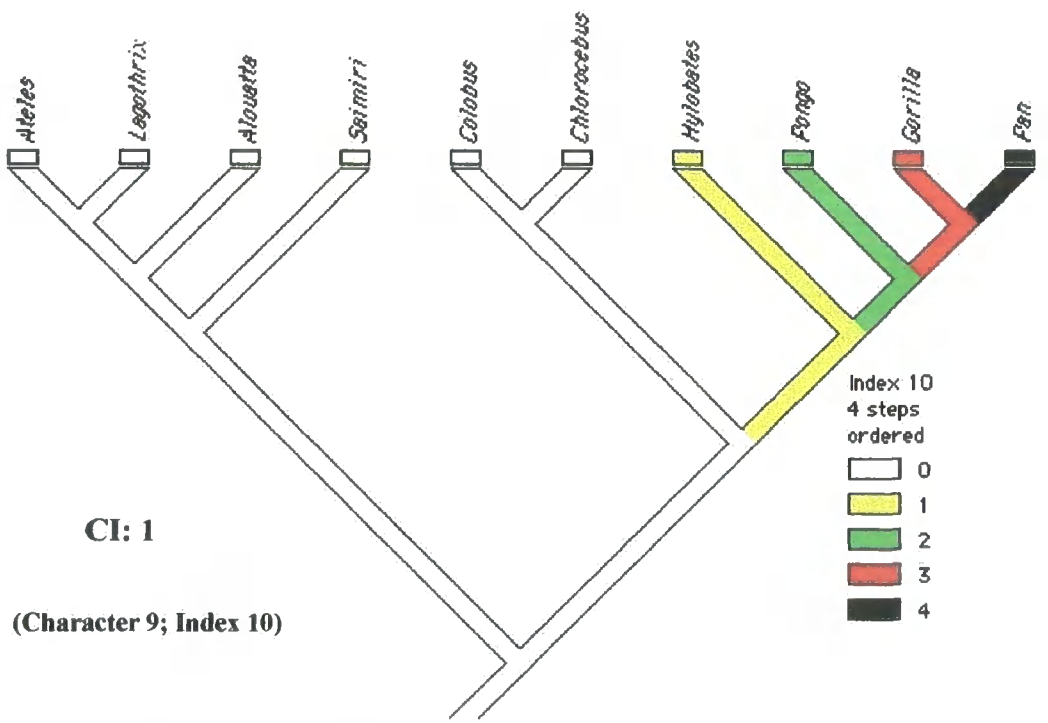

Figure 32: Relative Lunate Breadth.

State 0 = relatively narrow / State 4 = relatively broad

Character 5: Humeral Head Torsion Angle

Angle 2:

The results (Figures 21 and 23) show that no homoplasy is evident in this character. The African ape clade is synapomorphic, with *Gorilla* (130.33°) and *Pan* (127.88°) linked by their shared possession of very marked humeral head torsion. *Hylobates* (103.95°) and *Pongo* (106.88°) retain the primitive condition (shared with all of the ceboid taxa) of having moderate humeral head torsion. The cercopithecoid clade is derived, and *Chlorocebus* (72.43°) and *Colobus* (84.88°) are autapomorphic in having very little medial torsion of the head.

These results suggest that a medially orientated humeral head is not a synapomorphy of the extant Hominoidea (*contra* Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987), but is instead a shared derived trait of the African apes.

Character 6: Humeral Medial and Lateral Tochlear Keel Development

Index 6 (Medial and Lateral Trochlear Keel Development):

The results (Figures 22 and 24) show that homoplasy (in the form of convergence) may be evident between a number of taxa in this index. The hominid clade is linked by synapomorphy in its possession of a very well-developed lateral trochlear keel (LTK; although *Gorilla* has subsequently developed a slightly reduced LTK independently of *Pan* and *Pongo*). *Hylobates* and *Chlorocebus* are either convergent on each other or retain the primitive condition of having a moderately developed LTK, depending upon the reconstruction of the ancestral catarrhine and cercopithecoid nodes. The polarity of the Hominoidea is equivocal. *Colobus* and *Alouatta* are either convergent on each other or retain the primitive condition of having a weak LTK, depending upon the reconstruction of the ancestral anthropoid and catarrhine nodes. *Ateles*, *Saimiri* and *Lagothrix* are autapomorphic and possess undeveloped, poorly-developed and moderately-developed LTKs, respectively.

Index 7 (Trochlear Waisting):

The results (Figures 25 and 27) show that homoplasy is not evident in this index. Hominoidea is synapomorphic in having a markedly waisted trochlea. *Lagothrix* and *Saimiri* are autapomorphic in possessing moderate and minimal trochlear waisting, respectively. *Chlorocebus*, *Colobus*, *Alouatta* and *Ateles* retain the primitive condition of having a moderately waisted trochlea.

Summary of Character 6:

The results from these two indices are incongruent. Taken together, the results are equivocal as to whether the possession of prominent medial and lateral trochlear keels, separated by a deep trochlear groove is a synapomorphy of the extant hominoids. Index 7 indicates that this trait *is* a synapomorphy of extant hominoids, as suggested by Goodman (1963), Ciochon (1983), Andrews (1985) and Andrews and Martin (1987). Index 6 suggests that this feature is a synapomorphy of the extant hominids only, as suggested by Martin (1986). Both indices clearly show that hominids can be distinguished from other anthropoids by their prominent lateral trochlear keel.

Overall, the results show that hominids (in particular, *Pongo* and *Pan*) exhibit a high degree of medial and lateral trochlear keel development and also have very deep trochlear grooves. LTK development in *Hylobates* does not appear to be as marked as that of hominids.

Character 7: Ulnar Olecranon Process Length

Index 8:

The results (Figures 26 and 28) show that no homoplasy is evident in this character. The hominoid clade is synapomorphic in its possession of a markedly reduced olecranon process. Hominids are also synapomorphic in possessing a shorter olecranon process than hylobatids. *Ateles* is autapomorphic in possessing a medium length (compared with the other sampled taxa) olecranon process. *Ateles* does, however, show a trend towards the shortened olecranon process of the living apes. The cercopithecoids, and some ceboids (*Lagothrix* and *Saimiri*) retain the primitive condition of a moderate to long olecranon process. *Alouatta* is autapomorphic in having the longest olecranon process of the sampled taxa.

These results support the hypothesis, advanced by Goodman (1963), Ciochon (1983), Andrews (1985), Andrews and Martin (1987) and Harrison (1987), that a short olecranon process is a synapomorphy of all living apes, although hylobatids show less reduction than hominids.

Character 8: Ulnar Styloid Process Length

Index 9:

The results (Figures 29 and 31) show that homoplasy is not evident in this character. Hominids are synapomorphic in their possession of an extremely short ulnar styloid process (USP; although *Pan* has subsequently developed a slightly longer USP independently of *Pongo* and *Gorilla*). *Hylobates* retains the primitive condition of a moderately long USP, as do the cercopithecoids and atelines. *Saimiri* is autapomorphic in having a very long USP.

These results suggest that reduced ulnocarpal contact is not a synapomorphy of the extant hominoids (*contra* Goodman, 1963; Lewis, 1969, 1971a, b, 1972a, b; Corruccini, 1978; Ciochon, 1983; Andrews, 1985, Andrews and Martin, 1987; Harrison, 1987; Sarmiento, 1988), but rather, a shared derived trait of hominids, as suggested by Martin (1986). *Hylobates* retains a primitive, monkey-like morphology for this trait.

Character 9: Lunate Breadth

Index 10:

The results (Figures 30 and 32) show that no homoplasy is evident in this character. Hominoidea is synapomorphic, with all genera exhibiting relatively broader lunates than other anthropoid taxa. *Hylobates*, *Pongo*, *Gorilla* and *Pan* follow a morphocline from possessing a relatively narrow lunate (*Hylobates*) to having a relatively broad lunate (*Pan*). *Hylobates* has a significantly narrower lunate than hominids, closer in relative breadth to the ceboid monkeys (within one standard deviation of all four taxa). The cercopithecoids and ceboids retain the primitive condition of having a relatively very narrow lunate.

These results support Harrison's (1987) hypothesis that possession of a broad lunate is a synapomorphy of all extant hominoids. *Hylobates*, however, is

quite divergent from the hominid clade in its possession of a relatively narrower lunate.

Summary of Results for Extant Anthropoid Analysis

The results from the analysis of extant anthropoids show that five[43] out of the nine characters examined are synapomorphies of the extant Hominoidea: relatively wide manubrium, small glenoid fossa angle, well-developed medial and lateral trochlear keels, short ulnar olecranon process length and relatively broad lunate (Corruccini, 1978; Ciochon, 1983; Andrews, 1985, Andrews and Martin, 1987; Harrison, 1987). Two of the four remaining characters are shared derived for the hominid (short ulnar styloid process length; *contra* Lewis, 1969, 1971a, b, 1972a, b) and African ape/human (marked humeral head torsion; *contra* Andrews, 1985, Martin, 1986, Andrews and Martin, 1987; Harrison, 1987) clades. One trait appears to reflect absolute differences in body size between taxa (humeral head size). The remaining character (humeral head shape) does not distinguish extant hominoids from other taxonomic groups, and the frequently cited condition of 'globular/hemispherical' humeral head (usually interpreted as a hominoid synapomorphy; Goodman, 1963; Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987) was found not to be exhibited by living apes at all. Four of the nine characters (glenoid fossa angle, humeral head size, humeral head shape and medial and lateral trochlear keel development) exhibit homoplasy, in the form of convergence or reversal. None of these traits, however, show homoplasy between two or more extant hominoid taxa, therefore it is unlikely that hylobatids, pongines or African apes/humans evolved these traits independently of each other.

[43] Possibly four, if the character 'well-developed medial and lateral trochlear keels'is a hominid, rather than a hominoid, synapomorphy.

CHAPTER FIVE

CHARACTER ANALYSIS OF PALAEONTOLOGICAL CATARRHINE TRUNK AND FORELIMB MORPHOLOGY

Introduction

If parallelism is defined as homoplasy in two sister groups, then trying to detect parallelism on a cladogram composed solely of extant taxa is impossible (Eldredge and Cracraft, 1980). This is because the autapomorphies that develop independently in sister taxa that exhibit parallelism are always interpreted, on the grounds of parsimony, to be synapomorphies. In order to detect all three types of homoplasy, it is therefore necessary to include fossil taxa in an analysis (Lockwood and Fleagle, 1999). The inclusion of fossil taxa provides a test of the presumed homologies expressed by the codes assigned to living taxa (Wiley *et al.*, 1991). In this way, characters supported as synapomorphies based on the analysis of only extant taxa may be revealed to be homoplastic (Rae, 1997).

Materials

Taxa

A total of eleven postcranial specimens, from nine genera of fossil catarrhines, were included in this analysis, which takes place at the generic level. Measurements were taken from the published literature (Table 4). The ingroup consisted of five stem hominoids (*Dendropithecus*, *Kenyapithecus*, *Nyanzapithecus*, *Proconsul* and *Sivapithecus*), one stem hominid (*Dryopithecus*) and all extant non-human hominoid taxa[44]. Multiple outgroups were used in this analysis. A stem cercopithecoid (*Victoriapithecus*) and two stem catarrhines (*Aegyptopithecus* and *Pliopithecus*), together with the two extant cercopithecoid

[44] *Dendropithecus* has been placed as a stem hominoid (Fleagle, 1999), and as a stem catarrhine (Begun *et al.*, 1997). *Dryopithecus* has been placed as a stem hominid (Fleagle, 1999), and as a stem African ape/human (Begun *et al.*, 1997).

and four extant ceboid taxa examined in the previous analysis, were used here as successively more distant sister taxa.

Characters

It was not possible for all of the characters used in the analysis of extant anthropoids to be used in this analysis. Characters 1, 2, 3, 5, 7, 8, and 9 were excluded from this analysis, as no published data were available to quantify these traits in the sampled fossil taxa. Characters 4 and 6 ('humeral head shape' and 'medial and lateral trochlear keel development') were only obtainable for some of the relevant fossil taxa. For a description of the measurements taken and a discussion of the characters used, see Chapter Four.

Specimens

Table 4: Palaeontological Specimens included in this Analysis.

Accession Prefix	Specimen	Taxon	Reference(s)
DPC 1275	Humerus	*Aegyptopithecus*	Fleagle and Simons (1982), Rose (1988a, 1989)
KNM-RU 1675	Dist. humerus	*Dendropithecus*	Rose (1988a)
KNM-RU 2097	Dist. humerus	*Dendropithecus*	Rose (1988a)
RUD 53	Dist. humerus	*Dryopithecus*	Rose (1988a)
KNM-FT 2751	Dist. humerus	*Kenyapithecus*	Rose (1988a)
KNM-MB 21206	Prox. humerus	*Nyanzapithecus*	McCrossin (1992)
OE 304	Humerus	*Pliopithecus*	Gebo *et al.* (1988), Rose (1988a, 1989)
KNM-RU 2036AH	Dist. humerus	*Proconsul*	Rose (1988a)
KNM-RU 17376	Prox. humerus	*Proconsul*	Gebo *et al.* (1988), Rose (1989)
GSP 28062	Prox. humerus	*Sivapithecus*	Rose (1989)
KNM-MB 12044	Prox. humerus	*Victoriapithecus*	Harrison (1989), McCrossin (1992)

Aegyptopithecus zeuxis Simons, 1965

DPC 1275

This specimen is a complete humerus. The proximal end exhibits some crushing on the anterior surface and abrasion on the margins of the articular surface (Fleagle and Simons, 1982). The head is orientated almost directly

posteriorly, as in strepsirhines and some (quadrupedal) anthropoids, and is mediolaterally narrow with a head length/head width index of 108[45] (Fleagle and Simons, 1982), in contrast to the broad head seen in extant apes and some atelin monkeys. The most proximal margin of the articular surface is approximately level with the proximal aspect of the greater tuberosity (Fleagle and Simons, 1978, 1982). The bicipital groove is broad and shallow (Fleagle and Simons, 1982). On the distal end an entepicondylar foramen is evident, just proximal to the medial aspect of the trochlea, this is a primitive feature found in strepsirhines and ceboid monkeys (and *Pliopithecus*), and is not present in any living catarrhine (Fleagle and Simons, 1978). The medial epicondyle is large and projects medioposteriorly. The trochlea is relatively wide compared to the capitulum, and its medial edge exhibits a slight flare (intermediate between that of extant strepsirhines and cercopithecoids; Rose, 1988a). The lateral aspect of the trochlea is bounded by a low ridge that separates it from the capitulum (Fleagle and Simons, 1982), but lacks the prominent lateral keel and overall spool-shape of the extant hominoid trochlea. The capitulum is rounded (not spherical) like that of extant strepsirhines. The olecranon fossa is shallow and broad, in contrast to its deep, narrow appearance in living apes (Fleagle and Simons, 1982; Rose, 1988a).

***Pliopithecus* Gervais, 1849**

***P. vindobonensis* Zapfe and Hürzeler, 1957**

OE 304

This specimen is a complete humerus from Neudorf, in the former Czechoslovakia (Zapfe, 1958). The proximal articular surface is elevated slightly above the greater tuberosity (as in most anthropoids; McCrossin, 1992). The bicipital groove is relatively broad and shallow as in most ceboids and strepsirhines. The head exhibits what Zapfe (1958) describes as moderate torsion (121°), though this figure is within the range of values for extant hominoid humeral head torsion (especially *Hylobates*; Gebo, 1996). The shaft is straight, as in most primates except some extant cercopithecoids (Rose, 1994). An entepicondylar foramen is present (Zapfe, 1958) on the distal end, a primitive feature found in strepsirhines and platyrrhines (and *Aegyptopithecus*), and not

[45] Rose (1989) suggests an index of 115.2, indicating an even narrower head.

present in any extant catarrhine (Fleagle and Simons, 1982). The olecranon fossa is triangular in shape and quite shallow. The trochlea exhibits a weak lateral keel, and is separated from the relatively large capitulum by an indistinct, shallow *zona conoidea*. In both these features and in overall morphology OE 304 most closely resembles extant strepsirhines and platyrrhines (Zapfe, 1958), and probably represents an adaptation to arboreal quadrupedalism (possibly with some terrestrial progression; Rose, 1994).

***Victoriapithecus* Von Koenigswald, 1969**

KNM-MB 12044

This specimen consists of a proximal left humerus from Maboko Island, Kenya (Harrison, 1989). The head is narrower mediolaterally than it is long anteroposteriorly, with a head length/head breadth index of 115.65 (Harrison, 1989; McCrossin, 1992), a value comparable with that of most pronograde quadrupeds. The posteroproximal margin of the articular surface is only moderately convex and is only slightly elevated above the level of the greater tuberosity (McCrossin, 1992), as in most arboreal quadrupeds, but contrasting with the marked convexity and proximal extension of the articular surface above the greater tuberosity in extant hominoids and some atelin monkeys. These features indicate that when the humerus is in forward flexion (i.e., the arm is circumducted above the head) the range of rotation is limited compared with when the humerus is more extended (Harrison, 1989). This contrasts with the extensive potential for abduction and rotation at the glenohumeral joint in living apes and spider monkeys (Andrews and Groves, 1976; Harrison, 1989). The bicipital groove is shallow and broad as in arboreal quadrupedal cercopithecids and in contrast to extant hominoids and *Ateles* (Fleagle and Simons, 1982; Rose, 1988a). Overall, the morphology of the KNM-MB 12044 humeral head indicates that a relatively wide range of motion was possible at the glenohumeral joint and in most respects resembles that of arboreal cercopithecids (Harrison, 1989).

***Dendropithecus* Andrews and Simons, 1977**

***D. macinnesi* Le Gros Clark and Leakey, 1950**

(a) KNM-RU 1675

This specimen is a distal humerus.

(b) KNM-RU 2097

This specimen is a fragmentary distal humerus and shaft from Rusinga Island, Kenya (Le Gros Clark and Thomas, 1951). It is well-preserved, but lacks most of the proximal end including the articular surface and most of the tuberosities. The shaft is relatively straight and slender, contrasting with that of most cercopithecoids. The bicipital groove is shallow as in extant arboreal quadrupeds (Fleagle and Simons, 1982). Le Gros Clark and Thomas (1951) suggest that the proximal shaft features on this specimen indicate that the humeral head would have been orientated posteriorly (an angle of torsion of 108°) as in extant cercopithecoids. On the distal end, the medial epicondyle is large and projects directly medially as in extant hominoids (Le Gros Clark and Thomas, 1951; Andrews and Simons, 1977). The entepicondylar foramen, typical of strepsirhines, platyrrhines and stem catarrhines is absent (Feldesman, 1982). The olecranon fossa is relatively broad and moderately shallow (Le Gros Clark and Thomas, 1951). The distal articular surface is broad (Andrews and Simons, 1977) and exhibits a strongly-defined medial ridge separated from a weak lateral keel by a relatively shallow trochlear groove (Le Gros Clark and Thomas, 1951). The capitulum is small and globular in shape (Andrews and Simons, 1977), and is separated from the trochlea by a relatively broad, shallow *zona conoidea* (Le Gros Clark and Thomas, 1951; Rose, 1988a). Overall, the morphology of KNM-RU 2097 suggests an adaptation to arboreal quadrupedalism (Le Gros Clark and Thomas, 1951; Feldesman, 1982; Rose, 1988a).

The values for KNM-RU 1675 and KNM-RU 2097 differ considerably for index 6. The degree of difference, however, falls within the intraspecific variation expressed by extant taxa for this index. The mean of KNM-RU 1675 and KNM-RU 2097 was therefore used in index 6 and 7.

***Proconsul africanus* Hopwood, 1933**

(a) KNM-RU 2036AH

This specimen is the distal two-thirds of a left humerus (Napier and Davis, 1959). The proximal quarter of the shaft and the head is missing, and there has been some compression and angulation in the mid-shaft region, but the distal articular surface is well preserved. Napier and Davis (1959) argued that the head would have exhibited some medial torsion (somewhere intermediate between that

of extant hominoids and extant cercopithecoids) had it been preserved, a conjecture later substantiated by Walker and Pickford (1983) based on another *P. africanus* humeral specimen. Overall, the proximal shaft morphology is more similar to that of quadrupedal monkeys than living apes. On the distal end, the medial epicondyle is intermediate in breadth between that of *Pan* and *Ateles* on the one hand and *Presbytis*, *Cercopithecus* and Ceboids on the other (Napier and Davis, 1959). Napier and Davis (1959) suggest that the distal articular surface most closely resembles that of *Pan*. The medial ridge of the trochlea is large, well-rounded and is separated from the prominent lateral keel by a relatively deep groove (Napier and Davis, 1959). This is similar to the morphology found in living apes, although the lateral ridge is not as large or sharply defined as it is in hominids, it is more prominent than in extant cercopithecoids (Napier and Davis, 1959). The capitulum is well-rounded and globular (Napier and Davis, 1959). The articular surface of the entire distal end is markedly extended posteriorly, indicating a extensive potential for extension at the elbow joint (Napier and Davis, 1959). All of these features appear to be mechanically consistent with maintaining stability in the elbow joint in all positions of flexion/extension and pronation/supination and indicate that the distal end of KNM-RU 2036AH is closer in morphology to extant apes than to extant cercopithecoids (Napier and Davis, 1959).

(b) KNM-RU 17376 (? *Dendropithecus macinnesi*)

This specimen is a proximal right humerus from Rusinga Island, Kenya (Gebo *et al.*, 1988), comprising the head and proximal shaft. There is some abrasion around the anterior margin of the tuberosities and the medial edge of the articular surface. The articular surface of the head is almost a hemisphere that faces posterosuperiorly and rises proximally three millimetres above the greater tuberosity (Gebo *et al.*, 1988). Well-defined grooves separate the articular surface from the two tuberosities, which, together with the intertubercular sulcus, bound the anterior margin of the articular surface almost symmetrically. The bicipital groove appears to be relatively shallow (though the abrasion to the greater tuberosity may accentuate this; Gebo *et al.*, 1988), as in arboreal quadrupeds. The KNM-RU 17376 specimen probably represents an individual that weighed 8-10kg.

***Kenyapithecus Wickeri* Leakey, 1962**

KNM-FT 2751

This specimen is the distal one-third of a right humerus from Fort Ternan, Kenya (Andrews and Walker, 1976). It is well-preserved except for a few minor cracks and the main fracture on the shaft. The shaft is compressed anteroposteriorly, broad mediolaterally, and oval in cross-section (Andrews and Walker, 1976). The medial epicondyle is abbreviated and orientated posteromedially, in contrast to the extended, medially disposed entepicondyle of extant hominoids (McCrossin and Benefit, 1994). The abbreviation and retroflexion of the medial epicondyle probably reflects a reduced emphasis on digital grasping and may suggest an adaptation for terrestrial or semi-terrestrial progression (McCrossin and Benefit, 1994, 1997). The distal articular surface is broad mediolaterally and shallow proximodistally. The trochlea is relatively broad compared to the capitulum, with prominent medial and lateral keels and a moderately depressed groove (McCrossin and Benefit, 1997). The capitulum is globular in shape (Andrews and Walker, 1976) and is separated from the lateral margin of the trochlea by a deep, narrow *zona conoidea* (McCrossin and Benefit, 1994). The olecranon fossa is very deep and triangular in outline, suggesting a large potential for extension and hyperextension (Rose, 1988a). Morphologically, KNM-FT 2751 is most similar to extant apes[46] (McCrossin and Benefit, 1994), particularly hominids (Feldesman, 1982).

***Nyanzapithecus pickfordi* Harrison, 1986**

KNM-MB 21206

This specimen of a proximal right humerus comes from the Maboko Island locality in Kenya, and has been attributed to *Nyanzapithecus pickfordi* by McCrossin (1992). The specimen consists of a fragment of a proximal humerus, broken at the surgical neck. The head is orientated posteroproximally and is mediolaterally narrower than it is anteroposteriorly long (McCrossin, 1992). This orientation is most similar to that of some New World monkeys (e.g., cebines) and contrasts with the more proximomedially directed, and mediolaterally broader, humeral head found in extant hominoids and *Ateles* (Fleagle and Simons, 1982).

[46] McHenry and Corruccini (1975), however, suggested that KNM-FT 2751 is unique, and has morphometric affinities with Old World monkeys rather than apes.

The articular surface is globular-shaped, rises proximally above the greater tuberosity (as it does in most anthropoids, with the exception of some terrestrial cercopithecoids) and extends anteriorly toward the margin of the bicipital groove (McCrossin, 1992). Both tuberosities are large. The bicipital groove is broad and shallow (McCrossin, 1992) like those of most anthropoids, and contrasts with the deep, narrow intertubercular sulcus of living apes (except *Pongo*) and spider monkeys (Fleagle and Simons, 1982). The shaft is compressed anteroposteriorly and broad mediolaterally.

***Dryopithecus* Lartet, 1856**

***D. brancoi* Schlosser, 1901**

RUD 53

This specimen comes from the site of Rudabánya, in northeastern Hungary and consists of a fragment of the distal end of a left humerus, preserving a nearly complete distal articular surface and a short length of shaft (Begun, 1992c). The trochlea is relatively broad compared to the capitulum, with prominent medial and lateral keels separated by a deep groove (Begun, 1992c). The well-defined lateral ridge is separated from the spherical-like capitulum by a deep, narrow *zona conoidea* (Begun, 1992c). Begun (1992c) argues that the lateral keel is very strongly developed relative to trochlear depth (within one standard deviation of the means for *Pongo* and *Hylobates* for this trait). The olecranon fossa is deep and roughly triangular-shaped, indicating a hyperextension capability at the elbow joint, as in living apes (Begun, 1992c). The medial epicondyle is large and projects posteromedially. Begun (1992c) concludes that RUD 53 is morphologically similar to extant hominids, despite having a relatively smaller capitulum, a shallower trochlear groove and an abbreviated entepicondyle (possibly the result of damage).

***Sivapithecus* Pilgrim, 1910**

GSP 28062

This specimen consists of a partial proximal right humerus, preserving the head and a short length of the proximal shaft (Rose, 1989). Erosion is evident around the margins of the articular surface and bicipital groove. The articular surface is relatively broader mediolaterally than in strepsirhines, relatively deeper

proximodistally than in cercopithecoids, and relatively longer anteroposteriorly than in extant hominoids (Rose, 1989). In living apes, the articular surface of the head is not present (or is present in a limited fashion) between the tuberosities, which are anteriorly placed (Rose, 1989). This contrasts with most other anthropoids and strepsirhines. In GSP 28062, the proximal articular surface is similar to that of cebines (e.g., *Cebus* and *Saimiri*) in that it is partially sandwiched between the tuberosities (Rose, 1989). The proximal extremity of the articular surface of the head is superior to the greater tuberosity, as in extant hominoids (though the head also rises above the tuberosities in some strepsirhines, ceboids and arboreal cercopithecoids; Rose, 1989). The placement of the tuberosities can be expressed in terms of an intertuberosity angle (see Figure 4, Chapter Four). In GSP 28062 (as in most non-hominoid primates), the intertuberosity angle is acute, which contrasts with the wider angulation of the tuberosities and resultant obtuse intertuberosity angle in extant hominoids and atelin monkeys (Rose, 1989).

Methods

Raw fossil data were collected from the literature and converted into indices to focus comparisons on the shape and relative size of the areas in question, rather than on their absolute size. The values exhibited by the fossil genera were compared with those of the extant taxa, to generate codes for a character analysis (for an assessment of the comparability of these data sets, see Appendix). A fossil taxon (or taxa) that expressed a value closest to a particular extant taxon was given identical coding. This information was pooled to form a data matrix of both extant and fossil forms. The matrix was entered into the MacClade computer program and cladograms were generated to show the distribution of character states among all sampled taxa. The genera were this time forced to fit the tree topologies specified by two recent phylogenetic studies: Begun *et al.*'s (1997) and Fleagle's (1999). The resulting cladograms were then scrutinised to see if the distribution of character states in this analysis supported or refuted the hypothesized shared derived status of the nine characters examined, and/or highlighted evidence of synapomorphy/homoplasy. This formed the basis for the results section below.

Results

Table 5: Data Matrix for Extant Anthropoid and Fossil Catarrhine Taxa.

TAXA	INDICES											
	1	2	3	4	5	6	7	8	9	10	A1	A2
Alouatta	1	2	5	7	3	4	1	4	2	0	5	2
Ateles	5	3	4	3	1	6	1	2	2	0	3	2
Chlorocebus	0	1	1	4	3	2	1	3	2	0	5	0
Colobus	1	2	2	3	2	4	1	3	2	0	5	1
Gorilla	2	5	0	2	2	1	3	0	0	3	4	3
Hylobates	2	3	3	0	0	2	3	1	2	1	0	2
Lagothrix	5	2	5	6	2	3	2	3	2	0	4	2
Pan	4	4	1	1	1	0	3	0	1	4	1	3
Pongo	3	4	3	3	2	0	3	0	0	2	2	2
Saimiri	0	0	5	5	1	5	0	3	3	0	4	2
**Aegyptopithecus* (DPC 1275)	?	?	5	7	3	3	1	?	?	?	?	?
**Pliopithecus* (OE 304)	?	?	5	5	2	2	2	?	?	?	?	?
**Nyanzapithecus* (MB 21206)	?	?	0	7	3	?	?	?	?	?	?	?
**Proconsul* (RU 17376)	?	?	4	7	3	?	?	?	?	?	?	?
**Sivapithecus* (GSP 28062)	?	?	5	7	3	?	?	?	?	?	?	?
**Victoriapithecus* (MB 12044)	?	?	1	7	3	?	?	?	?	?	?	?
**Dendropithecus* (Mean)	?	?	?	?	?	3	2	?	?	?	?	?
**Dryopithecus* (RUD 53)	?	?	?	?	?	0	3	?	?	?	?	?
**Kenyapithecus* (FT 2751)	?	?	?	?	?	2	3	?	?	?	?	?
**Proconsul* (RU 2036AH)	?	?	?	?	?	0	3	?	?	?	?	?

*Denotes fossil taxon.

Character 4: Humeral Head Shape

Index 3 (PD depth / ML width):

Fleagle's (1999) Topology:

In this topology (Figure 34), *Nyanzapithecus* is placed as a stem hominoid and is convergent on *Gorilla* in having a humeral head that is the widest, relative to depth, of all the sampled taxa. *Pan* is converged upon by *Chlorocebus* and *Victoriapithecus* in having a very wide head. *Hylobates* and *Pongo* are linked by synapomorphy in their possession of moderately wide humeral heads, although

Sivapithecus (the sister taxon of *Pongo* in this topology) has undergone a reversal to the primitive condition of having a head that is equally wide as it is deep. *Proconsul* is convergent on *Ateles* in having a head that is almost as wide as it is deep. The New World monkeys (except *Ateles*) and stem catarrhine taxa retain the primitive condition of having a humeral head that is approximately equally wide as it is deep.

Begun *et al.*'s (1997) Topology:

This topology (Figure 35) differs from Fleagle's (1999) only in its placement of *Nyanzapithecus* as a stem hominid. This change renders the ancestral hominid node equivocal, thus making it unclear whether *Hylobates* and *Pongo* are linked by synapomorphy or are convergent on each another.

Index 4 (AP length / ML width):

Fleagle's (1999) Topology:

In this topology (Figure 37), *Pan* and *Gorilla* are synapomorphic in their possession of humeral heads that are markedly wider than they are long. The ancestral hominoid, hominid and African ape/human nodes are equivocal, therefore it is uncertain whether *Pongo* or *Hylobates* are linked by synapomorphy with the African apes or are autapomorphic. Regardless of this uncertainty, *Pongo* is convergent on *Colobus* and *Ateles* in having a humeral head that is slightly wider than it is long. *Sivapithecus* displays a radically different condition from its sister taxon *Pongo*, in having a head that is much longer than it is wide. *Hylobates* exhibits the most extreme condition of the hominoid taxa, with a head that is much wider than it is long. The extant apes, extant cercopithecoids and *Ateles* are distinct from the other taxa in their possession of relatively wide humeral heads. In contrast, the stem hominoids (*Proconsul*, *Nyanzapithecus*) and stem hominid (*Sivapithecus*) in this analysis all possess humeral heads that are longer than they are wide.

Begun *et al.*'s (1997) Topology:

In this topology (Figure 38), the placement of *Nyanzapithecus* as a stem hominid raises the possibility that the ancestral hominoid and hominid nodes can be reconstructed as having humeral heads that are equally long as they are wide. If this reconstruction were assumed then it would become most parsimonious to suggest that all extant apes evolved relatively wide humeral heads (albeit to differing degrees) independently from a common ancestor that possessed a relatively much longer head. The equivocal nature of the ancestral hominoid and hominid nodes precludes any definitive resolution of this problem.

Index 5 (AP length / PD depth):

Fleagle's (1999) Topology:

In this topology (Figure 40), *Pan* is converged upon by *Ateles* and *Saimiri* in having a humeral head that is relatively deep. *Pongo* and *Gorilla* are either linked by synapomorphy (with *Colobus*, *Lagothrix* and *Pliopithecus* all convergent on their condition) or, alternatively, have undergone character reversal to the condition of having a humeral head that is approximately equally long as it is deep, depending upon the reconstruction of the ancestral anthropoid and catarrhine nodes. Interestingly, *Sivapithecus* has again undergone a reversal to a markedly different condition to its sister taxon *Pongo*, in its possession of a head that is longer than it is deep. *Nyanzapithecus*, *Proconsul*, *Chlorocebus* and *Victoriapithecus* are either linked by synapomorphy with *Aegyptopithecus* and *Alouatta* convergent on their condition, or retain the primitive condition, depending upon the reconstruction of the ancestral anthropoid and catarrhine nodes. *Hylobates* is autapomorphic in possessing a humeral head that is markedly deeper than it is long.

Index 3

Humeral Head Shape PD/ML

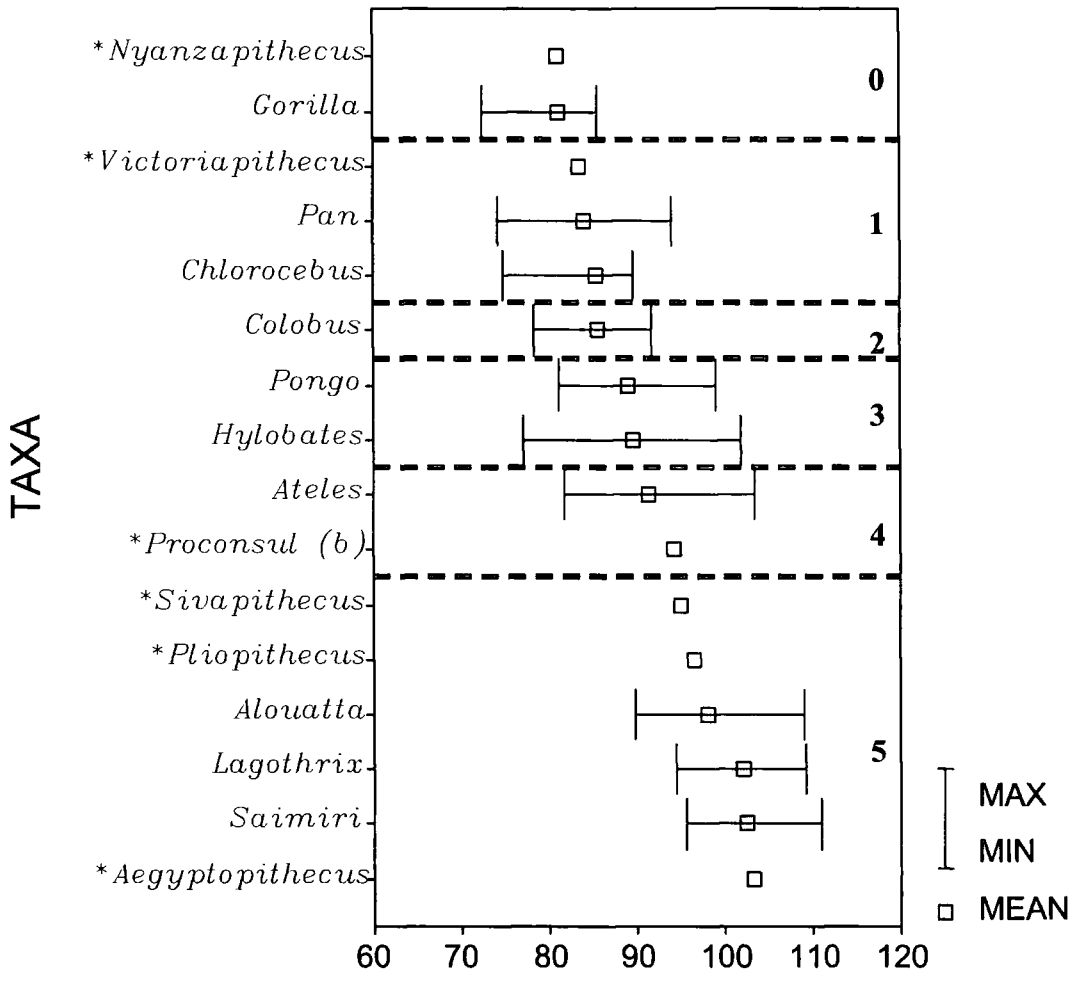

Figure 33: Univariate Chart for Humeral Head Shape PD/ML (Fossil).

Results and coding for humeral head shape PD/ML (Character 4; Index 3). In this and all subsequent univariate charts, fossil taxa are indicated by an asterisk (*). Summary data tables, giving sample sizes, arithmetic means, standard deviations and ranges are given in the Appendix.

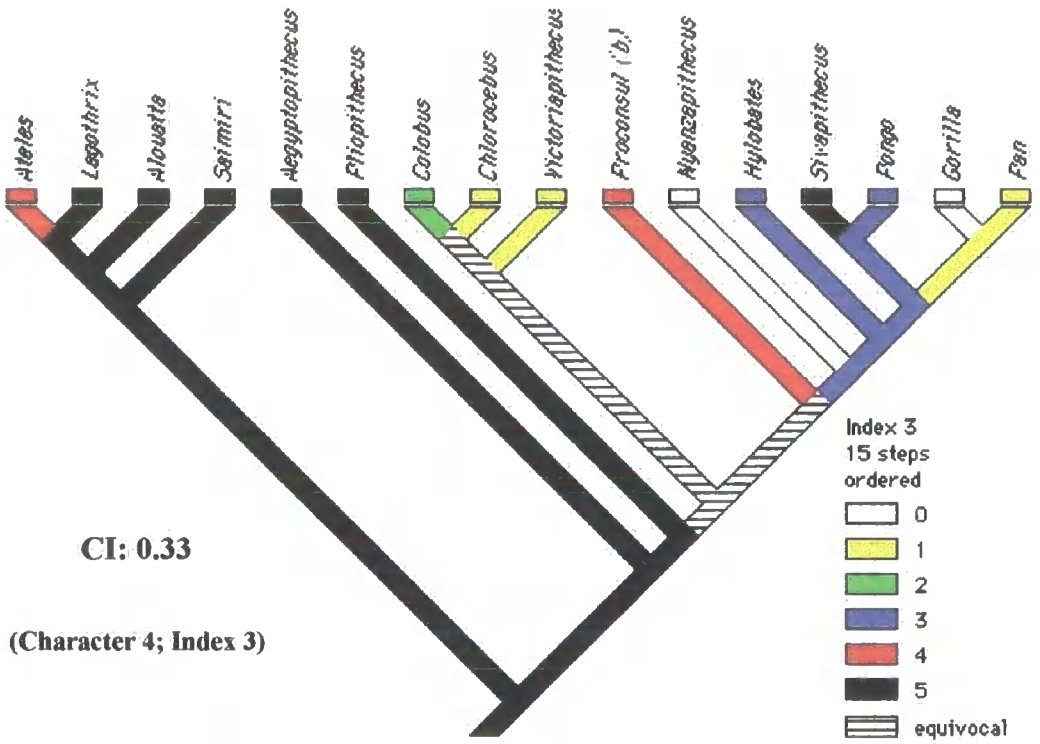

Figure 34: Humeral Head Shape PD/ML - Fleagle's (1999) Topology.

State 0 = wider ML than deep PD
State 5 = approximately equal values for PD depth and ML width

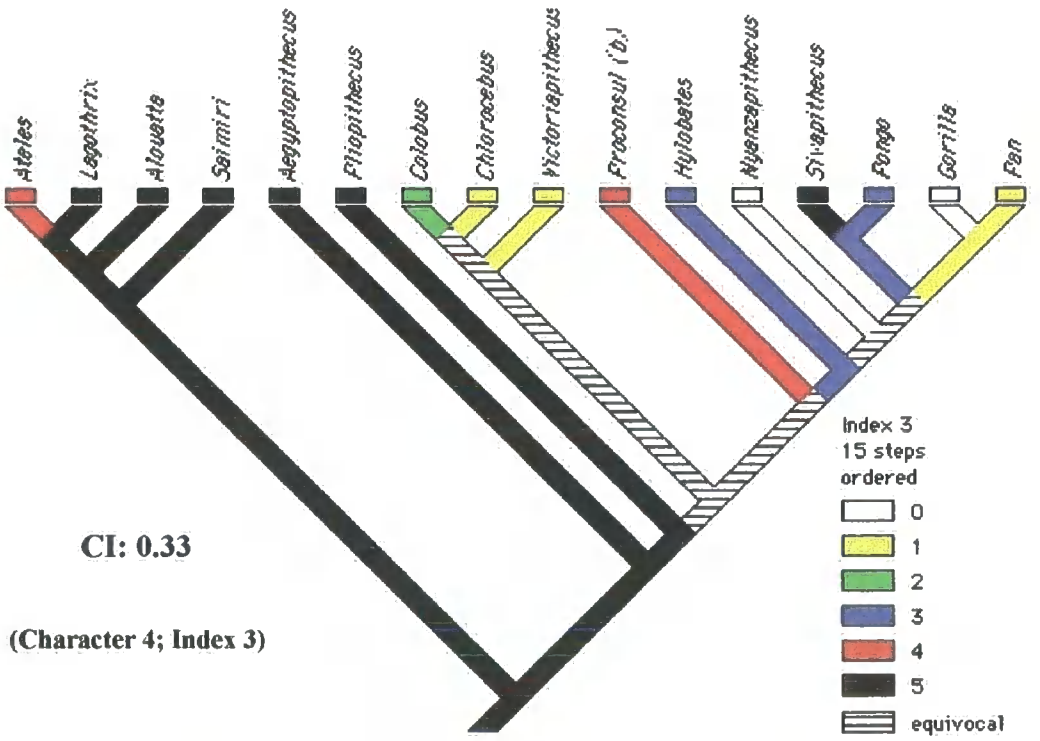

Figure 35: Humeral Head Shape PD/ML - Begun *et al.*'s (1997) Topology.

For descriptions of character states, see above.

Index 4

Humeral Head Shape AP/ML

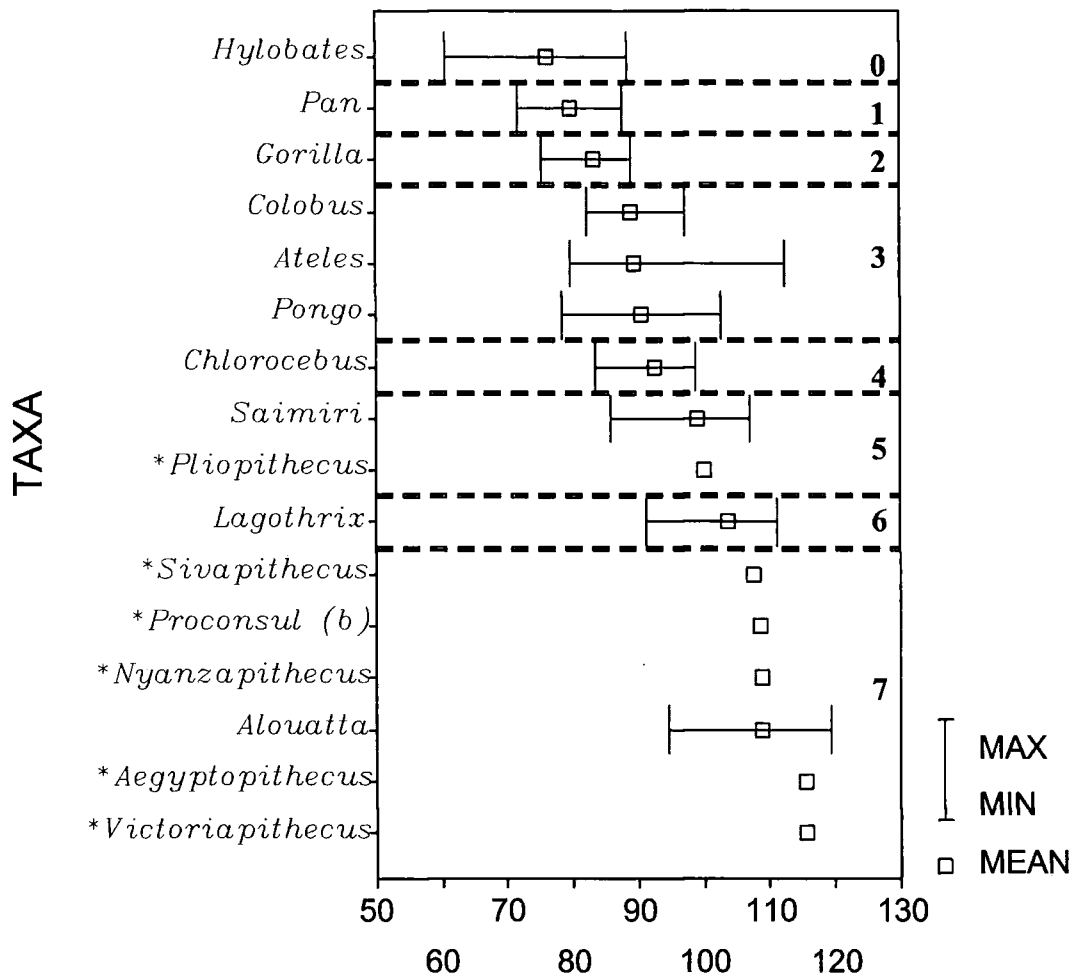

Figure 36: <u>**Univariate Chart for Humeral Head Shape AP/ML (Fossil).**</u>

Results and coding for humeral head shape AP/ML (Character 4; Index 4).

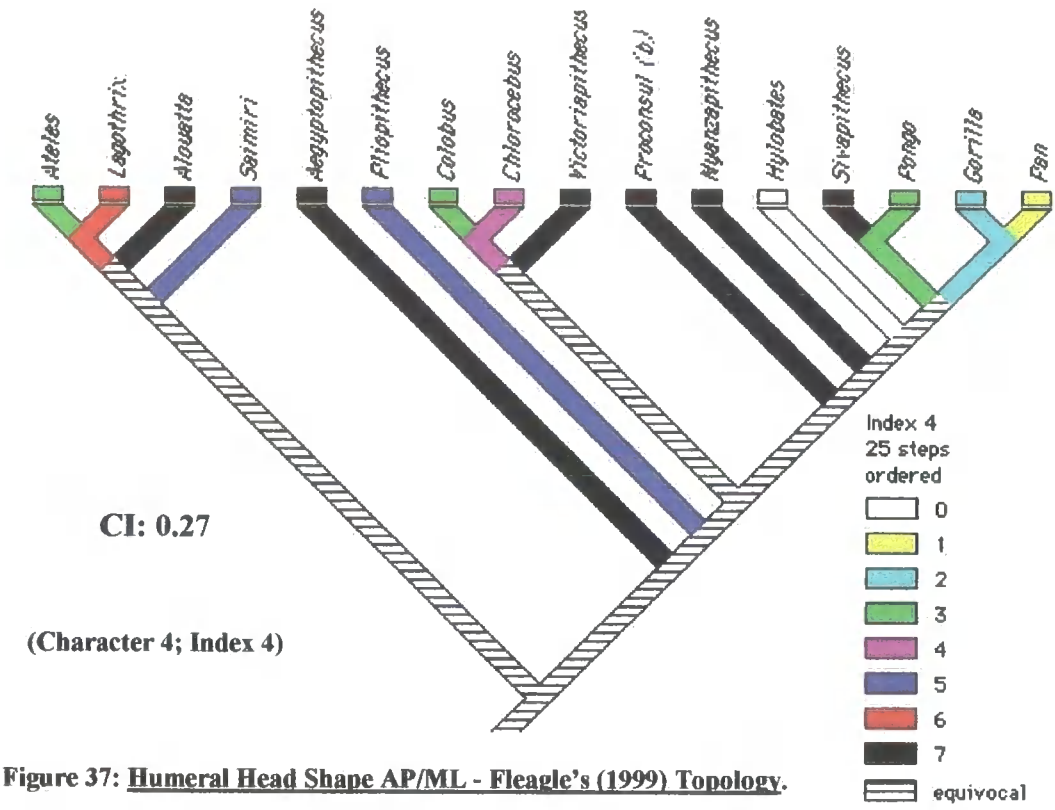

Figure 37: Humeral Head Shape AP/ML - Fleagle's (1999) Topology.

State 0 = wider ML than long AP
States 5 and 6 = approximately equal values for ML width and AP length
State 7 = longer AP than wide ML

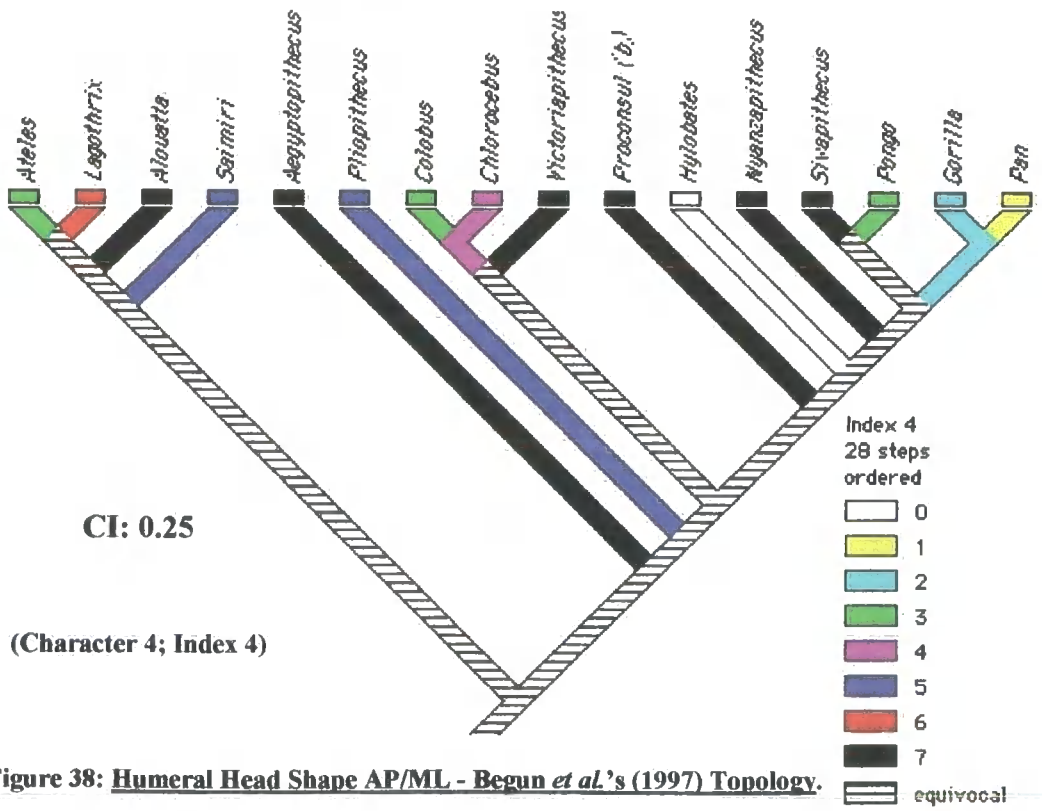

Figure 38: Humeral Head Shape AP/ML - Begun *et al.*'s (1997) Topology.

For description of character states, see above.

Index 5

Humeral Head Shape AP/PD

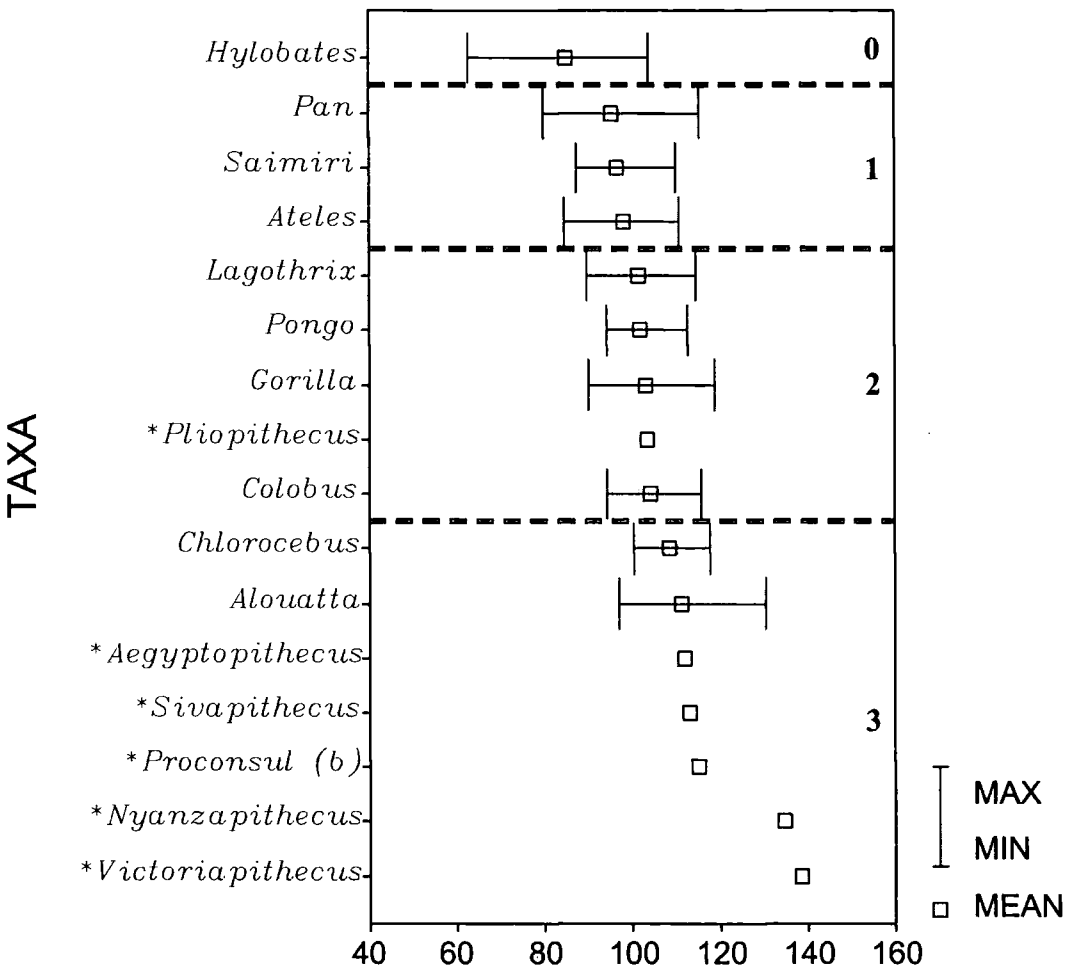

Figure 39: Univariate Chart for Humeral Head Shape AP/PD (Fossil).

Results and coding for humeral head shape AP/PD (Character 4; Index 5).

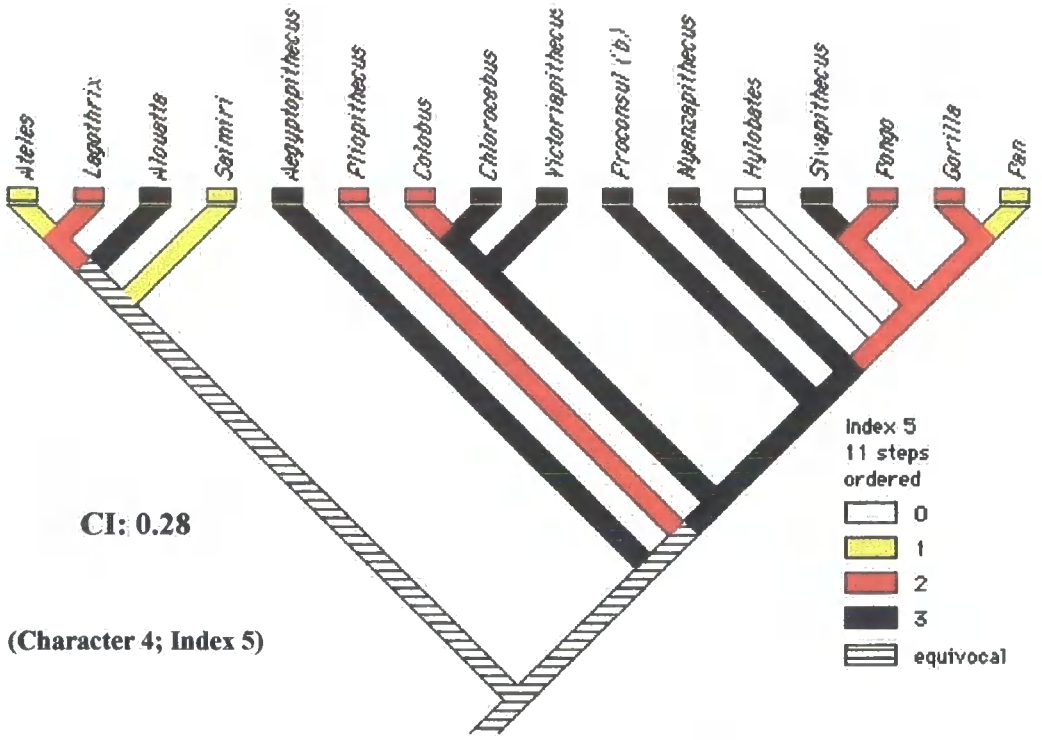

Figure 40: Humeral Head Shape AP/PD - Fleagle's (1999) Topology.

State 0 = deeper PD than long AP
State 2 = approximately equal values for AP length and PD depth
State 3 = longer AP than deep PD

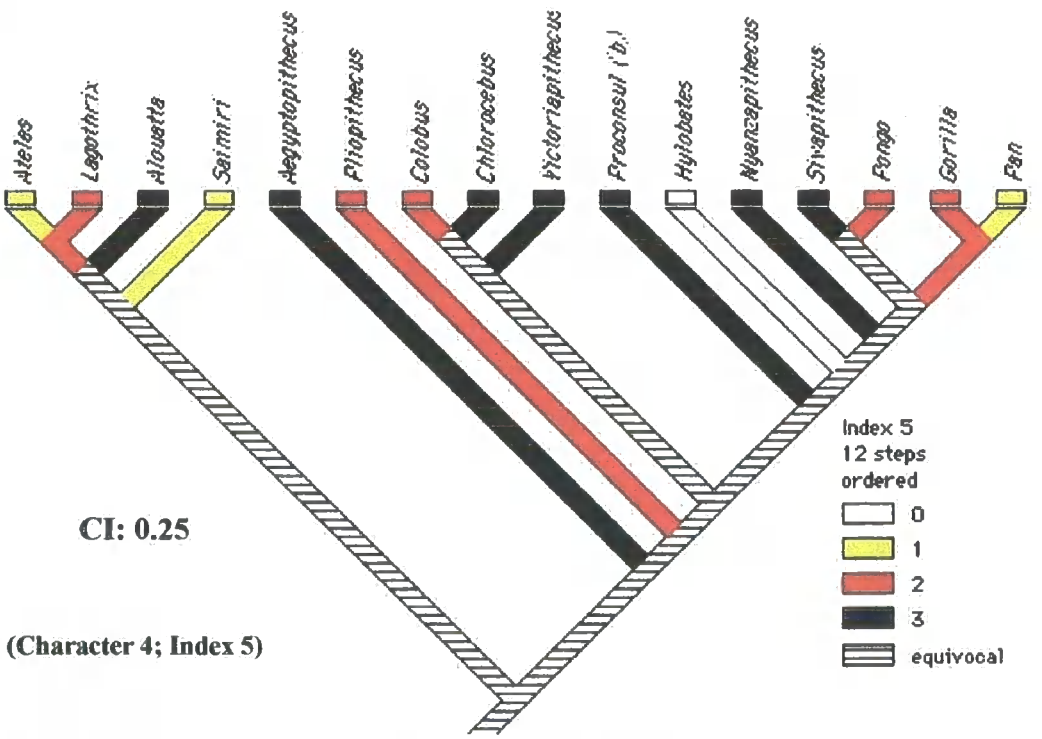

Figure 41: Humeral Head Shape AP/PD - Begun *et al.*'s (1997) Topology.

For descriptions of character states, see above.

Index 6

Medial & Lateral Trochlear Keel Development

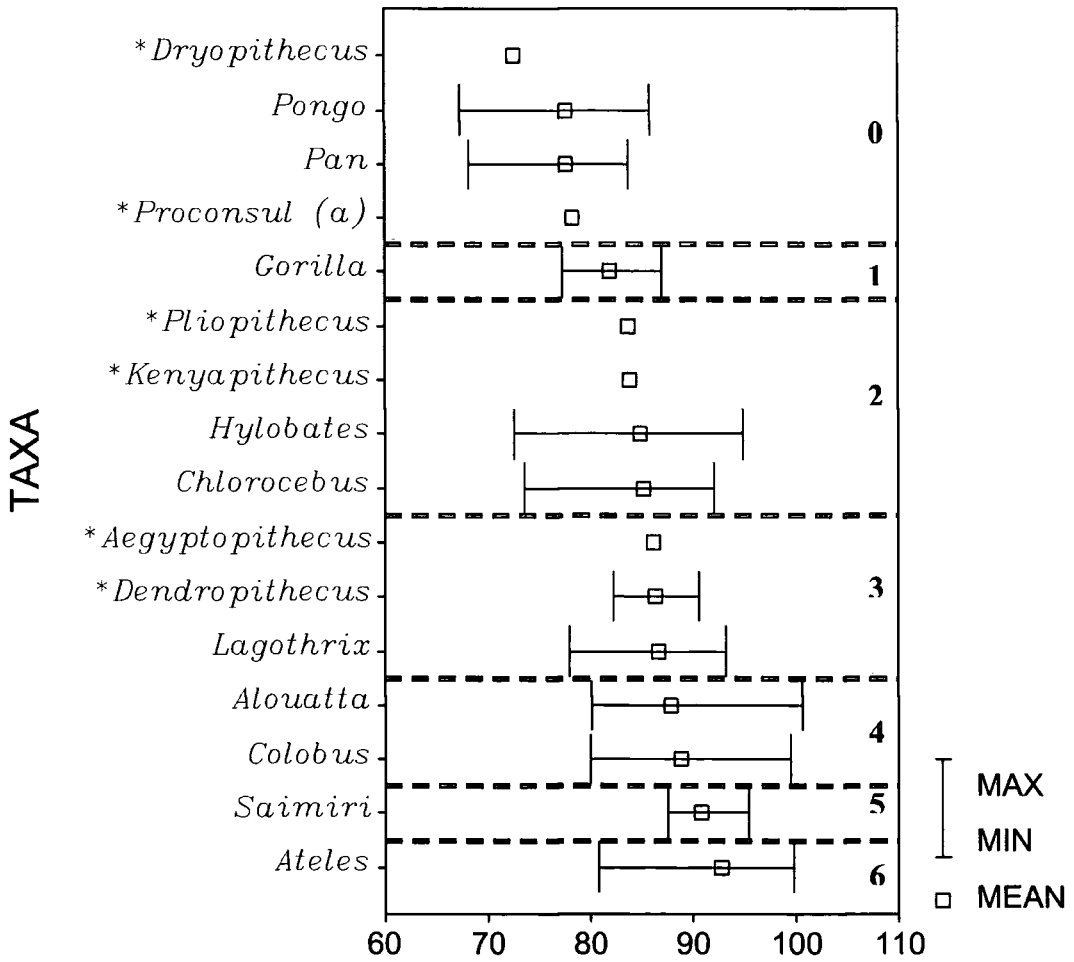

Figure 42: **Univariate Chart for Medial and Lateral Trochlear Keel Development (Fossil).**

Results and coding for medial and lateral trochlear keel development (Character 6; Index 6).

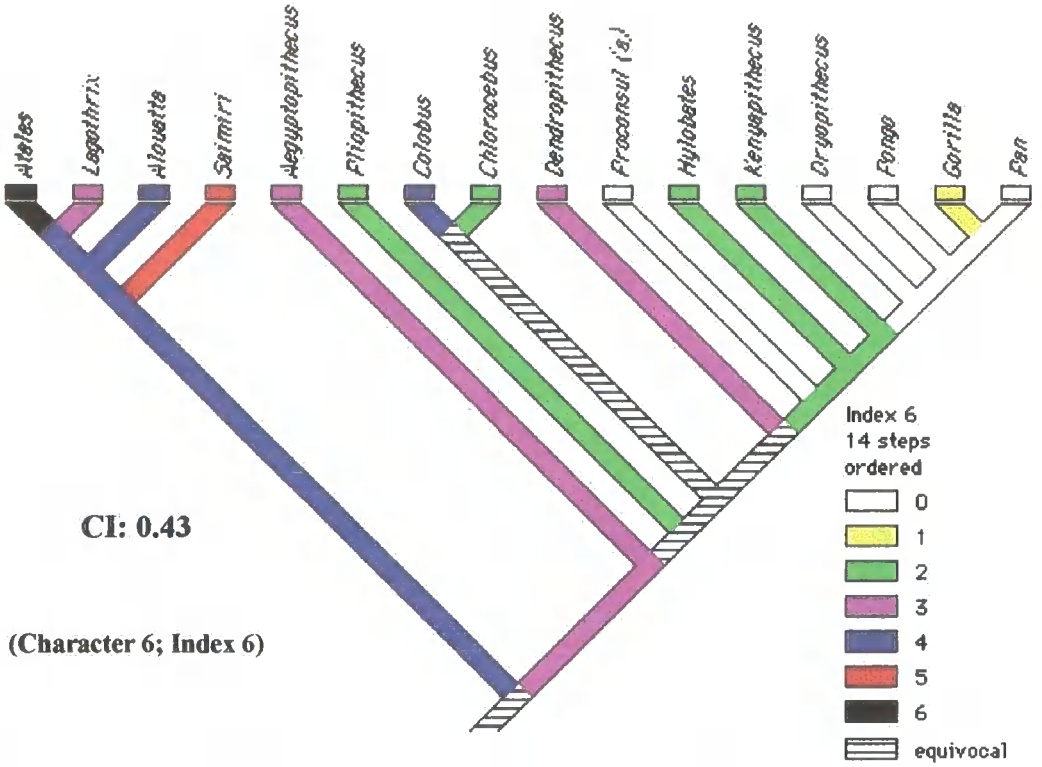

Figure 43: Medial and Lateral Trochlear Keel Development - Fleagle's (1999) Topology.

State 0 = very well-developed / State 6 = least developed

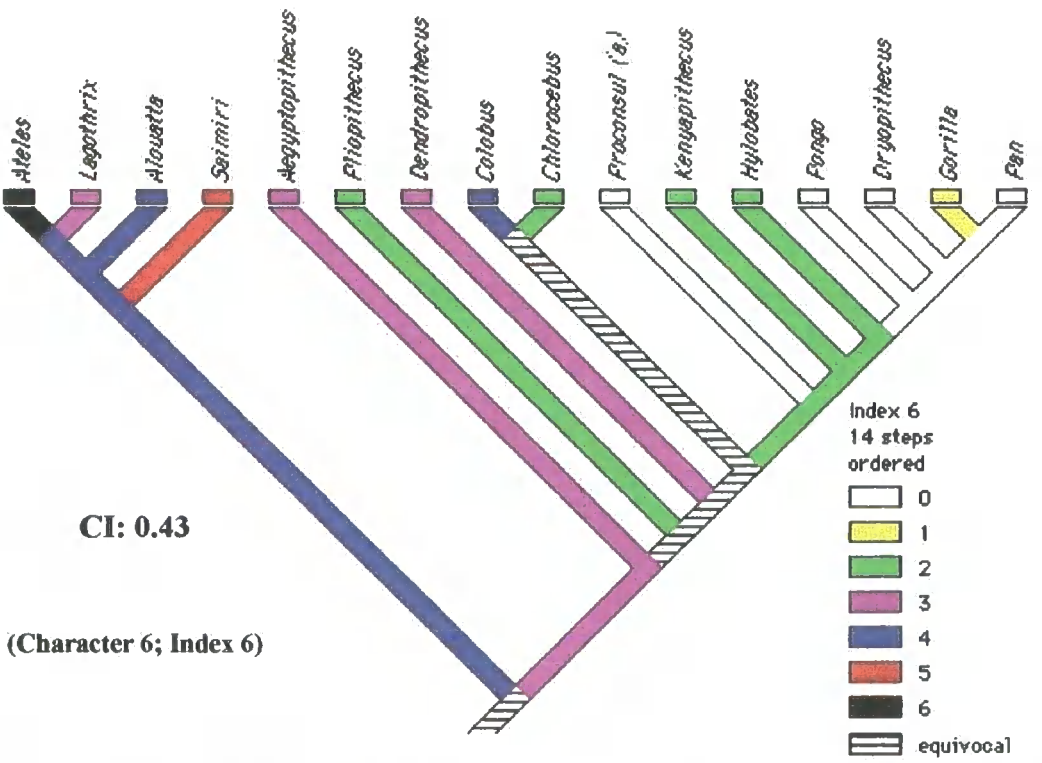

Figure 44: Medial and Lateral Trochlear Keel Development - Begun *et al.*'s (1997) Topology.

For descriptions of character states, see above.

Index 7

Trochlear Waisting

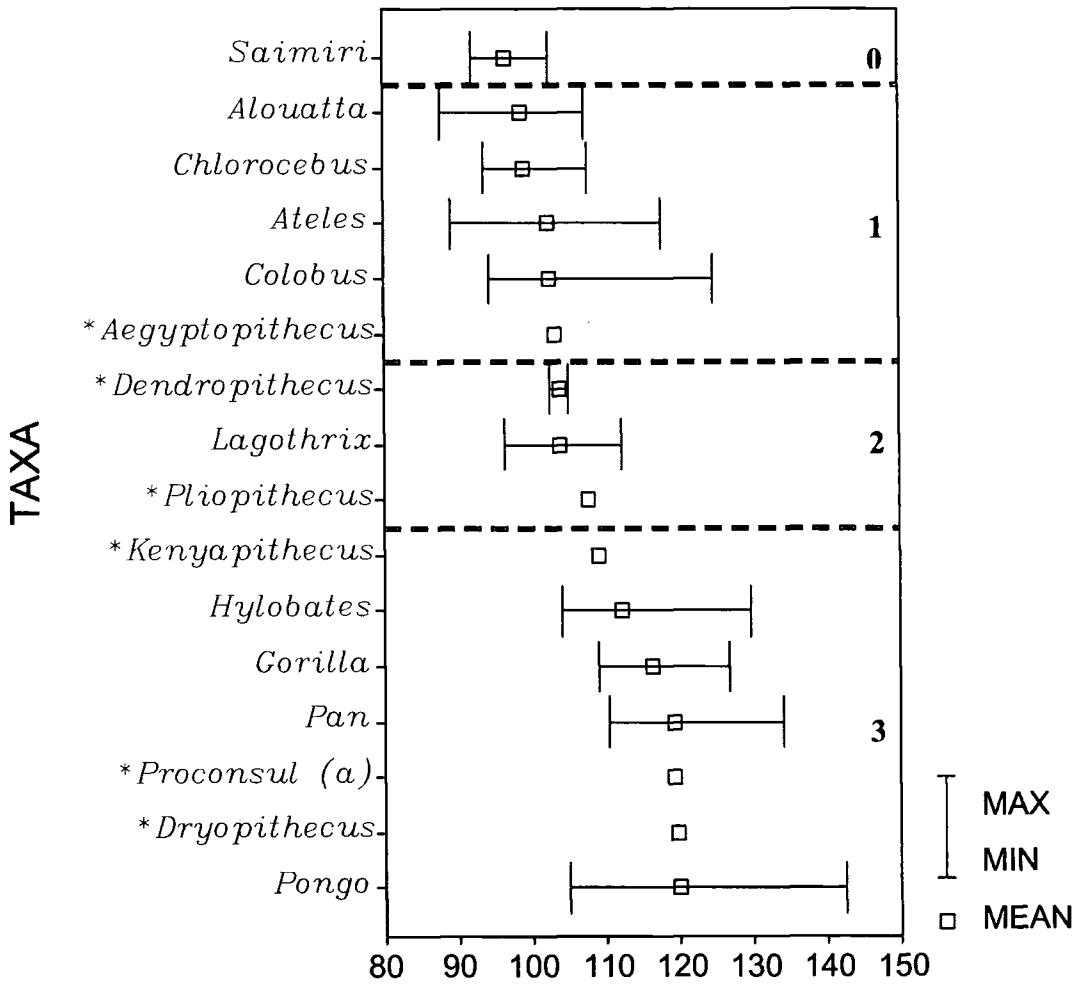

Figure 45: Univariate Chart for Trochlear Waisting (Fossil).

Results and coding for trochlear waisting (Character 6; Index 7).

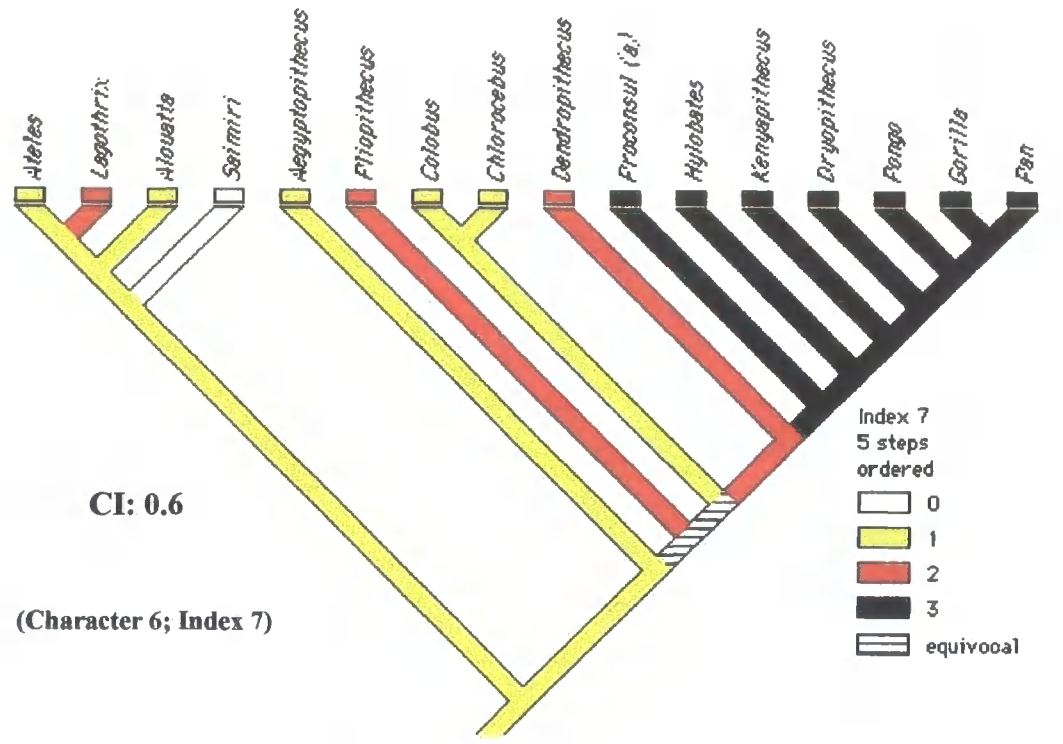

Figure 46: Trochlear Waisting - Fleagle's (1999) Topology.

State 0 = least waisted / State 3 = most waisted

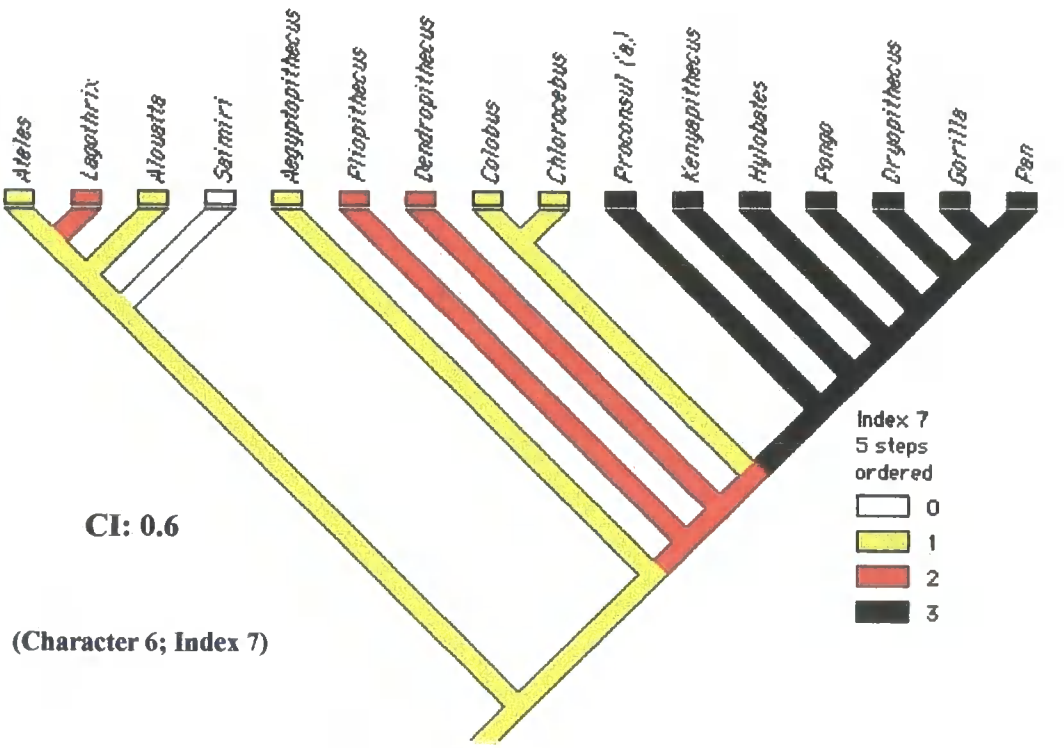

Figure 47: Trochlear Waisting - Begun *et al.*'s (1997) Topology.

For descriptions of character states, see above.

Begun *et al.*'s (1997) Topology:

Begun *et al.*'s (1997) placement of *Nyanzapithecus* as a stem hominid renders the ancestral hominoid and hominid nodes equivocal (Figure 41). These ancestral morphotypes could now be reconstructed as expressing either state 2 or 3. This further complicates the question of the polarity of these conditions and the relationships between the terminal taxa that exhibit them. *Pongo* and *Gorilla* would exhibit convergence if the ancestral hominid morphotype were reconstructed as state 3.

Summary of Character 4:

Overall, indices 3, 4 and 5 (Figures 33-41) indicate that extant hominoids are characterised by relatively wide (ML) humeral heads (*contra* Goodman, 1963; Ciochon, 1983; Andrews, 1985; Martin, 1986; Andrews and Martin, 1987; Harrison, 1987), while stem hominoids exhibit relatively long (AP) heads.

Sivapithecus displays a markedly different condition to its sister taxon (*Pongo*) in all three indices, having a head that is very long (AP) compared with its depth (PD) and, particularly, width (ML). *Proconsul* displays a similar morphology to *Sivapithecus*, although the head is slightly wider (ML). *Nyanzapithecus* displays a head that is both long (AP) and wide (ML), but quite shallow (PD).

Character 6: Medial and Lateral Trochlear Keel Development

Index 6: Lateral Trochlear Keel Development

Fleagle's (1999) Topology:

In this topology (Figure 43), *Dryopithecus* and *Kenyapithecus* are placed as stem hominids and *Proconsul* and *Dendropithecus* are placed as stem hominoids.

The results show that homoplasy (convergence) is evident in this index. *Pan*, *Gorilla*, *Pongo* and *Dryopithecus* are linked by synapomorphy and are converged upon by *Proconsul* in their possession of very marked lateral trochlear

keels (although *Gorilla* has subsequently independently developed a slightly less prominent LTK). *Hylobates* and *Kenyapithecus* both retain more primitive states and may converge on *Chlorocebus* and *Pliopithecus* in having a moderately developed LTK, depending upon the reconstruction of the ancestral catarrhine and hominoid nodes. *Dendropithecus* and *Aegyptopithecus* either exhibit symplesiomorphy or convergence, and both are convergent on *Lagothrix*, in their possession of a moderately prominent LTK. The other ceboids (*Ateles*, *Alouatta* and *Saimiri*) are autapomorphic in their possession of a weaker LTK.

Begun *et al.*'s (1997) Topology:

In this topology (Figure 44), *Kenyapithecus* is placed as a stem hominoid rather than a stem hominid, but since it retains a primitive condition (relative to hominids) for this trait (shared with *Hylobates*, *Chlorocebus* and *Pliopithecus*), this placement has little bearing on other taxonomic relationships. *Dryopithecus* is placed as a stem African ape rather than a stem hominid. This placement does not alter the synapomorphy exhibited by *Pan*, *Gorilla*, *Pongo* and *Dryopithecus*.

Index 7: Trochlear Waisting

Fleagle's (1999) Topology:

The results (Figure 46) show that all of the extant hominoids and all but one of the stem hominoids (*Dendropithecus*) are linked by synapomorphy, in having a markedly waisted trochlea. *Dendropithecus* and *Pliopithecus* are convergent on *Lagothrix* in displaying moderate trochlear waisting. *Aegyptopithecus*, *Alouatta*, *Ateles*, *Chlorocebus* and *Colobus* all share the primitive condition of having very little trochlear waisting. *Saimiri* is autapomorphic in possessing the least-waisted trochlea.

Begun *et al.*'s (1997) Topology:

The placement of *Dendropithecus* as a stem catarrhine in this topology (Figure 47) renders all of the stem hominoids (and extant hominoids) as synapomorphic, in their possession of highly waisted trochleae. The placement of

Dryopithecus as a stem African ape and *Kenyapithecus* as a stem hominoid does not alter the sequence of character evolution.

Summary of Character 6:

Indices 6 and 7 (Figures 42-47) indicate that *Pan*, *Pongo*, *Dryopithecus* and *Proconsul* exhibit the greatest development of the medial and lateral trochlear keels. In other respects, however, the results from these two indices are incongruent. Index 7 suggests that a well-developed lateral keel is synapomorphic for all stem and extant hominoids (with the exception of *Dendropithecus* in Fleagle's [1999] topology), as suggested by Goodman (1963), Ciochon (1983), Andrews (1985) and Andrews and Martin (1987). Index 6 suggests that well-developed medial and lateral keels are shared derived for hominids only (with *Proconsul* convergent on their condition), as suggested by Martin (1986).

Summary of Results for Fossil Catarrhine Analysis

The results from the analysis of fossil catarrhines show that well-developed medial and lateral trochlear keels are either a synapomorphy of the hominoid (Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987; Harrison, 1987) or hominid clade (Martin, 1986), while a globular/hemispherical humeral head is not a hominoid synapomorphy (*contra* Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987; Harrison, 1987). The character 'humeral head shape' does not distinguish hominoids from other taxonomic groups, and the character state 'globular/hemispherical' humeral head (previously interpreted as a hominoid synapomorphy; Ciochon, 1983; Andrews, 1985; Andrews and Martin, 1987; Harrison, 1987) is not exhibited by stem or extant hominoids and finds its greatest expression in *Lagothrix*. Homoplasy was evident in both characters, in the form of convergence and reversal, although no evidence of parallelism could be found. None of these traits, however, show homoplasy between two or more extant hominoid taxa, therefore it is unlikely that hylobatids, pongines or African apes/humans evolved these traits independently of each other.

CHAPTER SIX

DISCUSSION AND CONCLUSIONS

Introduction

In the preceding chapters, the pattern of character state change among hominoid taxa was examined using character analysis of the postcranial skeleton. The results of the analyses presented here indicate that: (1) some of the putative synapomorphies used to distinguish extant and stem hominoids from other anthropoid taxa are not in fact shared derived for this clade; (2) there is no homoplasy between living apes in the characters examined; and, (3) the supposed functional correlation of these traits with forelimb suspensory locomotion is unlikely. If these suppositions are correct, then a number of important questions are raised:

(1) If some of the characters hitherto interpreted as synapomorphies of the hominoid clade are not shared derived for this group, then what *are* the characteristics that distinguish hominoids from other anthropoid taxa?
(2) What are the implications for the phyletic status of fossil taxa that have previously been linked to extant hominoids (or individual hominoid genera) on the basis of these supposed synapomorphies?
(3) What do the characters that *are* interpreted here as synapomorphies of the hominoid, hominid and African ape/human clades tell us about the adaptations of the ancestral hominoid, hominid and African ape/human?
(4) What does the occurrence of homoplasy in four of the characters examined here tell us about ancestral hominoid, hominid and African ape/human adaptations?
(5) What does the fact that *Hylobates* and *Ateles* exhibit different conditions for eight of the nine characters examined here (as would not be expected if these characters are functionally linked with forelimb suspension) imply about the functional significance of these traits?

The following sections represent a discussion of possible answers to the above questions. Suggestions for further research are made and conclusions are drawn.

Hominoid Phylogeny

Extant Hominoid Synapomorphies

The extant Hominoidea is a group that has, historically, been distinguished from other anthropoid taxa on the basis of mainly postcranial (particularly trunk and forelimb) traits, although several craniofacial features also distinguish this group (Mann and Weiss, 1996; Pilbeam, 1996, 1997; Rae, 1999). Three[47] of the nine characters examined here, and interpreted by other workers as synapomorphies of the Hominoidea, have been shown by the analyses reported here not to be shared derived for this clade (one of the remaining putative synapomorphies, 'well-developed medial and lateral trochlear keels', may be shared derived for hominids only). If these three characters do not distinguish the hominoid clade from other anthropoids, then which characters do?

Five (possibly four[48]) of the nine characters used here have been shown to be synapomorphic for extant hominoids. Living apes are distinguished from cercopithecoids and quadrupedal ceboids by their shared possession of (1) a relatively broad manubrium (atelin taxa exhibit even broader manubria than extant hominoids and have developed this independently). *Pan*, *Pongo* and *Hylobates* can be distinguished from other anthropoids by their shared possession of (2) a small glenoid fossa angle (*Gorilla* has reversed to a primitive condition). All extant hominoids can be distinguished from other anthropoid taxa by their shared possession of (3) an abbreviated ulnar olecranon process, and (4) a relatively broad lunate. The results reported here are equivocal as to whether all extant apes are distinguished form other anthropoids by shared possession of (5) well-developed medial and lateral trochlear keels, or whether this applies only to the hominid clade (*Hylobates* and *Kenyapithecus* cannot be distinguished from

[47] The three characters are: globular humeral head shape; marked humeral head torsion; and, relatively short ulnar styloid process length.
[48] If the character 'well-developed medial and lateral trochlear keels' is a hominid, rather than a hominoid, synapomorphy.

Chlorocebus on the basis of lateral trochlear keel development; see Index 6, Figures 24, 43 and 44).

Larson (1998) has recently questioned the extent of hominoid postcranial similarities and synapomorphies, concluding that many of the characters that have been interpreted as shared derived for the hominoid clade actually exhibit morphological overlap with other anthropoid taxa. Out of thirty-five characters that had previously been interpreted as hominoid synapomorphies, only eight[49] were supported as shared derived for this clade (Larson, 1998). The results reported here support Larson's (1998) contention that hominoids display significant intergeneric morphological differences and are united by fewer derived postcranial features than was previously thought.

Fossil Hominoid Systematics

Fossil taxa are assigned a systematic position on the basis of features they share with living taxa that are hypothesized to be synapomorphic (Brooks and McLennon, 1991; Wiley *et al.*, 1991). The fact that some characteristics, previously thought to be diagnostic for living apes, have been shown here not to be shared derived for these taxa, has important implications for the phylogenetic status of fossil taxa that have been linked with the extant hominoid clade on the basis of such synapomorphies. If extant taxonomic groups cannot be differentiated by the presence or absence of a particular character state, then the usefulness of that character state for diagnosing the taxonomic placement of any fossil form must be seriously questioned (Sarmiento *et al.*, 2002).

For example, the character state 'globular/hemispherical humeral head shape', reported here not to be diagnostic for living apes, has been used by some workers (e.g., Harrison, 1986a; Sarmiento, 1987; Rose, 1994) to help justify the inclusion of certain fossil taxa (e.g., *Oreopithecus*) in the hominoid clade. The results reported here, however, have shown that extant hominoids are characterised by relatively wide (ML), rather than globular/hemispherical, humeral heads. If correct, this suggests that any fossil taxon that exhibits a

[49] The eight characters are: relatively broad shoulders, relatively broad sternal corpus, relatively elongated clavicle, humeral head shape AP/ML, well-developed medial and lateral trochlear keels, proximal ulnar less bilaterally compressed, short ulnar styloid process length and relatively broad lunate (Larson, 1998).

globular/hemispherical humeral head shape cannot be linked with the hominoid clade on this basis. Furthermore, these results have shown that stem hominoids are characterised by relatively long (AP) humeral heads, not wide[50] (ML) or globular/hemispherical humeral heads. These two points seem to indicate that the character 'humeral head shape' is not very useful for determining the relationships between fossil taxa and extant hominoids.

Hominoid Adaptations

Ancestral Hominoid Adaptations

In the absence of fossil candidates for the last common ancestor (LCA) of extant hominoids, it is necessary to reconstruct the morphology and adaptations of a hypothetical hominoid ancestor from the distribution of shared derived character states in living and stem forms, and their known functional significance (Begun, 1994).

Five (possibly four, see above) of the nine characters examined in the preceding analyses were shown to be synapomorphies of the extant hominoid clade: relatively wide manubrium, small glenoid fossa angle, well-developed medial and lateral trochlear keels, relatively short ulnar olecranon process length and relatively broad lunate. The results for one character, 'large humeral head size', may have been confounded by absolute differences in body size between taxa. In addition, four traits were found to exhibit homoplasy in the form of convergence or reversal: glenoid fossa angle, humeral head size, humeral head shape and medial and lateral trochlear keel development. None of these traits, however, exhibited homoplasy between two or more extant hominoid taxa; therefore it remains unlikely that hylobatids, pongines or African apes/humans evolved these traits independently of each other. What do these findings imply about the adaptations of the ancestral hominoid?

Possession of a broad manubrium is shown here to be a synapomorphy of the living apes (i.e., this trait was acquired by the LCA of the extant hominoids and has been inherited in all subsequent hominoid taxa). Several workers (e.g.,

[50] *Nyanzapithecus* exhibits a wide (ML) humeral head, relative to PD depth, but the head is still significantly longer (AP) than it is wide.

Goodman, 1963; Cartmill and Milton, 1977; Sarmiento, 1987; Gebo, 1996) have interpreted the broad manubria of hominoids to be related to the functional requirements of vertical climbing or forelimb suspensory locomotion. The distribution of character states for this trait, however, seem to indicate that possession of a wide manubrium may not be functionally linked with forelimb-dominated arboreal activities *per se*. This supposition is supported by the fact that *Pan* (essentially a digitigrade quadruped; Tuttle, 1986; Hunt, 1991a, b, 1992), has a relatively broader manubrium than any of the other hominoids, and by the fact that the almost exclusively quadrupedal *Gorilla* (Tuttle, 1986; Hunt, 1991b) exhibits the same condition as the almost exclusively forelimb suspensory *Hylobates* (Carpenter, 1976; Andrews and Groves, 1976; Hunt, 1991b).

The craniolateral orientation of the glenoid fossa is shown here to be a synapomorphy of the extant hominoids (with *Gorilla* exhibiting reversal). *Hylobates*, *Pan*, and *Pongo* possess glenoid fossae that are more cranially, than ventrolaterally directed. This means that it is most parsimonious for the hominoid LCA to be reconstructed as having had a relatively cranially directed glenoid fossa compared with other anthropoids.

Hylobates in particular has a very cranially orientated fossa with a mean angle of 102.75° compared with the next lowest of 113.47° for *Pan* and 114.57° for *Pongo*. The markedly divergent condition found in *Hylobates* is linked to the fact that the scapulae are placed higher on the thorax than in hominids (Andrews and Groves, 1976). This more cranially directed glenoid fossa has been functionally associated with increased mobility (and reduced stability) in the glenohumeral articulation (Ankel-Simons, 2000). *Gorilla* possesses a larger angle (118.53°) and therefore a more laterally facing glenoid fossa. Two of the New World monkey taxa (*Lagothrix* and *Saimiri*) display similar values to *Gorilla*. The fact that *Gorilla* has reversed to a condition similar to that of some extant ceboids is difficult to account for functionally, especially since *Pan* exhibits a markedly different condition and yet shares many of the same morphological and behavioural adaptations (Tuttle, 1969; Hunt, 1991b). Living humans also possess a laterally orientated glenoid fossa (Oxnard, 1963; Ankel-Simons, 2000), and this may indicate that the African ape/human common ancestor expressed this condition (in this scenario, *Pan* would be secondarily derived). The

cercopithecoids and *Alouatta* display the most ventrolaterally orientated glenoid fossae.

The analysis of humeral head size reported here has ostensibly shown that extant hominoids are synapomorphic in their possession of relatively large humeral heads. The humeral head of hominoids has previously been described as being relatively larger than those of other anthropoids and this has been correlated with forelimb-dominated (arboreal and terrestrial) locomotor habits (Harrison, 1987; Rose, 1989). If the results for this character are accurate, then the fact that the two most suspensory genera sampled here (*Hylobates* and *Ateles*) have relatively small humeral heads compared with the predominantly terrestrial African apes, would suggest that this trait is not linked to forelimb suspension. In addition, the possession by *Pongo* of a humeral head of similar relative size to the African apes would suggest that this feature is not associated with knuckle-walking.

The phylogenetic and functional signals from this character may have been obscured, however, possibly due to an inadequate control for allometric tendencies associated with body mass. Character state distributions for this trait (Figure 15) follow a trend roughly correlated with absolute body size. *Saimiri*, the smallest taxon sampled here (650-800g; Fleagle, 1999), also exhibits the smallest humeral head. *Chlorocebus* (3-8kg), *Colobus* (7.5-13.5kg), *Alouatta* (4-12kg) and *Lagothrix* (7-10kg) all display small to moderately sized heads. *Ateles* (7-9kg) and *Hylobates* (5-12kg) have slightly larger, medium sized heads, although they still cluster with other anthropoid taxa. *Pan* (♀33-45kg, ♂42-60kg), *Pongo* (♀37kg, ♂81kg) and *Gorilla* (♀70-90kg, ♂160-180kg) are markedly divergent in exhibiting by far the largest humeral heads. This trend appears to indicate that the use of the geometric mean of all measured variables as a surrogate size measure has not corrected for body mass differences between these taxa, although this method has been used successfully for other data sets (e.g., Mosimann and James, 1979). If this is the case, then the results for this trait reflect absolute, rather than relative humeral head size and therefore the character state 'relatively large humeral head size' cannot be supported as a hominoid synapomorphy.

The short ulnar olecranon process of extant hominoids is shown here to be a synapomorphy of this clade. The abbreviation of the ulnar olecranon process (together with the deep olecranon fossa on the distal humerus) has been

functionally associated with full extension and hyperextension capabilities at the elbow joint (Rose, 1988a), and for this reason is often judged to be implicated in forelimb suspensory activities (Rose, 1994, 1997). The fact that *Hylobates* retains a more primitive condition for this trait than hominids (*contra* Larson, 1998) suggests that this is not the case. *Ateles* follows a similar trend to living apes in this trait, without exhibiting full convergence on the hominoid condition. The fact that *Ateles* is the most suspensory non-hominoid taxon sampled and is more derived for this trait than any other extant ceboid or cercopithecoid, suggests some sort of link with suspensory behaviour, or other locomotor mode(s) necessitating similar mechanical capabilities.

A relatively broad lunate is shown here to be a shared derived characteristic of living apes, as suggested by Harrison (1987). The broadening of the lunate has been attributed to the expansion of the radial articular facet (Harrison, 1982, 1987). The functional significance of a broad lunate remains uncertain. It has been interpreted by some workers (e.g., Harrison, 1982; Sarmiento, 1988) as part of a suite of carpal adaptations to suspensory behaviour. The results reported here suggest that this is highly unlikely, as both *Hylobates* and *Ateles* display quite primitive conditions, while *Pongo*, and particularly the highly terrestrial African apes show a more derived condition.

The distribution of character states for this trait (Figure 32) suggests that the broadening of the lunate in living apes is correlated with an increase in body size. If there were an allometric tendency for lunates to increase in breadth as an artefact of large body size we would expect this to be evident in other large-bodied, non-hominoid primate taxa. The three ateline taxa (*Alouatta*, *Ateles* and *Lagothrix*) examined in this study have comparable body sizes to hylobatids, and yet all possess relatively narrower lunates than any living ape. Compared to the body mass of extant hominid taxa, however, atelines are relatively small-bodied. Perhaps a more valid comparison would be with the giant sub-fossil lemurs of Madagascar, as some of these taxa (e.g., *Archaeoindris*, *Lemuridotherium* and *Megaladapis*) exhibit a body size commensurate with that of extant hominids (Jungers, 1978, 1980; Vuillaume-Randriamanantena, 1988; Godfrey *et al.*, 1997; Hamrick *et al.*, 2000).

The analyses reported here show that the character 'well-developed medial and lateral trochlear keels' is either a synapomorphy of the hominoid or hominid

clade. Some workers have suggested that a well-developed LTK may be functionally correlated with vertical climbing (Sarmiento, 1987) or forelimb suspensory locomotion (Napier and Davis, 1959; Gebo, 1996). This is based on the supposition that the LTK acts as a stabilising agent in those primates who engage in suspensory locomotion, thus liberating the radius from its weight transmission role and permitting it to undergo a greater range of pronation/supination (Napier and Davis, 1959). The fact that *Hylobates* does not exhibit the most derived condition for this trait in Index 6, that *Pan* and *Gorilla* both show highly derived conditions, and that *Ateles* exhibits a highly primitive condition for this trait in both indices[51], suggests that LTK development is not functionally linked with forelimb suspensory locomotion (*contra* Napier and Davis, 1959; Gebo, 1996).

Rose (1988a) has previously suggested that development of the LTK is linked to forearm pronation during knuckle-walking. The LTK may prevent the proximal ulna from dislocating laterally (due to the sizable lateral stresses generated) during this movement. The fact that *Pongo* (a quadrumanous climber) and *Proconsul* (a pronograde arboreal quadruped) exhibit the greatest development of this trait seems incongruent with this hypothesis.

The fact that so many different taxa, with widely differing locomotor habits, exhibit the same condition of having a well-developed LTK and a high degree of trochlear waisting suggests that this character may not be functionally correlated with a particular extant mode of progression. It could be argued that a well-developed LTK evolved as an adaptation to suspensory behaviour early in the evolution of the hominoid clade and was subsequently 'retained' by the African apes and exapted for new purposes (i.e., knuckle-walking). Alternatively, it could be argued that the derived condition found in African apes is a product of phylogenetic 'lag' rather than adaptation (Richmond *et al.*, 2001).

The LCA of hominoids would therefore have possessed a wide manubrium, cranially orientated glenoid fossa, short ulnar olecranon process, broad lunate, and (possibly) well-developed medial and lateral trochlear keels. The hominoid ancestor may have possessed a relatively large humeral head,

[51] The suspensory atelin monkeys possess a prehensile tail, which may reduce stress in the forelimb joints and therefore reduce the need for stability in the elbow (as provided by the LTK) during hanging postures (Gebo, 1996).

though the validity of the results for this trait are uncertain. Despite being linked with forelimb suspensory activities by several workers, the distribution of character states in these analyses suggest that these traits are not functionally correlated with any forelimb-dominated arboreal activities (with the possible exception of 'relatively large humeral head size' and 'short olecranon process length'). Overall, the functional significance of these characters appears to be equivocal. The fact that these six characters cannot be unequivocally linked with a particular modern locomotor pattern severely reduces their diagnostic potential for reconstructing the adaptations of fossil and ancestral forms.

The inference that the hominoid LCA possessed a mediolaterally broad manubrium (probably indicating a transversely broad thorax), craniolaterally directed glenoid fossae, extensive flexion/extension and pronation/supination capabilities at the elbow and a broad lunate does not in itself shed light on basal hominoid adaptations, if the functional signal of these traits is unclear. The fact that all of the fossil hominoids sampled here (with the exception of *Dendropithecus*) exhibit moderate to marked development of the medial and lateral trochlear keels, does however, suggest that this trait evolved prior to the adoption of suspensory postures in the hominoid lineage.

Ancestral Hominid Adaptations

One (possibly two, see above) of the nine traits examined in the above analyses has been shown to be a synapomorphy of the hominid clade: short ulnar styloid process length. The reduction of ulnocarpal contact in hominids has been functionally linked to increased flexibility in the wrist joint, an adaptation that has been interpreted, variously, as facilitating forelimb suspensory locomotion (Lewis, 1971a, 1972b), cautious quadrupedalism (Cartmill and Milton, 1977), vertical climbing (Sarmiento, 1987, 1988) or knuckle-walking (Conroy and Fleagle, 1972).

Hylobates has been shown here to possess the least derived condition for this trait of all the hominoids; this suggests that this character may not be linked with forelimb suspension (*contra* Lewis, 1971a, 1972b), as pointed out by Cartmill and Milton (1977). (Cartmill and Milton's (1977) argument was based on the hominoid wrist morphology being converged upon by lorisine strepsirhines

who do not engage in suspensory activities. Lewis (1985), however, later showed that only hominoids have developed an intra-articular meniscus and that the lorisine ulnocarpal articulation is primitive). The fact that *Pongo* exhibits an equally derived condition to *Gorilla* suggests that this trait cannot be linked exclusively with knuckle-walking (*contra* Conroy and Fleagle, 1972), as suggested by Jenkins and Fleagle (1975). The association of this trait with cautious quadrupedalism and/or vertical climbing seems more likely, as all non-human hominids engage in these activities for at least a fraction of their locomotor repertoires (Hunt, 1991b).

The hominid LCA would have had a shortened ulnar styloid process. The reduction in styloid process length appears to have occurred prior to the divergence of the hominid lineage, possibly as a response to a locomotor repertoire heavily biased towards vertical climbing and/or cautious arboreal quadrupedalism. The African apes would have inherited this condition and, perhaps, exapted it for use in knuckle-walking.

Ancestral African Ape Adaptations

Marked humeral head torsion has been shown here to be a synapomorphy of the African ape/human clade. This character has previously been linked with forelimb-dominated suspensory behaviours (Le Gros Clark, 1971) and quadrumanous climbing. If this were the case, we would expect the most suspensory ceboid and hominoid taxa (*Ateles*, *Hylobates* and *Pongo*) to exhibit the most medial torsion of the humeral head. The fact that *Gorilla*, the most terrestrial of the extant apes, exhibits the greatest medial torsion suggests that this is not so.

Greater angles of humeral head torsion are biomechanically linked with craniolaterally directed glenoid fossae (Le Gros Clark, 1971; Larson, 1988). Dorsally positioned scapulae (as found in living apes) redirect the ventrally facing glenoid fossae of most anthropoids to a more craniolateral position (Gebo, 1996; Larson, 1996). If the humeral head was orientated posteriorly and articulated with this more superolaterally facing glenoid fossa, then the entire forelimb would be rotated to face laterally when at rest (Ankel-Simons, 2000).

It has been reported here that the African apes display the greatest degree of humeral head torsion of all anthropoids. These results support the hypothesis

put forward by Larson (1988) that marked humeral head torsion is functionally correlated with quadrupedalism, and in particular knuckle-walking, rather than forelimb-dominated arboreal activities. Presumably, this is because of the biomechanical need in hominoids who engage in this form of digitigrade quadrupedalism, to maintain an elbow joint that functions in a parasagittal plane with a scapula that is positioned dorsally (Larson, 1988, 1996). It has been suggested that hylobatids exhibit moderate, rather than marked humeral head torsion due to the extreme lateral rotation of the distal humerus that is necessary to perform rapid ricochetal brachiation (Larson, 1988, 1996). Although this may be the case for *Hylobates*, it does not account for the fact that *Pongo* also displays the primitive condition of having moderate torsion, and yet does not engage in ricochetal brachiation.

The LCA of the African ape/human clade would therefore have possessed a high degree of humeral head torsion. The functional signal for this character appears to be clear and indicates that marked medial torsion of the humeral head evolved as an adaptation to knuckle-walking, in primates that had inherited dorsally positioned scapulae.

Functional Significance of Hominoid Trunk and Forelimb Traits

The characters used in the above analyses have all been implicated in facilitating the behaviour of forelimb suspension (Larson, 1998). If this were the case, we would expect that the most suspensory taxa in these analyses (*Ateles* and *Hylobates*) would both exhibit the same condition for these traits. Which, if any, of the nine characters examined here can be functionally linked with forelimb-dominated arboreal activities?

The results show that *Hylobates* and *Ateles* share the same state (through convergence) in only one of the nine characters: relative humeral head size. The validity of the results for this trait have already been called into question, however, and thus it remains uncertain whether these two taxa are convergent on each other, or whether they display the same condition because they exhibit a similar body size. If *Hylobates* and *Ateles* were genuinely convergent on each other, it would be reasonable to suppose that this trait is correlated with forelimb-

suspensory activity. For most of the traits examined here, however, these two taxa display very divergent conditions.

The preceding analyses showed that most of the nine characters examined here are not as diagnostic of locomotor behaviour as previously thought. This raises the question of what this weak functional signal can be attributed to? Perhaps the LCAs of the hominoids, hominids and African ape/humans exhibited locomotor patterns that have no analogue in extant/modern forms; i.e., these traits represent an adaptation to an extinct locomotor mode. If so, this poses a severe problem in the attempt to reconstruct the ancestral adaptations of these clades. Alternatively, perhaps many of these traits are not as adaptive as previously thought; i.e., they are merely "architectural by-products" (Gould and Lewontin, 1979:147) of other adaptive traits.

Further Research

The present study has sought to ascertain the extent of homoplasy and synapomorphy in the superfamily Hominoidea. A number of suggestions for further research can be implied from the outcome of this study. Further study in this area would benefit from the use of a greater number and range of characters. The inclusion of cranial and other postcranial (hindlimb) characters in an analysis would be beneficial, as this would provide a broader anatomical perspective from which to evaluate the nature of the similarities between the hylobatids, pongines and African apes/humans. Characters that are also well-represented in the known hominoid fossil record would be particularly beneficial, as parallelism can only be diagnosed when fossil taxa are included in an analysis.

Summary and Conclusions

The analyses reported in this study show that five of the nine characters examined are hominoid synapomorphies: relatively wide manubrium, small glenoid fossa angle, well-developed medial and lateral trochlear keels, relatively short ulnar olecranon process length and relatively broad lunate. Of the remaining traits, one is shared derived for hominids (relatively short ulnar styloid process length), one is a synapomorphy of the African ape/human clade (marked humeral

head torsion), one is not diagnostic for apes at all (globular/round humeral head), and one reflects absolute differences in body size between taxa (large humeral head size). Four traits exhibit homoplasy, in the form of convergence or reversal: glenoid fossa orientation, relative humeral head size, humeral head shape and medial and lateral trochlear keel development. None of these traits, however, show homoplasy between two or more extant hominoid taxa; therefore it is unlikely that hylobatids, pongines or African apes/humans evolved these traits independently of each other.

One striking conclusion that can be drawn from these analyses is that the functional significance of eight of the nine characters examined (all except marked humeral head torsion) is equivocal. This severely reduces the diagnostic potential of these traits for reconstructing the adaptations of fossil and ancestral taxa. The weak functional signal produced by the traits examined here may be due to their having evolved as adaptations to ancestral (now extinct) locomotor patterns for which modern analogues do not exist.

This is supported by the fact that one of the characters that has been shown to be a hominoid synapomorphy (well-developed medial and lateral trochlear keels), and which has previously been linked to suspensory behaviour, appears to have arisen early in the evolution of the clade (before *Proconsul*). Since early and middle Miocene hominoids clearly exhibit morphology inconsistent with the employment of forelimb suspension (Rose, 1994; Pilbeam, 1996), and since well-developed LTKs are not exclusively associated with these arboreal quadrupeds, it seems reasonable to suppose that this trait (and possibly others) evolved as an adaptation to an extinct locomotor mode.

Three main conclusions can be drawn from this study: (1) some of the characteristics previously interpreted as synapomorphies for extant and stem hominoids are not in fact shared derived for this clade; (2) there is no homoplasy between extant hominoid genera in the features examined; and, (3) the association of these traits with forelimb suspensory locomotion is unlikely.

APPENDIX

Inter-observer Error

Data used in this study were collected both from specimens held in museum collections and from the published literature. The extant and fossil data were therefore measured by different workers. Only a few of the measurements taken on the extant specimens could be achieved from the literature. As a result, the only indices that could be meaningfully compared with the extant data were those of humeral head shape and medial and lateral trochlear keel development.

Data on fossil catarrhines were taken from various sources. Distal humerus values for all fossil taxa were taken from Rose (1988a, Table 1B). Proximal humerus values were taken from the following sources: (1) Rose (1989, Tables 2, 3A) - AP and PD values for *Aegyptopithecus*, *Pliopithecus* and *Proconsul*; (2) McCrossin (1992, Table 1) - *Nyanzapithecus*, all values and *Victoriapithecus* PD; (3) Harrison (1989, Table 2) *Victoriapithecus* AP and ML. ML values for *Aegyptopithecus* were the means of values in Fleagle and Simons (1982, Table 1) and Rose (1989, Tables 2, 3A). ML values for *Pliopithecus* and *Proconsul* were the means of values in Gebo *et al.* (1988, Table 1) and Rose (1989, Tables 2, 3A).

Rose (1988a, 1989) presented comparative data on extant taxa together with fossil data. This allowed the comparison of published data with that procured from museum collections for this study. Measurements for all humeral indices (Indices 3, 4, 5, 6 and 7) were found to be roughly comparable between the two data sets, thus indicating that the fossil data could be meaningfully compared with the extant data. Although data were found to be comparable across all taxa, for the purpose of brevity, the data presented for comparison here (Tables 6 and 7) represent a random selection of one taxon for each of the relevant indices.

Table 6: Data for Extant Anthropoids Presented in Rose (1988a, 1989).

Indices	Taxa	N	Mean	S.D.	Range
Index 3	*Saimiri*	20	102.6	3.4	97 – 110
Index 4	*Pongo*	12	90.5	6.0	81 – 98
Index 5	*Ateles*	14	96.4	5.4	86 – 102
Index 6	*Ateles*	10	93.1	3.9	88 – 99
Index 7	*Cercopithecus*	10	98.6	5.5	91 – 107

Table 7: Data for Extant Anthropoids Collected from the AMNH and NMNH.

Indices	Taxa	N	Mean	S.D.	Range
Index 3	*Saimiri*	12	102.54	4.98	95.58 – 111.01
Index 4	*Pongo*	16	90.57	6.02	78.40 – 102.57
Index 5	*Ateles*	18	98.19	8.68	84.62 – 110.66
Index 6	*Ateles*	18	92.76	5.17	80.86 – 99.79
Index 7	*Chlorocebus*	14	99.06	4.20	93.71 – 107.70

Summary Data Tables

The following tables summarise the extant and fossil data collected for this study. Sample sizes (N), arithmetic means, standard deviations (S.D.) and ranges are given for all ten indices and both angles. Data on extant anthropoids were taken from the collections of the American Museum of Natural History, New York, and the National Museum of Natural History, at the Smithsonian Institution, Washington D.C. Data on fossil catarrhines were taken from the literature; sources are given above and in Chapter Five, Table 4. For a list of indices and a discussion of measurements taken, see Chapter Four.

Table 8: Index 1 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Chlorocebus aethiops	14	94.70	15.99	74.10 – 129.67
Saimiri sciureus	12	94.89	12.17	75.39 – 113.73
*Alouatta**	12	97.10	37.97	57.67 – 169.61
*Colobus**	12	104.81	19.25	75.03 – 150.49
*Hylobates**	21	118.25	17.64	87.11 – 155.23
Gorilla gorilla	15	122.74	17.16	94.39 – 154.29
Pongo pygmaeus	15	124.92	12.30	99.45 – 143.54
Pan troglodytes	17	131.68	20.65	79.76 – 172.75
Lagothrix lagothrichca	12	155.01	13.26	137.37 – 177.10
*Ateles**	14	179.93	54.89	60.37 – 303.51

* For *Alouatta*, *Ateles*, *Colobus* and *Hylobates*, the samples were made up of specimens from several species of each genus. Samples for other genera were made up from a single species.

Table 9: Index 2 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Saimiri sciureus	12	9.14	0.47	8.36 – 9.91
Chlorocebus aethiops	14	15.18	1.48	12.32 – 17.48
Colobus	16	19.48	2.81	14.90 – 24.09
Alouatta	16	19.93	2.70	14.39 – 24.07
Lagothrix lagothrichca	14	20.81	1.92	16.82 – 24.47
Ateles	18	24.52	3.89	17.82 – 32.60
Hylobates	22	25.00	4.42	17.80 – 34.77
Pan troglodytes	17	64.72	8.46	51.12 – 83.46
Pongo pygmaeus	16	72.70	10.74	57.42 – 95.34
Gorilla gorilla	15	92.64	10.62	75.30 – 116.07

Table 10: Index 3 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
**Nyanzapithecus*	1	80.95	-	-
Gorilla gorilla	15	81.10	3.22	72.47 – 85.55
**Victoriapithecus*	1	83.48	-	-
Pan troglodytes	17	83.99	6.68	74.28 – 94.13
Chlorocebus aethiops	14	85.34	3.91	74.79 – 89.55
Colobus	16	85.64	4.79	78.26 – 91.78
Pongo pygmaeus	16	89.13	5.31	81.14 – 99.07
Hylobates	22	89.67	5.62	77.13 – 101.99
Ateles	18	91.39	6.03	81.74 – 103.37
**Proconsul* (b)	1	94.29	-	-
**Sivapithecus*	1	95.04	-	-
**Pliopithecus*	1	96.49	-	-
Alouatta	16	98.03	4.19	89.72 – 109.00
Lagothrix lagothrichca	14	102.16	4.50	94.46 – 109.18
Saimiri sciureus	12	102.54	4.98	95.58 – 111.01
**Aegyptopithecus*	1	103.23	-	-

* In this and all subsequent tables, fossil taxa are indicated by an asterisk.

Table 11: Index 4 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Hylobates	22	75.96	6.42	60.68 – 88.51
Pan troglodytes	17	79.57	5.31	71.64 – 87.55
Gorilla gorilla	15	83.31	3.78	75.22 – 88.90
Colobus	16	88.97	4.66	82.24 – 97.22
Ateles	18	89.57	8.33	79.75 – 112.45
Pongo pygmaeus	16	90.57	6.02	78.40 – 102.57
Chlorocebus aethiops	14	92.56	4.55	83.54 – 98.81
Saimiri sciureus	12	99.00	6.47	85.98 – 107.05
**Pliopithecus*	1	100.00	-	-
Lagothrix lagothrichca	14	103.61	5.82	91.38 – 111.15
**Sivapithecus*	1	107.44	-	-
**Proconsul* (b)	1	108.57	-	-
**Nyanzapithecus*	1	108.84	-	-
Alouatta	16	108.91	7.57	94.61 – 119.51
**Aegyptopithecus*	1	115.48	-	-
**Victoriapithecus*	1	115.65	-	-

Table 12: Index 5 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Hylobates	22	85.16	10.13	62.81 – 103.83
Pan troglodytes	17	95.35	10.43	80.05 – 115.33
Saimiri sciureus	12	96.72	7.63	87.29 – 110.05
Ateles	18	98.19	8.68	84.62 – 110.66
Lagothrix lagothrichca	14	101.59	7.12	89.68 – 114.49
Pongo pygmaeus	16	101.75	6.19	94.15 – 112.65
Gorilla gorilla	15	102.95	7.40	90.16 – 118.83
**Pliopithecus*	1	103.64	-	-
Colobus	16	104.06	5.83	94.07 – 115.92
Chlorocebus aethiops	14	108.57	5.09	100.43 – 117.52
Alouatta	16	111.29	9.27	96.78 – 130.54
**Aegyptopithecus*	1	111.88	-	-
**Sivapithecus*	1	113.04	-	-
**Proconsul* (b)	1	115.15	-	-
**Nyanzapithecus*	1	134.45	-	-
**Victoriapithecus*	1	138.54	-	-

Table 13: Index 6 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
**Dryopithecus*	1	72.70	-	-
Pongo pygmaeus	16	77.68	4.98	67.45 – 85.95
Pan troglodytes	17	77.79	3.65	68.17 – 83.71
**Proconsul* (a)	1	78.40	-	-
Gorilla gorilla	15	81.99	2.42	77.32 – 87.08
**Pliopithecus*	1	83.70	-	-
**Kenyapithecus*	1	84.00	-	-
Hylobates	22	84.90	5.24	72.66 – 94.98
Chlorocebus aethiops	14	85.17	5.15	73.63 – 92.08
**Aegyptopithecus*	1	86.30	-	-
**Dendropithecus*	2	86.45	-	82.30 – 90.60
Lagothrix lagothrichca	14	86.71	4.65	78.03 – 93.21
Alouatta	15	87.86	5.79	80.12 – 100.59
Colobus	16	88.86	3.83	79.93 – 99.49
Saimiri sciureus	12	90.89	2.38	87.50 – 95.40
Ateles	18	92.76	5.17	80.86 – 99.79

Table 14: Index 7 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Saimiri sciureus	12	96.48	2.59	92.11 – 102.40
Alouatta	15	98.58	4.84	87.68 – 107.20
Chlorocebus aethiops	14	99.06	4.20	93.71 – 107.70
Ateles	18	102.32	6.55	89.18 – 117.82
Colobus	16	102.51	6.67	94.32 – 124.83
**Aegyptopithecus*	1	103.20	-	-
**Dendropithecus*	2	103.85	-	102.60 - 105.10
Lagothrix lagothrichca	14	103.92	4.47	96.42 – 112.32
**Pliopithecus*	1	107.80	-	-
**Kenyapithecus*	1	109.20	-	-
Hylobates	22	112.17	6.70	103.98 – 129.82
Gorilla gorilla	15	116.43	4.87	109.07 – 126.86
Pan troglodytes	17	119.35	6.65	110.54 – 133.99
**Proconsul* (a)	1	119.40	-	-
**Dryopithecus*	1	119.80	-	-
Pongo pygmaeus	16	120.10	10.61	105.00 – 142.46

Table 15: Index 8 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Pongo pygmaeus	16	0.24	0.17	0.02 – 0.57
Pan troglodytes	17	0.25	0.14	0.05 – 0.47
Gorilla gorilla	15	0.45	0.19	0.11 – 0.94
Hylobates	19	0.66	0.26	0.29 – 1.25
Ateles	15	3.71	0.40	3.05 – 4.32
Chlorocebus aethiops	14	4.81	0.51	4.29 – 5.85
Lagothrix lagothrichca	14	5.01	0.55	4.22 – 6.21
Saimiri sciureus	12	5.19	0.50	4.54 – 6.11
Colobus	12	5.26	0.79	3.81 – 6.69
Alouatta	14	6.95	0.74	5.31 – 7.94

Table 16: Index 9 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Gorilla gorilla	15	0.71	0.37	0.22 – 1.46
Pongo pygmaeus	16	1.42	0.73	0.29 – 2.60
Pan troglodytes	17	2.48	0.80	1.39 – 4.01
Hylobates	19	9.52	2.48	5.95 – 15.60
Alouatta	14	9.73	2.28	6.23 – 13.86
Colobus	12	9.88	1.79	8.02 – 13.67
Ateles	16	10.34	2.55	6.47 – 15.32
Chlorocebus aethiops	14	11.52	2.64	6.69 – 18.53
Lagothrix lagothrichca	14	11.63	2.2	8.96 – 15.19
Saimiri sciureus	12	18.90	3.28	12.06 – 23.06

Table 17: Index 10 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Colobus	12	56.01	5.49	47.92 – 66.54
Chlorocebus aethiops	12	56.13	4.23	48.60 – 61.65
Saimiri sciureus	12	57.24	6.08	46.44 – 66.31
Ateles	13	58.00	6.69	45.23 – 66.45
Lagothrix lagothrichca	13	60.37	8.11	52.04 – 75.38
Alouatta	12	60.72	5.98	51.73 – 70.64
Hylobates	17	63.06	6.31	52.00 – 74.43
Pongo pygmaeus	15	69.92	3.87	62.38 – 76.11
Gorilla gorilla	13	73.51	8.09	60.68 – 88.28
Pan troglodytes	17	79.02	5.89	61.63 – 87.23

Table 18: Angle 1 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Hylobates	20	102.75	9.07	92 – 128
Pan troglodytes	17	113.47	3.97	106 – 120
Pongo pygmaeus	15	114.57	5.16	106 – 125
Ateles	16	117.13	5.33	109 – 126
Saimiri sciureus	12	117.83	2.86	112 – 122
Gorilla gorilla	15	118.53	7.41	110 – 141
Lagothrix lagothrichca	14	118.61	3.87	111 – 125
Colobus	12	124.42	3.73	116 – 129
Alouatta	14	125.86	4.29	117 – 132
Chlorocebus aethiops	14	126.00	4.13	120 – 132

Table 19: Angle 2 (sample size / mean / standard deviation / range).

Taxa	N	Mean	S.D.	Range
Chlorocebus aethiops	14	72.43	7.12	55 – 84
Colobus	16	84.88	10.35	62 – 105
Saimiri sciureus	12	101.33	10.24	85 – 116
Alouatta	16	103.06	6.62	86 – 115
Hylobates	21	103.95	14.23	80 – 138
Lagothrix lagothrichca	14	104.71	4.34	99 – 112
Pongo pygmaeus	16	106.88	13.92	83 – 141
Ateles	18	110.39	6.10	98 – 118
Pan troglodytes	17	127.88	10.26	106 – 150
Gorilla gorilla	15	130.33	8.16	118 – 149

REFERENCES

Aiello, L.C. (1981a) Locomotion in the Miocene Hominoidea. In C.B. Stringer (ed.): *Aspects of Human Evolution*, pp. 63-98. Taylor and Francis: London.

Aiello, L.C. (1981b) The allometry of primate body proportions. *Symp. Zool. Soc. Lond.* **48**:331-358.

Aiello, L.C. (1984) Applications of allometry: the postcrania of the higher primates. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.): *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 170-179. Edinburgh University Press: Edinburgh.

Aiello, L.C. and Dean, C. (1990) *An Introduction to Human Evolutionary Anatomy*. Academic Press: London.

Alba, D.M., Moyà-Solà, S., Köhler, M. and Rook, L. (2001) Heterochrony and the cranial anatomy of *Oreopithecus*: some cladistic fallacies and the significance of developmental constraints in phylogenetic analysis. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 284-315. Cambridge University Press: Cambridge.

Allbrook, D. and Bishop, W.W. (1963) New fossil hominoid material from Uganda. *Nature* **197**:1187-1190.

Andrews, P.J. (1985) Family group systematics and evolution among catarrhine primates. In E. Delson (ed.): *Ancestors: The Hard Evidence*, pp. 14-22. Alan R. Liss: New York.

Andrews, P.J. (1992) Evolution and environment in the Hominoidea. *Nature* **360**:641-646.

Andrews, P.J. and Cronin, J.E. (1982) The relationships of *Sivapithecus* and *Ramapithecus* and the evolution of the orang-utan. *Nature* **297**:541-546.

Andrews, P.J. and Groves, C.P. (1976) Gibbons and brachiators. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 4. Suspensory Behaviour, Locomotion, and other Behaviours of Captive Gibbons; Cognition*, pp. 167-218. S. Karger: Basel.

Andrews, P.J., Harrison, T., Martin, L.B. and Pickford, M.H.L. (1981) Hominoid primates from a new Miocene locality named Meswa Bridge in Kenya. *J. Hum. Evol.* **10**:123-128.

Andrews, P.J. and Martin, L.B. (1987) Cladistic relationships of extant and fossil hominoids. *J. Hum. Evol.* **16**:101-118.

Andrews, P.J. and Simons, E.L. (1977) A new African Miocene gibbon-like genus, *Dendropithecus* (Hominoidea, Primates) with distinctive postcranial adaptations: its significance to origin of Hylobatidae. *Folia Primatol.* **28**:161-169.

Ankel-Simons, F. (2000) *Primate Anatomy: An Introduction. Second edition.* Academic Press: San Diego.

Archie, J.W. (1985) Methods for coding variable morphological features for numerical taxonomic analysis. *Syst. Zool.* **34**:325-345.

Ashton, E.H. and Oxnard, C.E. (1963) The musculature of the primate shoulder. *Trans. Zool. Soc. Lond.* **29**:553-650.

Ashton, E.H. and Oxnard, C.E. (1964a) Functional adaptations in the primate shoulder girdle. *Proc. Zool. Soc. Lond.* **142**:49-66.

Ashton, E.H. and Oxnard, C.E. (1964b) Locomotor patterns in primates. *Proc. Zool. Soc. Lond.* **142**:1-28.

Avis, V. (1962) Brachiation: the crucial issue in man's ancestry. *Southwestern J. Anthropol.* **18**:119-148.

Ax, P. (1985) Stem species and the stem lineage concept. *Cladistics* **1**:279-287.

Azzaroli, A., Boccaletti, M., Delson, E., Moratti, G. and Torre, D. (1986) Chronological and paleogeographical background to the study of *Oreopithecus bambolii*. *J. Hum. Evol.* **15**:533-540.

Baldwin, J.D. (1985) The behaviour of squirrel monkeys (*Saimiri*) in natural environments. In L.A. Rosenblum and C.L. Coe (eds.): *Handbook of Squirrel Monkey Research*, pp. 35-53. Plenum Press: New York.

Baldwin, L.A. and Teleki, G. (1976) Patterns of gibbon behaviour on Hall's Island, Bermuda. A preliminary ethogram for *Hylobates lar*. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 4. Suspensory Behaviour, Locomotion, and other Behaviours of Captive Gibbons; Cognition*, pp. 21-105. S. Karger: Basel.

Beard, K.C., Teaford, M.F. and Walker, A.C. (1986) New wrist bones of *Proconsul africanus* and *P. nyanzae* from Rusinga Island, Kenya. *Folia Primatol.* **47**:97-118.

Begun, D.R. (1988a) Catarrhine phalanges from the late Miocene (Vallesian) of Rudabánya, Hungary. *J. Hum. Evol.* **17**:413-438.

Begun, D.R. (1988b) Diversity and affinities of *Dryopithecus*. *Am. J. Phys. Anthropol.* **75**:185.

Begun, D.R. (1992a) *Dryopithecus crusafonti* sp. nov., a new Miocene hominoid species from Can Ponsic (northeastern Spain). *Am. J. Phys. Anthropol.* **87**:291-309.

Begun, D.R. (1992b) Miocene fossil hominids and the chimp-human clade. *Science* **257**:1929-1933.

Begun, D.R. (1992c) Phyletic diversity and locomotion in primitive European hominids. *Am. J. Phys. Anthropol.* **87**:311-340.

Begun, D.R. (1993) New catarrhine phalanges from Rudabánya (northeastern Hungary) and the problem of parallelism and convergence in hominoid postcranial morphology. *J. Hum. Evol.* **24**:373-402.

Begun, D.R. (1994) Relations among the great apes and humans: new interpretations based on the fossil great ape *Dryopithecus*. *Yearb. Phys. Anthropol.* **37**:11-63.

Begun, D.R. (2000) Middle Miocene hominoid origins. *Science* **287**:2375a.

Begun, D.R. (2001) African and Eurasian Miocene hominoids and the origins of the Hominidae. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 231-253. Cambridge University Press: Cambridge.

Begun, D.R. and Kordos, L. (1997) Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 291-316. Plenum Press: New York.

Begun, D.R., Teaford, M.F. and Walker, A.C. (1994) Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *J. Hum. Evol.* **26**:89-165.

Begun, D.R., Ward, C.V. and Rose, M.D. (1997a) Events in hominoid evolution. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 389-415. Plenum Press: New York.

Begun, D.R., Ward, C.V. and Rose, M.D. (eds.) (1997b) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations.* Plenum Press: New York.

Benefit, B.R. and McCrossin, M.L. (1995) Miocene hominoids and hominid origins. *Annu. Rev. Anthropol.* **24**:237-256.

Benefit, B.R. and McCrossin, M.L. (1997) New fossil evidence bearing on the relationships of *Nyanzapithecus* and *Oreopithecus*. *Am. J. Phys. Anthropol.* **Supplement 24**:74.

Benefit, B.R. and McCrossin, M.L. (2000) Middle Miocene hominoid origins. *Science* **287**:2375a.

Bilsborough, A. (1992) *Human Evolution*. Blackie Academic & Professional: Glasgow.

Boschetto, H.B., Brown, F.H. and McDougall, I. (1992) Stratigraphy of the Lothidok Range, northern Kenya, and K/Ar ages of its Miocene primates. *J. Hum. Evol.* **22**:47-71.

Brooks, D.R. (1996) Explanations of homoplasy at different levels of biological organization. In M.J. Sanderson and L. Hufford (eds.): *Homoplasy: The Recurrence of Similarity in Evolution*, pp. 3-36. Academic Press: San Diego.

Brooks, D.R. and McLennon, D.A. (1991) *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. University of Chicago Press: Chicago.

Brown, B. and Ward, S.C. (1988) Basicranial and facial topography in *Pongo* and *Sivapithecus*. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 247-260. Oxford University Press: New York.

Brown, L. (ed.) (1993) *The New Shorter Oxford English Dictionary*. Oxford University Press: New York.

Canavez, F.C., Moreira, M.A.M., Ladasky, J.J., Pissinatti, A., Parham, P. and Seuánez, H. (1999) Molecular phylogeny of New World primates (Platyrrhini) based on β2-microglobulin DNA sequences. *Mol. Phylogenet. Evol.* **12**:74-82.

Cant, J.G.H. (1986) Locomotion and feeding postures of spider and howling monkeys: field study and evolutionary interpretation. *Folia Primatol.* **46**:1-14.

Cant, J.G.H., Youlatos, D. and Rose, M.D. (2001) Locomotor behaviour of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. *J. Hum. Evol.* **41**(2):141-166.

Carpenter, C.R. (1976) Suspensory behaviour of gibbons. *Hylobates lar* a photoessay. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 4. Suspensory Behaviour, Locomotion, and other Behaviours of Captive Gibbons; Cognition*, pp. 1-20. S. Karger: Basel.

Cartmill, M. (1982) Assessing tarsier affinities: is anatomical description phylogenetically neutral? *Geobios (mém. spéc.)* **6**:279-287.

Cartmill, M. (1994) A critique of homology as a morphological concept. *Am. J. Phys. Anthropol.* **94**:115-123.

Cartmill, M. and Milton, K. (1974) The lorisform wrist joint. *Am. J. Phys. Anthropol.* **41**:471.

Cartmill, M. and Milton, K. (1977) The lorisform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *Am. J. Phys. Anthropol.* **47**:249-272.

Cela-Conde, C.J. (1998) The problem of hominoid systematics, and some suggestions for solving it. *S. Afr. J. Sci.* **94**:255-262.

Chappill, J.A. (1989) Quantitative characters in phylogenetic analysis. *Cladistics* **5**:217-234.

Chivers, D.J. (1972) The siamang and the gibbon in the Malay Peninsula. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 1. Evolution, Ecology, Behaviour, and Captive Maintenance*, pp. 103-135. S. Karger: Basel.

Ciochon, R.L. (1983) Hominoid cladistics and the ancestry of modern apes and humans: a summary statement. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 783-843. Plenum Press: New York.

Ciochon, R.L. and Corruccini, R.S. (eds.) (1983) *New Interpretations of Ape and Human Ancestry.* Plenum Press: New York.

Collard, M. and Wood, B.A. (2001a) Homoplasy and the early hominid masticatory system: inferences from analyses of extant hominoids and papionins. *J. Hum. Evol.* **41**(3):167-194.

Collard, M. and Wood, B.A. (2001b) How reliable are current estimates of fossil catarrhine phylogeny? An assessment using extant great apes and Old World

monkeys. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 118-150. Cambridge University Press: Cambridge.

Conroy, G.C. (1990) *Primate Evolution.* W.W. Norton & Company: New York.

Conroy, G.C. and Fleagle, J.G. (1972) Locomotor behaviour in living and fossil pongids. *Nature* **237**:103-104.

Corruccini, R.S. (1978a) Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *J. Hum. Evol.* **7**:307-321.

Corruccini, R.S. (1978b) Primate skeletal allometry and hominoid evolution. *Evolution* **32**:752-758.

Corruccini, R.S., Ciochon, R.L. and McHenry, H.M. (1976) The postcranium of Miocene hominoids: were dryopithecines merely "dental apes"? *Primates* **17**:205-223.

Cracraft, J. (1979) Phylogenetic analysis, evolutionary models, and paleontology. In J. Cracraft and N. Eldredge (eds.): *Phylogenetic Analysis and Paleontology*, pp. 7-39. Columbia University Press: New York.

Day, M.H. (1979) The locomotor interpretation of fossil primate postcranial bones. In M.E. Morbeck, H. Preuschoft and N. Gomberg (eds.): *Environment, Behaviour, and Morphology: Dynamic Interactions in Primates*, pp. 245-258. Gustav Fischer: New York.

Dean, D. and Delson, E. (1992) Second gorilla or third chimp? *Nature* **359**:676-677.

Defler, T.R. (1999) Locomotion and posture in *Lagothrix lagothricha*. *Folia Primatol.* **70**:313-327.

Delson, E. (1979) *Oreopithecus* is a cercopithecoid after all. *Am. J. Phys. Anthropol.* **50**:431-432.

Delson, E. (1986) An anthropoid enigma: historical introduction to the study of *Oreopithecus bambolii*. *J. Hum. Evol.* **15**:523-531.

Delson, E. and Szalay, F.S. (1985) Reconstruction of the 1958 skeleton of *Oreopithecus bambolii* and its comparison to other catarrhines. *Am. J. Phys. Anthropol.* **66**:163.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G. and Dechow, P.C. (2000) Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. *Anth. Papers Am. Mus. Nat. Hist.* **83**:1-159.

Dennett, D.C. (1995) *Darwin's Dangerous Idea: Evolution and the Meanings of Life*. Simon and Schuster: New York.

Disotell, T.R. (1996) The phylogeny of Old World monkeys. *Evol. Anthropol.* **5**:18-24.

Dixson, A.F. (1981) *The Natural History of the Gorilla*. Weidenfeld and Nicolson: London.

Doran, D.M. (1992) Comparison of instantaneous and bout sampling methods: a case study of adult male chimpanzee locomotor behaviour and substrate use. *Am. J. Phys. Anthropol.* **89**:85-99.

Doran, D.M. (1993) Comparative locomotor behaviour of chimpanzees and bonobos: the influence of morphology on locomotion. *Am. J. Phys. Anthropol.* **91**:83-98.

Eldredge, N. (1979) Cladism and common sense. In J. Cracraft and N. Eldredge (eds.): *Phylogenetic Analysis and Paleontology*, pp. 165-198. Columbia University Press: New York.

Eldredge, N. and Cracraft, J. (1980) *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press: New York.

Ellefson, J.O. (1974) A natural history of white-handed gibbons in the Malayan peninsula. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes*

on the Lesser Apes, Vol. 3. Natural History, Social Behaviour, Reproduction, Vocalizations, Prehension, pp. 1-136. S. Karger: Basel.

Erikson, G.E. (1963) Brachiation in New World monkeys and in anthropoid apes. *Symp. Zool. Soc. Lond.* **10**:135-163.

Etter, H.F. (1973) Terrestrial adaptations in the hands of Cercopithecinae. *Folia Primatol.* **20**:331-350.

Farris, J.S. (1982) Outgroups and parsimony. *Syst. Zool.* **31**:328-334.

Farris, J.S. (1983) The logical basis of phylogenetic analysis. In N.I. Platnick and V.A. Funk (eds.): *Advances in Cladistics, Vol. 2. Proceedings of the second meeting of the Willi Hennig Society*, pp. 7-36. Columbia University Press: New York.

Farris, J.S. (1990) Phenetics in camouflage. *Cladistics* **6**:91-100.

Fedigan, L. and Fedigan, L.M. (1988) *Cercopithecus aethiops*: a review of field studies. In A. Gautier-Hion, F. Bourliere, J.P. Gautier and J. Kingdon (eds.): *A Primate Radiation: Evolutionary Biology of the African Geunons*, pp. 389-411. Cambridge University Press: Cambridge.

Feldesman, M.B. (1976) The primate forelimb: a morphometric study of locomotor diversity. *Univ. Oregon Anthropol. Papers*, **No. 10.** University of Oregon: Eugene.

Feldesman, M.B. (1982) Morphometric analysis of the distal humerus of some Cenozoic catarrhines: the late divergence hypothesis revisited. *Am. J. Phys. Anthropol.* **59**:73-95.

Filler, A.G. (1981) Anatomical specializations in the hominoid lumbar region. *Am. J. Phys. Anthropol.* **54**:218.

Fleagle, J.G. (1976) Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol.* **26**:245-269.

Fleagle, J.G. (1980) Locomotion and posture. In D.J. Chivers (ed.): *Malayan Forest Primates*, pp. 191-207. Plenum Press: New York.

Fleagle, J.G. (1983) Locomotor adaptations of Oligocene and Miocene hominoids and their phyletic implications. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 301-324. Plenum Press: New York.

Fleagle, J.G. (1984) Are there any fossil gibbons? In H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.): *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 431-447. Edinburgh University Press: Edinburgh.

Fleagle, J.G. (1999) *Primate Adaptation and Evolution*. Academic Press: San Diego.

Fleagle, J.G. and Kay, R.F. (1983) New interpretations of the phyletic position of Oligocene hominoids. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 181-210. Plenum Press: New York.

Fleagle, J.G. and Mittermeier, R.A. (1980) Locomotor behaviour, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* **52**:301-314.

Fleagle, J.G., Mittermeier, R.A. and Skopec, A.L. (1981) Differential habitat use by *Cebus apella* and *Saimiri sciureus* in central Surinam. *Primates* **22**:361-367.

Fleagle, J.G. and Simons, E.L. (1978) Humeral morphology of the earliest apes. *Nature* **276**:705-707.

Fleagle, J.G. and Simons, E.L. (1982) The humerus of *Aegyptopithecus zeuxis*: a primitive anthropoid. *Am. J. Phys. Anthropol.* **59**:175-193.

Fleagle, J.G., Simons, E.L. and Conroy, G.C. (1975) Ape limb bone from the Oligocene of Egypt. *Science* **189**:135-137.

Gaffney, E.S. (1979) An introduction to the logic of phylogeny reconstruction. In J. Cracraft and N. Eldredge (eds.): *Phylogenetic Analysis and Paleontology*, pp. 79-111. Columbia University Press: New York.

Gautier-Hion, A., Bourliere, F., Gautier, J.P. and Kingdon, J. (eds.) (1988) *A Primate Radiation: Evolutionary Biology of the African Guenons.* Cambridge University Press: Cambridge.

Gebo, D.L. (1996) Climbing, brachiation and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am. J. Phys. Anthropol.* **101**:55-92.

Gebo, D.L., Beard, K.C., Teaford, M.F., Walker, A.C., Larson, S.G., Jungers, W.L. and Fleagle, J.G. (1988) A hominoid proximal humerus from the early Miocene of Rusinga Island, Kenya. *J. Hum. Evol.* **17**:393-401.

Gebo, D.L. and Chapman, C.A. (1995) Positional behaviour in five sympatric Old World monkeys. *Am. J. Phys. Anthropol.* **97**:49-76.

Gebo, D.L., MacLatchy, L.M., Kityo, R., Deino, A., Kingston, J.D. and Pilbeam, D.R. (1997) A hominoid genus from the early Miocene of Uganda. *Science* **276**:401-404.

Gittins, S.P. (1983) Use of the forest canopy by the agile gibbon. *Folia Primatol.* **40**:134-144.

Godfrey, L.R., Jungers, W.L., Reed, K.E., Simons, E.L. and Ghatrath, P.S. (1997) Inferences about past and present primate communities in Madagascar. In S.M. Goodman and B.D. Patterson (eds.): *Natural Change and Human Impact in Madagascar*, pp. 218-256. Smithsonian Institution Press: Washington, DC.

Goodman, M. (1963) Man's place in the phylogeny of the primates as reflected in serum proteins. In S.L. Washburn (ed.): *Classification and Human Evolution*, pp. 204-234. Methuen & Co. Ltd: London.

Goodman, M., Bailey, W.J., Hayasaka, K., Stanhope, M.J., Slightom, J.L. and Czelusniak, J. (1994) Molecular evidence on primate phylogeny from DNA sequences. *Am. J. Phys. Anthropol.* **94**:3-24.

Goodman, M., Tagle, D.A., Fitch, D.H.A., Bailey, W.J., Czelusniak, J., Koop, B.F., Benson, P. and Slightom, J.L. (1990) Primate evolution at the DNA level and a classification of hominoids. *J. Mol. Evol.* **30**:260-266.

Gosliner, T.M. and Ghiselin, M.T. (1984) Parallel evolution in opistobranch gastropods and its implications for phylogenetic methodology. *Syst. Zool.* **33**:255-274.

Gould, S.J. and Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* **205**:581-598.

Groves, C.P. (1972) Systematics and phylogeny of gibbons. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 1. Evolution, Ecology, Behaviour, and Captive Maintenance*, pp. 1-89. S. Karger: Basel.

Groves, C.P. (1986) Systematics of the great apes. In D.R. Swindler and J. Erwin (eds.): *Comparative Primate Biology, Vol. 1. Systematics, Evolution, and Anatomy*, pp. 187-217. Alan R. Liss, Inc.: New York.

Groves, C.P. and Paterson, J.D. (1991) Testing hominoid phylogeny with the PHYLIP programs. *J. Hum. Evol.* **20**:167-183.

Hall, B.K. (1994) Introduction. In B.K. Hall (ed.): *Homology: The Hierarchical Basis of Comparative Biology*, pp. 1-19. Academic Press: San Diego.

Hamrick, M.W., Simons, E.L. and Jungers, W.L. (2000) New wrist bones of the Malagasy giant subfossil lemurs. *J. Hum. Evol.* **38**:635-650.

Harrison, G.A. and Weiner, J.S. (1963) Some considerations in the formulation of theories of human phylogeny. In S.L. Washburn (ed.): *Classification and Human Evolution*, pp. 75-84. Methuen and Co. Ltd: London.

Harrison, T. (1982) *Small-Bodied Apes from the Miocene of East Africa.* Ph.D. thesis. University College: London.

Harrison, T. (1985) African oreopithecids and the origin of the family. *Am. J. Phys. Anthropol.* **66**:180.

Harrison, T. (1986a) A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. *J. Hum. Evol.* **15**:541-583.

Harrison, T. (1986b) New fossil anthropoids from the middle Miocene of East Africa and their bearing on the origin of the Oreopithecidae. *Am. J. Phys. Anthropol.* **71**:265-284.

Harrison, T. (1986c) The phylogenetic relationships of the Oreopithecidae. *Am. J. Phys. Anthropol.* **69**:212.

Harrison, T. (1987) The phylogenetic relationship of the early catarrhine primates: a review of the current evidence. *J. Hum. Evol.* **16**:41-80.

Harrison, T. (1988) A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatol.* **50**:59-108.

Harrison, T. (1989) New postcranial remains of *Victoriapithecus* from the middle Miocene of Kenya. *J. Hum. Evol.* **18**:3-54.

Harrison, T. (1991) The implications of *Oreopithecus bambolii* for the origins of bipedalism. In B. Senut and Y. Coppens (eds.): *Origine(s) de la Bipedie Chez les Hominides*, pp. 235-244. Cahiers de Paléoanthropologie, CNRS: Paris.

Harrison, T. and Rook, L. (1997) Enigmatic anthropoid or misunderstood ape? The phylogenetic status of *Oreopithecus bambolii* reconsidered. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 327-362. Plenum Press: New York.

Hennig, W. (1965) Phylogenetic systematics. *Annu. Rev. Entomol.* **10**:97-116.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press: Urbana, IL.

Hollihn, U. (1984) Bimanual suspensory behaviour: morphology, selective advantages and phylogeny. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.): *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 85-95. Edinburgh University Press: Edinburgh.

Hopwood, A.T. (1933) Miocene primates from British East Africa. *Ann. Mag. Nat. Hist.* **10**(11):96-98.

Hunt, K.D. (1991a) Mechanical implications of chimpanzee positional behaviour. *Am. J. Phys. Anthropol.* **86**:521-536.

Hunt, K.D. (1991b) Positional behaviour in the Hominoidea. *Int. J. Primatol.* **12**:95-118.

Hunt, K.D. (1992) Positional behavior of the *Pan troglodytes* in Mahale Mountains and Gombe Stream National Parks, Tanzania. *Am. J. Phys. Anthropol.* **87**:83-105.

Hunt, K.D., Cant, J.G.H., Gebo, D.L., Rose, M.D., Walker, S.E. and Youlatos, D. (1996) Standardized descriptions of primate locomotor and postural modes. *Primates* **37**:363-387.

Isbell, L.A., Pruetz, J.D., Lewis, M. and Young, T.P. (1998) Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. *Am. J. Phys. Anthropol.* **105**:199-207.

Jenkins, F.A., Jr., Dombrowski, P.J. and Gordon, E.P. (1978) Analysis of the shoulder in brachiating spider monkeys (*Ateles geoffroyi*). *Am. J. Phys. Anthropol.* **48**:65-76.

Jenkins, F.A., Jr. and Fleagle, J.G. (1975) Knuckle-walking and the functional anatomy of the wrists in living apes. In R.H. Tuttle (ed.): *Primate Functional Morphology and Evolution*, pp. 213-227. Mouton: The Hague.

Jungers, W.L. (1978) The functional significance of skeletal allometry in *Megaladapis* in comparison to living prosimians. *Am. J. Phys. Anthropol.* **49**:303-314.

Jungers, W.L. (1980) Adaptive diversity in subfossil Malagasy prosimians. *Z. Morph. Anthropol.* **71**:177-186.

Jungers, W.L. (1984) Scaling of the hominoid locomotor skeleton with special reference to the lesser apes. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.): *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 146-169. Edinburgh University Press: Edinburgh.

Jungers, W.L. (1985) Body size and scaling of limb proportions in primates. In W.L. Jungers (ed.): *Size and Scaling in Primate Biology*, pp. 345-381. Plenum Press: New York.

Jungers, W.L. (1987) Size and morphometric affinities of the appendicular skeleton in *Oreopithecus bambolii* (IGF 11778). *J. Hum. Evol.* **16**:445-456.

Jungers, W.L., Falsetti, A.B. and Wall, C.E. (1995) Shape, relative size, and size-adjustments in morphometrics. *Yearb. Phys. Anthropol.* **38**:137-161.

Kappelman, J., Kelley, J., Pilbeam, D.R., Sheikh, K.A., Ward, S.C., Anwar, M., Barry, J.C., Brown, B., Hake, P., Johnson, N.M., Raza, S.M. and Shah, S.M.I. (1991) The earliest occurrence of *Sivapithecus* from the middle Miocene Chinji Formation of Pakistan. *J. Hum. Evol.* **21**:61-73.

Kelley, J. (1988) A new large species of *Sivapithecus* from the Siwaliks of Pakistan. *J. Hum. Evol.* **17**:305-324.

Kelley, J. (1997) Paleobiological and phylogenetic significance of life history in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 173-208. Plenum Press: New York.

Kelley, J., Ward, S.C., Brown, B., Hill, A. and Downs, W. (2000) Middle Miocene hominoid origins. *Science* **287**:2375a.

Kluge, A. and Farris, J.S. (1969) Quantitative phyletics and the evolution of anurans. *Syst. Zool.* **18**:1-32.

Köhler, M. and Moyà-Solà, S. (1997) Ape-like or hominid-like? The positional behaviour of *Oreopithecus bambolii* reconsidered. *Proc. Natl. Acad. Sci. USA* **94**:11747-11750.

Köhler, M., Moyà-Solà, S. and Alba, D.M. (2001) Eurasian hominoid evolution in the light of recent *Dryopithecus* findings. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 192-212. Cambridge University Press: Cambridge.

Kordos, L. and Begun, D.R. (2001) Primates from Rudabánya: allocation of specimens to individuals, sex and age categories. *J. Hum. Evol.* **40**(1):17-39.

Lankester, E.R. (1870) On the use of the term Homology in modern Zoology, and the distinction between homogenetic and homoplastic agreements. *Ann. Mag. Nat. Hist.* **6**(4):34-43.

Larson, S.G. (1988) Subscapularis function in gibbons and chimpanzees: implications for interpretation of humeral head torsion in hominoids. *Am. J. Phys. Anthropol.* **76**:449-462.

Larson, S.G. (1992) Are the similarities in forelimb morphology among the hominoid primates due to parallel evolution? *Am. J. Phys. Anthropol.* **Supplement 14**:106.

Larson, S.G. (1995) New characters for the functional interpretation of primate scapulae and proximal humeri. *Am. J. Phys. Anthropol.* **98**:13-35.

Larson, S.G. (1996) Estimating humeral torsion on incomplete fossil anthropoid humeri. *J. Hum. Evol.* **31**:239-257.

Larson, S.G. (1998) Parallel evolution in the hominoid trunk and forelimb. *Evol. Anthropol.* **6**(5):87-99.

Larson, S.G. and Stern, J.T., Jr. (1992) Further evidence for the role of supraspinatus in quadrupedal monkeys. *Am. J. Phys. Anthropol.* **87**:359-363.

Lauder, G.V. (1981) Form and function: structural analysis in evolutionary morphology. *Paleobiology* **7**:430-442.

Lauder, G.V. (1982) Historical biology and the problem of design. *J. Theor. Biol.* **97**:57-67.

Lauder, G.V. (1994) Homology, form, and function. In B.K. Hall (ed.): *Homology: The Hierarchical Basis of Comparative Biology*, pp. 151-196. Academic Press: San Diego.

Lauder, G.V. (1995) On the inference of function from structure. In J.J. Thomason (ed.): *Functional Morphology in Vertebrate Paleontology,* pp. 1-18. Cambridge University Press: Cambridge.

Le Gros Clark, W.E. (1971) *The Antecedents of Man: An Introduction to the Evolution of Primates. Third edition.* Edinburgh University Press: Edinburgh.

Le Gros Clark, W.E. and Leakey, L.S.B. (1951) The Miocene Hominoidea of East Africa. *Fossil Mamm. Afr. (Br. Mus. Nat. Hist.)* **1**:1-117.

Le Gros Clark, W.E. and Thomas, D.P. (1951) Associated jaws and limb bones of *Limnopithecus macinnesi. Fossil Mamm. Afr. (Br. Mus. Nat. Hist.)* **3**:1-27.

Leakey, L.S.B. (1962) A new lower Pliocene fossil primate from Kenya. *Ann. Mag. Nat. Hist.* **13**(4):689-696.

Leakey, L.S.B. (1967) An early Miocene member of Hominidae. *Nature* **213**:155-163.

Leakey, R.E.F. and Leakey, M.G. (1986) A second new Miocene hominoid from Kenya. *Nature* **324**:146-148.

Leakey, R.E.F., Leakey, M.G. and Walker, A.C. (1988) Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. Phys. Anthropol.* **76**:289-307.

Lewis, O.J. (1969) The hominoid wrist joint. *Am. J. Phys. Anthropol.* **30**:251-267.

Lewis, O.J. (1971a) Brachiation and the early evolution of the Hominoidea. *Nature* **230**:577-579.

Lewis, O.J. (1971b) The contrasting morphology found in the wrist joint of semibrachiating monkeys and brachiating apes. *Folia Primatol.* **16**:248-256.

Lewis, O.J. (1972a) Evolution of the hominoid wrist. In R.H. Tuttle (ed.): *The Functional and Evolutionary Biology of Primates,* pp. 207-222. Aldine-Atherton: Chicago, Ill.

Lewis, O.J. (1972b) Osteological features characterising the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus* (*Proconsul*) *africanus*. *Am. J. Phys. Anthropol.* **36**:45-58.

Lewis, O.J. (1974) The wrist articulations of the Anthropoidea. In F.A. Jenkins, Jr. (ed.): *Primate Locomotion*, pp. 143-169. Academic Press: New York.

Lewis, O.J. (1985) Derived morphology of the wrist articulations and theories of hominoid evolution. Part I: the lorisine joints. *J. Anat.* **140**:447-460.

Lewis, O.J., Hamshere, R.J. and Bucknill, T.M. (1970) The anatomy of the wrist joint. *J. Anat.* **106**(3):539-552.

Lockwood, C.A. and Fleagle, J.G. (1999) The recognition and evaluation of homoplasy in primate and human evolution. *Yearb. Phys. Anthropol.* **42**:189-232.

MacKinnon, J. (1974a) *In Search of the Red Ape*. Collins: London.

MacKinnon, J. (1974b) The behaviour and ecology of wild orang-utans (*Pongo pygmaeus*). *Animal Behaviour* **22**:3-74.

MacLatchy, L.M., Gebo, D.L., Kityo, R. and Pilbeam, D.R. (2000) Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *J. Hum. Evol.* **39**:159-183.

Madar, S. (1994) Humeral shaft morphology of *Sivapithecus*. *Am. J. Phys. Anthropol.* **Supplement 20**:140.

Maddison, W.P., Donoghue, M.J. and Maddison, D.R. (1984) Outgroup analysis and parsimony. *Syst. Zool.* **33**:83-103.

Maddison, W.P. and Maddison, D.R. (1989) Interactive analysis of phylogeny and character evolution using the computer program MacClade. *Folia Primatol.* **53**:190-202.

Maddison, W.P. and Maddison, D.R. (1992) *MacClade: Analysis of Phylogeny and Character Evolution.* (Version 3.0). Sinauer Associates: Sunderland Massachusetts.

Mann, A. and Weiss, M. (1996) Hominoid phylogeny and taxonomy: a consideration of the molecular and fossil evidence in an historical perspective. *Mol. Phylogenet. Evol.* **5**(1):169-181.

Martin, L.B. (1986) Relationships among extant and extinct great apes and humans. In B.A. Wood, L.B. Martin and P.J. Andrews (eds.): *Major Topics in Primate and Human Evolution*, pp. 161-187. Cambridge University Press: Cambridge.

Martin, R.D. (1990) *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Princeton University Press: Princeton, NJ.

Mayr, E. (1981) Biological classification: towards a synthesis of opposing methodologies. *Science* **214**:510-516.

McCrossin, M.L. (1992) An oreopithecid proximal humerus from the middle Miocene of Maboko Island, Kenya. *Int. J. Primatol.* **13**:659-677.

McCrossin, M.L. (1994) Semi-terrestrial adaptations of *Kenyapithecus*. *Am. J. Phys. Anthropol.* **Supplement 18**:142-143.

McCrossin, M.L. (1997) New postcranial remains of *Kenyapithecus* and their implications for understanding the origins of hominoid terrestriality. *Am. J. Phys. Anthropol.* **Supplement 24**:164.

McCrossin, M.L. and Benefit, B.R. (1994) Maboko Island and the evolutionary history of Old World monkeys and apes. In R.S. Corruccini and R.L. Ciochon (eds.): *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*, pp. 95-122. Prentice Hall: Englewood Cliffs, NJ.

McCrossin, M.L. and Benefit, B.R. (1997) On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the middle Miocene of eastern Africa. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 241-267. Plenum Press: New York.

McGraw, W.S. (1996) Cercopithecid locomotion, support use, and support availability in the Tai Forest, Ivory Coast. *Am. J. Phys. Anthropol.* **100**:507-522.

McGraw, W.S. (1998) Comparative locomotion and habitat use of six monkeys in the Tai Forest, Ivory Coast. *Am. J. Phys. Anthropol.* **105**:493-510.

McHenry, H.M. and Corruccini, R.S. (1975) Distal humerus in hominoid evolution. *Folia Primatol.* **23**:227-244.

McHenry, H.M. and Corruccini, R.S. (1983) The wrist of *Proconsul africanus* and the origin of hominoid postcranial adaptations. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 353-367. Plenum Press: New York.

Meireles, C.M., Czelusniak, J., Schneider, M.P.C., Muniz, J.A.P.C., Brigido, M.C., Ferreira, H.S. and Goodman, M. (1999) Molecular phylogeny of ateline New World monkeys (Platyrrhini, Atelinae) based on γ-globin gene sequences: evidence that *Brachyteles* is the sister group of *Lagothrix*. *Mol. Phylogenet. Evol.* **12**:10-30.

Mendel, F.C. (1976) Postural and locomotor behaviour of *Alouatta palliata* on various substrates. *Folia Primatol.* **26**:36-53.

Mittermeier, R.A. (1978) Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatol.* **30**:161-193.

Mittermeier, R.A. and Fleagle, J.G. (1976) The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a reevaluation of the locomotor category semibrachiation. *Am. J. Phys. Anthropol.* **45**:235-256.

Miyamoto, M.M., Slightom, J.L. and Goodman, M. (1987) Phylogenetic relations of humans and African apes from DNA sequences in the ψη-globin region. *Science* **238**:369-273.

Moore, J. and Willmer, P. (1997) Convergent evolution in invertebrates. *Biol. Rev.* **72**:1-60.

Morbeck, M.E. (1979) Forelimb use and positional adaptation in *Colobus guereza*: integration of behavioural, ecological, and anatomical data. In M.E. Morbeck, H. Preuschoft and N. Gomberg (eds.): *Environment, Behaviour, and*

Morphology: Dynamic Interactions in Primates, pp. 95-117. Gustav Fischer: New York.

Morbeck, M.E. (1983) Miocene hominoid discoveries from Rudabánya: implications from the postcranial skeleton. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 369-404. Plenum Press: New York.

Morbeck, M.E. and Zihlman, A.L. (1988) Body composition and limb proportions. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 285-297. Oxford University Press: Oxford.

Mosimann, J.E. and James, F.C. (1979) New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* **33**(1):444-459.

Moyà-Solà, S. and Köhler, M. (1993) Recent discoveries of *Dryopithecus* shed new light on evolution of great apes. *Nature* **365**:543-545.

Moyà-Solà, S. and Köhler, M. (1995) New partial cranium of *Dryopithecus* Lartet, 1863 (Hominoidea, Primates) from the upper Miocene of Can Llobateres, Barcelona, Spain. *J. Hum. Evol.* **29**:101-139.

Moyà-Solà, S. and Köhler, M. (1996) A *Dryopithecus* skeleton and the origins of great-ape locomotion. *Nature* **379**:156-159.

Moyà-Solà, S., Köhler, M. and Rook, L. (1999) Evidence of hominid-like precision grip capability in the hand of the Miocene ape *Oreopithecus*. *Proc. Natl. Acad. Sci. USA* **96**:313-317.

Moynihan, M. (1976) *The New World Primates. Adaptive Radiation and the Evolution of Social Behaviour, Languages, and Intelligence*. Princeton University Press: Princeton, N.J.

Napier, J.R. (1963) Brachiation and brachiators. *Symp. Zool. Soc. Lond.* **10**:183-195.

Napier, J.R. (1967) Evolutionary aspects of primate locomotion. *Am. J. Phys. Anthropol.* **27**:333-342.

Napier, J.R. and Davis, P.R. (1959) The forelimb skeleton and associated remains of *Proconsul africanus*. *Fossil Mamm. Afr. (Br. Mus. Nat. Hist.)* **16**:1-70.

Napier, J.R. and Napier, P.H. (1967) *A Handbook of Living Primates*. Academic Press: London.

Napier, J.R. and Napier, P.H. (eds.) (1970) *Old World Monkeys: Evolution, Systematics, and Behaviour.* Academic Press: New York.

O'Conner, B.L. (1975) The functional morphology of the cercopithecoid wrist and inferior radioulnar joints, and their bearing on some problems in the evolution of the Hominoidea. *Am. J. Phys. Anthropol.* **43**:113-122.

Owen, R. (1848) *On the Archetype and Homologies of the Vertebrate Skeleton.* John Van Voorst: London.

Oxnard, C.E. (1963) Locomotor adaptations in the primate forelimb. *Symp. Zool. Soc. Lond.* **10**:165-182.

Oxnard, C.E. (1967) The functional morphology of the primate shoulder as revealed by comparative anatomical, osteometric and discriminant function techniques. *Am. J. Phys. Anthropol.* **26**:219-240.

Oxnard, C.E. (1968) A note on the fragmentary Sterkfontein scapula. *Am. J. Phys. Anthropol.* **28**:213-217.

Oxnard, C.E. (1986) Comparative anatomy of the primates: old and new. In D.R. Swindler and J. Erwin (eds.): *Comparative Primate Biology, Vol. 1. Systematics, Evolution, and Anatomy*, pp. 719-763. Alan R. Liss, Inc.: New York.

Panchen, A.L. (1994) Richard Owen and the concept of homology. In B.K. Hall (ed.): *Homology: The Hierarchical Basis of Comparative Biology*, pp. 21-62. Academic Press: San Diego.

Pickford, M.H.L. (1985) A new look at *Kenyapithecus* based on recent discoveries in Western Kenya. *J. Hum. Evol.* **14**:113-143.

Pickford, M.H.L. (1986) A reappraisal of *Kenyapithecus*. In J.G. Else and P.C. Lee (eds.): *Primate Evolution*, pp. 163-171. Cambridge University Press: Cambridge.

Pilbeam, D.R. (1982) New hominoid skull material from the Miocene of Pakistan. *Nature* **295**:232-234.

Pilbeam, D.R. (1986) Hominoid evolution and hominid origins. *Am. Anthropol.* **88**:295-312.

Pilbeam, D.R. (1996) Genetic and morphological records of the Hominoidea and hominid origins: a synthesis. *Mol. Phylogenet. Evol.* **5**:155-168.

Pilbeam, D.R. (1997) Research on Miocene hominoids and hominid origins: the last three decades. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 13-28. Plenum Press: New York.

Pilbeam, D.R., Barry, J.C., Meyer, G.E., Shah, S.M.I., Pickford, M.H.L., Bishop, W.W., Thomas, H. and Jacobs, L.L. (1977a) Geology and palaeontology of Neogene strata of Pakistan. *Nature* **270**:684-689.

Pilbeam, D.R., Meyer, G.E., Badgley, C., Rose, M.D., Pickford, M.H.L., Behrensmeyer, A.K. and Shah, S.M.I. (1977b) New hominoid primates from the Siwaliks of Pakistan and their bearing on hominoid evolution. *Nature* **270**:689-695.

Pilbeam, D.R., Rose, M.D., Barry, J.C. and Shah, S.M.I. (1990) New *Sivapithecus* humeri from Pakistan and the relationship of *Sivapithecus* and *Pongo*. *Nature* **348**:237-239.

Pilbeam, D.R. and Simons, E.L. (1971) Humerus of *Dryopithecus* from Saint Gaudens, France. *Nature* **229**:408-409.

Pilbeam, D.R. and Young, N.M. (2001) *Sivapithecus* and hominoid evolution: some brief comments. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the*

Neogene Hominoid Primates of Eurasia, pp. 349-364. Cambridge University Press

Pimentel, R.A. and Riggins, R. (1987) The nature of cladistic data. *Cladistics* **3**(3):201-209.

Poe, S. and Wiens, J.J. (2000) Character selection and the methodology of morphological phylogenetics. In J.J. Wiens (ed.): *Phylogenetic Analysis of Morphological Data*, pp. 20-36. Smithsonian Institution Press: Washington, D.C.

Pounds, J.A. (1991) Habitat structure and morphological patterns in arboreal vertebrates. In S. Bell, E. McCoy and H. Mushinksy (eds.): *Habitat Structure: The Physical Arrangement of Objects in Space*, pp. 109-119. Chapman and Hall: New York.

Preuschoft, H., Chivers, D.J., Brockelman, W.Y. and Creel, N. (eds.) (1984) *The Lesser Apes: Evolutionary and Behavioural Biology.* Edinburgh University Press: Edinburgh.

Prost, J.H. (1965) A definitional system for the classification of primate locomotion. *Am. Anthropol.* **67**:1198-1214.

Quicke, D.L.J. (1993) *Principles and Techniques of Contemporary Taxonomy.* Blackie Academic and Professional: Glasgow.

Rae, T.C. (1993) *Phylogenetic Analysis of Proconsulid Facial Morphology.* Ph.D. thesis. State University of New York: Stony Brook, NY.

Rae, T.C. (1997) The early evolution of the hominoid face. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 59-77. Plenum Press: New York.

Rae, T.C. (1998) The logical basis for the use of continuous characters in phylogenetic systematics. *Cladistics* **14**:221-228.

Rae, T.C. (1999) Mosaic evolution in the origin of the Hominoidea. *Folia Primatol.* **70**:125-135.

Remis, M.J. (1995) Effects of body size and context on the arboreal activities of lowland gorillas in the Central African Republic. *Am. J. Phys. Anthropol.* **97**:413-434.

Remis, M.J. (1998) The gorilla paradox: the effects of body size and habitat on the positional behaviour of lowland and mountain gorillas. In E. Strasser, J.G. Fleagle, A.L. Rosenberger and H.M. McHenry (eds.): *Primate Locomotion: Recent Advances*, pp. 95-106. Plenum Press: New York.

Reynolds, T.R. (1985) Stresses on the limbs of quadrupedal primates. *Am. J. Phys. Anthropol.* **67**:351-362.

Richard, A. (1970) A comparative study of the activity patterns and behaviour of *Alouatta villosa* and *Ateles geoffroyi*. *Folia Primatol.* **12**:241-263.

Richmond, B.G. (1999) Eurasian hominoid evolution. *Evol. Anthropol.* 7(6):194-196.

Richmond, B.G., Begun, D.R. and Strait, D.S. (2001) Origin of human bipedalism: the knuckle-walking hypothesis revisited. *Yearb. Phys. Anthropol.* **44**:70-105.

Richmond, B.G. and Whalen, M. (2001) Forelimb function, bone curvature and phylogeny of *Sivapithecus*. In L. de Bonis, G.D. Koufos and P.J. Andrews (eds.): *Hominoid Evolution and Climatic Change in Europe, Vol. 2: Phylogeny of the Neogene Hominoid Primates of Eurasia*, pp. 326-348. Cambridge University Press: Cambridge.

Röhrer-Ertl, O. (1988) Research history, nomenclature, and taxonomy of the orang-utan. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 7-18. Oxford University Press: Oxford.

Rollinson, J. and Martin, R.D. (1981) Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symp. Zool. Soc. Lond.* **48**:377-427.

Rook, L., Bondioli, L., Köhler, M., Moyà-Solà, S. and Macchiarelli, R. (1999) *Oreopithecus* was a bipedal ape after all: evidence from the iliac cancellous architecture. *Proc. Natl. Acad. Sci. USA* **96**:8795-8799.

Rose, M.D. (1979) Positional behaviour of natural populations: some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In M.E. Morbeck, H. Preuschoft and N. Gomberg (eds.): *Environment, Behaviour, and Morphology: Dynamic Interactions in Primates*, pp. 75-93. Gustav Fischer: New York.

Rose, M.D. (1983) Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both? In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 405-417. Plenum Press: New York.

Rose, M.D. (1984) Hominoid postcranial specimens from the middle Miocene Chinji Formation, Pakistan. *J. Hum. Evol.* **13**:503-516.

Rose, M.D. (1986) Further hominoid postcranial specimens from the late Miocene Nagri Formation of Pakistan. *J. Hum. Evol.* **15**:333-367.

Rose, M.D. (1988a) Another look at the anthropoid elbow. *J. Hum. Evol.* **17**:193-224.

Rose, M.D. (1988b) Functional anatomy of the cheiridia. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 299-310. Oxford University Press: Oxford.

Rose, M.D. (1989) New postcranial specimens of catarrhines from the middle Miocene Chinji Formation, Pakistan: descriptions and a discussion of proximal humeral functional morphology in anthropoids. *J. Hum. Evol.* **18**:131-162.

Rose, M.D. (1992a) Kinematics of the trapezium-1st metacarpal joint in extant anthropoids and Miocene hominoids. *J. Hum. Evol.* **22**:255-266.

Rose, M.D. (1992b) Quadrupedalism in Miocene hominoids. *Am. J. Phys. Anthropol.* **Supplement 14**:141.

Rose, M.D. (1994) Quadrupedalism in some Miocene catarrhines. *J. Hum. Evol.* **26**:387-411.

Rose, M.D. (1996) Functional morphological similarities in the locomotor skeleton of Miocene catarrhines and platyrrhine monkeys. *Folia Primatol.* **66**:7-14.

Rose, M.D. (1997) Functional and phylogenetic features of the forelimb in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 79-100. Plenum Press: New York.

Rose, M.D., Leakey, M.G., Leakey, R.E.F. and Walker, A.C. (1992) Postcranial specimens of *Simiolus enjiessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. *J. Hum. Evol.* **22**:171-237.

Rose, M.D., Nakano, Y. and Ishida, H. (1996) *Kenyapithecus* postcranial specimens from Nachola, Kenya. *Afr. Stud. Monogr.* **24**:3-56.

Rosenberger, A.L. (1983) Tale of tails: parallelism and prehensility. *Am. J. Phys. Anthropol.* **60**:103-107.

Rosenberger, A.L. and Delson, E. (1985) The dentition of *Oreopithecus bambolii*: systematic and paleobiological implications. *Am. J. Phys. Anthropol.* **66**(1):222-223.

Rosenberger, A.L. and Strier, K.B. (1989) Adaptive radiation of ateline primates. *J. Hum. Evol.* **18**:717-750.

Ross, C., Williams, B.A. and Kay, R.F. (1998) Phylogenetic analysis of anthropoid relationships. *J. Hum. Evol.* **35**(3):221-306.

Rumbaugh, D.M. (ed.) (1972) *Gibbon and Siamang. A Series of Volumes on the Lesser Apes. Vol. 1. Evolution, Ecology, Behaviour, and Captive Maintenance.* S. Karger: Basel.

Ruvolo, M. (1997) Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol. Biol. Evol.* **14**(3):248-265.

Ruvolo, M., Disotell, T.R., Allard, M.W., Brown, W.M. and Honeycutt, R.L. (1991) Resolution of the African hominoid trichotomy by use of a mitochondrial gene sequence. *Proc. Natl. Acad. Sci. USA* **88**:1570-1574.

Sanders, W.J. and Bodenbender, B.E. (1994) Morphometric analysis of lumbar vertebra UMP67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. *J. Hum. Evol.* **26**:203-237.

Sanderson, M.J. and Hufford, L. (1996a) Homoplasy and the evolutionary process: an afterword. In M.J. Sanderson and L. Hufford (eds.): *Homoplasy: The Recurrence of Similarity in Evolution*, pp. 327-330. Academic Press: San Diego.

Sanderson, M.J. and Hufford, L. (eds.) (1996b) *Homoplasy: The Recurrence of Similarity in Evolution.* Academic Press: San Diego.

Sankhyan, A.R. (1985) Late occurrence of *Sivapithecus* in Indian Siwaliks. *J. Hum. Evol.* **14**:573-578.

Sarich, V.M. and Wilson, A.C. (1967) Immunological time scale for hominid evolution. *Science* **158**:1200-1203.

Sarmiento, E.E. (1987) The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *Am. Mus. Nov.* **2881**:1-44.

Sarmiento, E.E. (1992) Terrestrial traits in the hands and feet of gorillas. *Am. J. Phys. Anthropol.* **Supplement 14**:146-147.

Sarmiento, E.E. (1994) Terrestrial traits in the hands and feet of gorillas. *Am. Mus. Nov.* **3091**:1-56.

Sarmiento, E.E. and Oates, J.F. (2000) The Cross River gorillas: a distinct subspecies, *Gorilla gorilla diehli* Matschie 1904. *Am. Mus. Nov.* **3304**:1-55.

Sarmiento, E.E., Stiner, E. and Mowbray, K. (2002) Morphology-based systematics (MBS) and problems with fossil hominoid and hominid systematics. *Anat. Rec. (New Anat.)* **269**(1):50-66.

Schmitt, D. (1998) Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World monkeys. In E. Strasser, J.G. Fleagle, A.L.

Rosenberger and H.M. McHenry (eds.): *Primate Locomotion: Recent Advances*, pp. 175-200. Plenum Press: New York.

Schoch, R.M. (1986) *Phylogeny Reconstruction in Paleontology*. Van Nostrand Reinhold: New York.

Schultz, A.H. (1930) The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* **2**:303-438.

Schultz, A.H. (1969) *The Life of Primates*. Weidenfeld and Nicolson: London.

Schultz, A.H. (1970) The comparative uniformity of the Cercopithecoidea. In J.R. Napier and P.H. Napier (eds.): *Old World Monkeys: Evolution, Systematics, and Behaviour*, pp. 39-51. Academic Press: New York.

Schultz, A.H. (1973) Age changes, variability and generic differences in body proportions of recent hominoids. *Folia Primatol.* **19**:338-359.

Schultz, M. (1986) The forelimb of the Colobinae. In D.R. Swindler and J. Erwin (eds.): *Comparative Primate Biology, Vol. 1. Systematics, Evolution, and Anatomy*, pp. 559-669. Alan R. Liss, Inc.: New York.

Schwartz, J.H. (1988) History, morphology, paleontology, and evolution. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 69-85. Oxford University Press: Oxford.

Shea, B.T. (1988) Phylogeny and skull form in the hominoid primates. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 233-245. Oxford University Press: Oxford.

Sherwood, R.J., Ward, S.C., Hill, A., Duren, D.L., Brown, B. and Downs, W. (2002) Preliminary description of the *Equatorius africanus* partial skeleton (KNM-TH 28860) from Kipsaramon, Tugen Hills, Baringo District, Kenya. *J. Hum. Evol.* **42**:63-73.

Shoshani, J., Groves, C.P., Simons, E.L. and Gunnell, G.F. (1996) Primate phylogeny: morphological vs molecular results. *Mol. Phylogenet. Evol.* **5**(1):102-154.

Simon, C. (1983) A new coding procedure for morphometric data with an example from periodical cicada wing veins. In J. Felsenstein (ed.): *Numerical Taxonomy*, pp. 378-383. Springer-Verlag: Berlin.

Simons, E.L. (1962) Fossil evidence relating to the early evolution of primate behaviour. *Ann. N. Y. Acad. Sci.* **102**:282-294.

Simons, E.L. (1965) New fossil apes from Egypt and the initial differentiation of the Hominoidea. *Nature* **205**:135-139.

Simons, E.L. (1967a) Fossil primates and the evolution of some primate locomotor systems. *Am. J. Phys. Anthropol.* **26**:241-254.

Simons, E.L. (1967b) The earliest apes. *Sci. Am.* **217**(6):28-35.

Simons, E.L. (1970) The deployment and history of Old World monkeys (Cercopithecidae, Primates). In J.R. Napier and P.H. Napier (eds.): *Old World Monkeys: Evolution, Systematics, and Behaviour*, pp. 97-137. Academic Press: New York.

Simons, E.L. (1972) *Primate Evolution: An Introduction to Man's Place in Nature.* Macmillan: New York.

Simpson, G.G. (1945) The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* **85**:1-350.

Simpson, G.G. (1961) *Principles of Animal Taxonomy.* Columbia University Press: New York.

Slowinski, J. (1993) "Unordered" versus "Ordered" characters. *Syst. Biol.* **42**(2):155-165.

Sokal, R.R. and Rohlf, F.J. (1995) *Biometry. Third edition.* W.H. Freeman and Co: New York.

Spoor, F.C., Sondaar, P.Y. and Hussain, S.T. (1991) A new hominoid hamate and first metacarpal from the late Miocene Nagri Formation of Pakistan. *J. Hum. Evol.* **21**:413-424.

Srikosamatara, S. (1984) Notes on the ecology and behaviour of the hoolock gibbon. In H. Preuschoft, D.J. Chivers, W.Y. Brockelman and N. Creel (eds.): *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 242-257. Edinburgh University Press: Edinburgh.

Stern, J.T., Jr. and Jungers, W.L. (1985) Body size and proportions of the locomotor skeleton in *Oreopithecus bambolii*. *Am. J. Phys. Anthropol.* **66**:233.

Stern, J.T., Jr. and Oxnard, C.E. (1973) Primate locomotion: some links with evolution and morphology. *Primatologia* **4**:1-93.

Stevens, P.F. (1980) Evolutionary polarity of character states. *Annu. Rev. Ecol. Syst.* **11**:333-358.

Strasser, E. and Delson, E. (1987) Cladistic analysis of cercopithecid relationships. *J. Hum. Evol.* **16**:81-99.

Strasser, E., Fleagle, J.G., Rosenberger, A.L. and McHenry, H.M. (eds.) (1998) *Primate Locomotion: Recent Advances.* Plenum Press: New York.

Straus, W.L., Jr. (1949) The riddle of man's ancestry. *Q. Rev. Biol.* **24**(3):200-223.

Straus, W.L., Jr. (1961) Primate taxonomy and *Oreopithecus*. *Science* **133**:760-761.

Straus, W.L., Jr. (1963) The classification of *Oreopithecus*. In S.L. Washburn (ed.): *Classification and Human Evolution*, pp. 146-177. Aldine: Chicago.

Sugardjito, J. and van Hooff, J.A.R.A.M. (1986) Age-sex class differences in the positional behaviour of the Sumatran orang-utan *Pongo pygmaeus abelli* in the Gunung Leuser National Park, Indonesia. *Folia Primatol.* **47**(1):14-25.

Susman, R.L. (1979) Comparative and functional morphology of hominoid fingers. *Am. J. Phys. Anthropol.* **50**:215-236.

Susman, R.L., Badrian, N.L. and Badrian, A.J. (1980) Locomotor behaviour of *Pan Paniscus* in Zaire. *Am. J. Phys. Anthropol.* **53**:69-90.

Szalay, F.S. and Berzi, A. (1973) Cranial anatomy of *Oreopithecus*. *Science* **180**:183-185.

Szalay, F.S. and Delson, E. (1979) *Evolutionary History of the Primates.* Academic Press: New York.

Szalay, F.S. and Langdon, J.H. (1985) Evolutionary morphology of the foot in *Oreopithecus*. *Am. J. Phys. Anthropol.* **66**:237.

Szalay, F.S. and Langdon, J.H. (1986) The foot of *Oreopithecus*: an evolutionary assessment. *J. Hum. Evol.* **15**:585-621.

Takahashi, L.K. (1990) Morphological basis of arm-swinging: multivariate analyses of the forelimbs of *Hylobates* and *Ateles*. *Folia Primatol.* **54**:70-85.

Temerin, L.A. and Cant, J.G.H. (1983) The evolutionary divergence of Old World monkeys and apes. *Am. Nat.* **122**(3):335-351.

Thorington, R.W., Jr. (1985) The taxonomy and distribution of squirrel monkeys (*Saimiri*). In L.A. Rosenblum and C.L. Coe (eds.): *Handbook of Squirrel Monkey Research*, pp. 1-33. Plenum Press: New York.

Tuttle, R.H. (1967) Knuckle-walking and the evolution of hominoid hands. *Am. J. Phys. Anthropol.* **26**:171-206.

Tuttle, R.H. (1969) Knuckle-walking and the problem of human origins. *Science* **166**:953-961.

Tuttle, R.H. (1972a) Functional and evolutionary biology of hylobatid hands and feet. In D.M. Rumbaugh (ed.): *Gibbon and Siamang. A Series of Volumes on the Lesser Apes, Vol. 1. Evolution, Ecology, Behaviour, and Captive Maintenance*, pp. 136-206. S. Karger: Basel.

Tuttle, R.H. (ed.) (1972b) *The Functional and Evolutionary Biology of Primates.* Aldine-Atherton: Chicago, Ill.

Tuttle, R.H. (1974) Darwin's apes, dental apes, and descent of man: normal science in evolutionary anthropology. *Curr. Anthropol.* **15**:389-398.

Tuttle, R.H. (1975a) Parallelism, brachiation and hominoid phylogeny. In W. Lackett and F.S. Szalay (eds.): *Phylogeny of the Primates: A Multidisciplinary Approach*, pp. 447-480. Plenum Press: New York.

Tuttle, R.H. (ed.) (1975b) *Primate Functional Morphology and Evolution.* Mouton: The Hague.

Tuttle, R.H. (1986) *Apes of the World: Their Social Behaviour, Communication, Mentality and Ecology*. Noyes Publications: New Jersey.

Tuttle, R.H. and Cortright, G.W. (1988) Positional behaviour, adaptive complexes, and evolution. In J.H. Schwartz (ed.): *Orang-utan Biology*, pp. 311-330. Oxford University Press: Oxford.

van Valen, L.M. (1982) Homologies and causes. *J. Morph.* **173**:305-312.

Von Koenigswald, G.H.R. (1969) Miocene Cercopithecoidea and Oreopithecoidea from the Miocene of East Africa. In L.S.B. Leakey (ed.): *Fossil Vertebrates of Africa, Vol. 1*, pp. 39-52. Academic Press: New York.

Vuillaume-Randriamanantena, M. (1988) The taxonomic attributions of giant subfossil lemur bones from Ampasambazimba: *Archaeoindris* and *Lemuridotherium. J. Hum. Evol.* **17**:379-391.

Wake, D.B. (1991) Homoplasy: the result of natural selection, or evidence of design limitations? *Am. Nat.* **138**:543-567.

Wake, D.B. (1996) Introduction. In M.J. Sanderson and L. Hufford (eds.): *Homoplasy: The Recurrence of Similarity in Evolution*, pp. xvii-xxv. Academic Press: San Diego.

Walker, A.C. (1997) *Proconsul*: function and phylogeny. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 209-224. Plenum Press: New York.

Walker, A.C. and Pickford, M.H.L. (1983) New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In R.L. Ciochon and R.S. Corruccini

(eds.): *New Interpretations of Ape and Human Ancestry*, pp. 325-351. Plenum Press: New York.

Walker, A.C. and Rose, M.D. (1968) Fossil hominoid vertebra from the Miocene of Uganda. *Nature* **217**:980-981.

Walker, A.C., Teaford, M.F. and Leakey, R.E.F. (1986) New information concerning the R114 *Proconsul* site, Rusinga Island, Kenya. In J.G. Else and P.C. Lee (eds.): *Primate Evolution*, pp. 143-149. Cambridge University Press: Cambridge.

Walker, A.C., Teaford, M.F., Martin, L.B. and Andrews, P.J. (1993) A new species of *Proconsul* from the early Miocene of Rusinga/Mfangano Islands, Kenya. *J. Hum. Evol.* **25**:43-56.

Ward, C.V. (1993) Torso morphology and locomotion in *Proconsul nyanzae*. *Am. J. Phys. Anthropol.* **92**:291-328.

Ward, C.V. (1997) Functional anatomy and phyletic implications of the hominoid trunk and hindlimb. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 101-130. Plenum Press: New York.

Ward, C.V., Begun, D.R. and Rose, M.D. (1997) Function and phylogeny in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 1-12. Plenum Press: New York.

Ward, C.V., Walker, A.C., Teaford, M.F. and Odhiambo Nengo, I. (1993) Partial skeleton of *Proconsul nyanzae* from Mfwangano Island, Kenya. *Am. J. Phys. Anthropol.* **90**:77-111.

Ward, S.C. (1997) The taxonomy and phylogenetic relationships of *Sivapithecus* revisited. In D.R. Begun, C.V. Ward and M.D. Rose (eds.): *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 269-290. Plenum Press: New York.

Ward, S.C. and Brown, B. (1986) The facial skeleton of *Sivapithecus indicus*. In D.R. Swindler and J. Erwin (eds.): *Comparative Primate Biology, Vol. 1. Systematics, Evolution, and Anatomy*, pp. 413-452. Alan R. Liss, Inc.: New York.

Ward, S.C., Brown, B., Hill, A., Kelley, J. and Downs, W. (1999) *Equatorius*: a new hominoid genus from the middle Miocene of Kenya. *Science* **285**:1382-1386.

Ward, S.C. and Kimbel, W.H. (1983) Subnasal alveolar morphology and the systematic position of *Sivapithecus*. *Am. J. Phys. Anthropol.* **61**:157-171.

Ward, S.C. and Pilbeam, D.R. (1983) Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan. In R.L. Ciochon and R.S. Corruccini (eds.): *New Interpretations of Ape and Human Ancestry*, pp. 211-238. Plenum Press: New York.

Washburn, S.L. (1963) Behaviour and human evolution. In S.L. Washburn (ed.): *Classification and Human Evolution*, pp. 190-203. Methuen & Co. Ltd: London.

Watrous, L. and Wheeler, Q. (1981) The outgroup comparison method of character analysis. *Syst. Zool.* **30**:1-11.

White, T.D. and Folkens, P.A. (2000) *Human Osteology. Second edition.* Academic Press: San Diego.

Wiens, J.J. (2000) Coding morphological variation within species and higher taxa for phylogenetic analysis. In J.J. Wiens (ed.): *Phylogenetic Analysis of Morphological Data*, pp. 115-145. Smithsonian Institution Press: Washington, DC.

Wiley, E.O. (1979) Ancestors, species, and cladograms: remarks on the symposium. In J. Cracraft and N. Eldredge (eds.): *Phylogenetic Analysis and Paleontology*, pp. 211-225. Columbia University Press: New York.

Wiley, E.O., Siegel-Causey, D., Brooks, D.R. and Funk, V.A. (1991) The complete cladist: a primer of phylogenetic procedures. *Univ. Kans. Mus. Nat. Hist. Spec. Publ.* **19**:1-158.

Youlatos, D. (1996) Atelines, apes and wrist joints. *Folia Primatol.* **67**:193-198.

Yunis, J.J. and Prakash, O. (1982) The origin of man: a chromosomal pictorial legacy. *Science* **215**:1525-1530.

Zelditch, M.L., Swiderski, D.L. and Fink, W.L. (2000) Discovery of phylogenetic characters in morphometric data. In J.J. Wiens (ed.): *Phylogenetic Analysis of Morphological Data*, pp. 37-83. Smithsonian Institution Press: Washington, D.C.

Zihlman, A.L. (1992) Locomotion as a life history character: the contribution of anatomy. *J. Hum. Evol.* **22**:315-325.